ENTOMOFAUNAL DYNAMICS AND BIOCHEMISTRY OF LITTER DECOMPOSITION IN AN EVERGREEN FOREST WITH SPECIAL REFERENCE TO SYSTEMATICS OF DUNG BEETLES (COLEOPTERA: SCARABAEINAE)

Thesis submitted to the
UNIVERSITY OF CALICUT
in partial fulfillment of the requirements for the award of the degree of
DOCTOR OF PHILOSOPHY IN ZOOLOGY

By
Anu Anto

Under the guidance of
Dr. Sabu K. Thomas

P.G. & RESEARCH DEPARTMENT OF ZOOLOGY, LITTER ENTOMOLOGY UNIT
ST. JOSEPH'S COLLEGE, DEVAGIRI, CALICUT, KERALA, INDIA
2006

P.G. & RESEARCH DEPARTMENT OF ZOOLOGY
ST. JOSEPH'S COLLEGE, DEVAGIRI
CALICUT - 673 008, KERALA, INDIA
Phone: +91- 495-2352145 (O)
+91-9447349744(M)
E-mail: sabukthomas@gmail.com

Dr. Sabu K. Thomas
Selection Grade Lecturer

21-11-2006

Certificate

Certified that the thesis entitled **"Entomofaunal dynamics and biochemistry of litter decomposition in an evergreen forest with special reference to systematics of dung beetles (Coleoptera: Scarabaeinae)"** submitted by Ms. Anu Anto to the University of Calicut for the award of the degree of Doctor of Philosophy in Zoology is a bonafide record of research work done by her in this department under my guidance and supervision. This has not previously been formed the basis for any award of degree or diploma.

Ms. Anu Anto has successfully completed the preliminary qualifying examination prescribed by the University of Calicut.

Dr. Sabu K. Thomas

Declaration

I do hereby declare that the thesis entitled **"Entomofaunal dynamics and biochemistry of litter decomposition in an evergreen forest with special reference to systematics of dung beetles (Coleoptera: Scarabaeinae)"** submitted to the University of Calicut for the award of the Degree of Doctor of Philosophy in Zoology has not been submitted for the award of any other degree or diploma and represents the original work done by me.

Calicut
21-11-2006

Anu Anto

Acknowledgments

I wish to thank the many people who have helped me through this adventure. First and foremost, I would like to extend my sincere thanks and appreciation to my supervisor, Dr. Sabu K. Thomas for providing me with the opportunity to do this study, in addition to his assistance and understanding throughout the development of this thesis. Interacting with him all these years has been a very stimulating and rewarding experience, both academically and personally.

I am extremely happy to record my profound sense of gratitude to Prof. A.T. Thomas, Head of the Department and all other staff members of Department of Zoology, St. Joseph's College, Devagiri, Calicut for their constant encouragement through out the period. I am thankful to all the non-teaching staff of the Dept. of Zoology for their valuable co-operation and help.

With immense pleasure I express my sincere thanks to Rev. Fr. Joseph Vayalil CMI, Principal, St. Joseph's College, Devagiri, Calicut for providing all the necessary facilities during the course of my work.

I would like to acknowledge the Council of Scientific and Industrial Research (CSIR) of India for providing financial assistance through their Research Fellowship (JRF/SRF-NET) and also to the Kerala Forest and Wild Life Department for providing permission and facilities in the study region.

I am also greatly indebted to many people who have contributed a significant amount of their time to help me in the field, the laboratory, with the statistical approach and in other numerous ways. I would like to start by giving my deepest thanks to Mr. Thomachan K.T., Senior Lecturer, Department of Economics, St. Joseph's College, Devagiri for relieving my statistical anxieties with valuable advice. Large appreciation also goes out to my colleagues Vinod K.V & Vineesh P.J. who volunteered a large number of hours helping me out in the field and in the laboratory. Special thanks to Vinod K.V for his assistance in taking photographs. I also acknowledge and appreciate all other colleagues especially Abhitha, Shiju, Anish, Manoj, Usha and Jobi, who showed keen interest in my work and had always lent a helping hand in this endeavor.

The following experts helped me identify insect material: V.V. Ramamurthy (Curculionidae), T.C. Narendran (Chalcidae), Mikael Sorenson (Ptillidae), K.A. Karmaly (Ants), Merkl Otto (Tenebrionidae), Nivedita Saha (Isoptera), Pawel Jaloszynski (Scydmaenidae), Mohanasundaram (Mites), Mahalingam (Orthoptera), Varadarajan (Thrips), George. E Ball (Carabidae) and also to Paul Schoolmesters for verifying dung beetle specimens.

This thesis was the most exciting and rewarding journey I have ever undertaken. I dedicate it to my family because they made it possible. I wish to thank my parents; they bore me, raised me, supported me, taught me and loved me. My brothers Arun & Anand and my brother- in-law Jobin lent their helping hand by collecting several books and journal articles for this thesis work. My in-laws also supported me without whose love and advice I simply wouldn't have reached this far.

I have reserved my last note of heartfelt love and gratitude for my husband, Jimmy Mathew, always encouraging me to pursue my interests; giving me tremendous emotional support, sharing the everyday joys and sorrows involved in the different stages of my work that making it possible to achieve my dream of completing a doctoral thesis. My daughter Riya who was the silent victim of my temperament during the course of work also deserves a special mention here.

For their wholehearted co-operation and prayers and all those who have been instrumental in my research work either directly or indirectly and whose name/s I may have failed to record.

Above all I bow my head before the God for blessing with health and confidence to carry out the work successfully.

Anu Anto

To my family…

It's little things that run the world

-E.O. Wilson

Contents

1.

General Introduction

Forest organisms are greatly diverse both taxonomically and ecologically and they occupy a wide range of microhabitats, consume many kinds of food resources and are active in different seasons and/or different times of day (Toda & Kitching 1999). Although the magnitude of biodiversity present on earth is largely unknown and its estimates remain highly controversial (Erwin 1982) most workers agree that much, if not, most of biodiversity are represented by arthropod inhabitants of evergreen tropical rainforests (Wilson 1988). The lowland tropical rainforest is the most species rich terrestrial ecosystem harbouring more than 50-75% of all living organisms on approximately 6-7% of land area (Linsenmair 1990; Wilson 1992). The determinants and primary causes of this gradient and mechanisms responsible for the maintenance of this high diversity are manifold and widely discussed (Blackburn & Gaston 1996; Connell 1978; MacArthur 1969; Paine 1996) since noted by the first naturalists (Wallace 1869). However, being located in under-developed or developing countries, the pressure of these forests are very high and as a result many areas are getting degraded.

An unexpected high species richness of arthropods which even resulted in new global estimations of biodiversity were recorded in studies of the rainforest canopy (Basset 1991; Basset & Kitching 1991; Erwin 1995; Floren & Linsenmair 1994; Gaston & Hudson 1994; Stork 1987) and were also confirmed for the forest floor studies of different insect groups (Bruehl et al. 1998; Fittkau & Klinge 1973; Stork 1988). With this, the picture of a stratum with an especially high biodiversity emerged. Above and below ground organisms are critical for the biogeochemical cycles that sustain the Earth and this constitutes the main resource of energy and matter for an extraordinarily diverse community of soil organisms connected by highly complex interactions (Hättenschwiler et al. 2005). Above ground diversity might promote below ground diversity – or vice versa- by increasing the variety of food resources (litter quality and composition) the range of environmental conditions (temperature and humidity) or the structural complexity of the habitat (Anderson 1994; Hooper et al. 2000). In spite of this, there is limited knowledge on the extent to which the biota below ground and the functions they perform are dependant on the biota above ground and vice versa (Wolters et al. 2000).

Similarly, the ecosystem consequences of the diversity of litter organisms are little understood, except for some keystone species or ecosystem engineers such as earthworms, termites, and ants (Jones et al. 1994; Anderson 1995). Below ground communities also affect nutrient availability and detritus build up. Feedbacks through these mechanisms could influence the diversity of above ground communities, although evidence for such feedback is mixed (Hooper et al. 2000). In addition, removal of specific below ground top predators can induce a cascade of effects down the food chain that alters the mineralization of available plant nutrients (Santos et al. 1981). Understanding patterns of belowground biological diversity is a matter of renewed urgency because of the steady anthropogenic destruction of natural ecosystems worldwide.

The close relationship between the vegetation change and soil Carbon dynamics (Jobbágy & Jackson 2000) suggests that any disruption of the coupling between plants and soil organisms as a result of global change may have deleterious consequence for functioning of terrestrial ecosystems. Moreover, the agents of global change (such as land use, climate and atmospheric inputs), acting either individually or in combination, may lead to non-linear changes in above and below ground relationships with effects varying in distribution and intensity around the globe (Heal et al.1997). Changes in the species composition of this component of the belowground community may significantly alter the nitrogen transfer to plants.

Due to urbanization and increased agricultural practices, natural forests are disappearing or transforming into plantation forests at alarming rates world wide (Laurance 1999), which appears to be the single greatest threat to the world's biological diversity (Whitmore 1990; Huston 1994). In landscapes worldwide, ongoing fragmentation and clearance of native habitat is spawning complex mosaics of natural, semi-natural and human-dominated habitats. Apart from the preservation of a huge amount of the world's overall biodiversity, tropical rainforests are of unique importance due to their ecosystem services for climate stabilization as major carbon stores, for erosion prevention and for global and local water balance (Laurance 1998; Linsenmair 1997). They are of great importance in understanding complex processes of nutrient recycling and may contribute valuable data to studies of comparative biodiversity, forest management and conservation (Stork 1988; Kremen et al. 1993; Hoekstra at al.

1995). It has been estimated that by 1990, 24% of the lowland tropical rainforests on Earth had been cleared (Turner & Corlett 1996). As the extent of relatively natural habitat shrinks, the future of biodiversity depends increasingly on the conservation potential of existing forests and remnants of native habitat embedded in landscapes devoted primarily to human activities.

Lavelle et al (1993) suggested that biological systems of regulation of organic matter turnover are most strongly expressed in moist tropical situations where optimal conditions of temperature and humidity remove the higher-level constraints of climate over biota. With a wide array of bioclimatic and topographic conditions, the Western Ghats, fringing the Arabian sea coastline of Indian peninsula has a high level of biodiversity and endemism and at the same time it is also a most threatened region due to various land practices and other developmental activities and has accordingly earned the status as one of the 25 biodiversity 'hotspots' (WCMC 1992; Myers 1988). In spite of the fact that the South Western Ghats montane rainforests are the most species rich ecoregion in the Deccan peninsula (Rawat et al. 2001), the forest belt in the region is already extremely attenuated and fragmented and is now under maximum destructive pressure (Nair 1991). Nearly three-fourths of the natural vegetation in the ecoregion has been cleared or converted, and the remaining severely fragmented forests are one of the major conservation priorities in a global scale due to their fragility, biological richness, high rates of endemism and multiple anthropogenic threats (Pascal 1991). In the past it had been ravaged by the European planters and subsequently for the ply wood industry.

With post-independence period. a whole combination of factors came to affect them calamitously. Developmental schemes in particular the river valley projects, roads, resettlement schemes, mining industries accelerated timber working and large scale conversion of natural forests to the so called fast growing commercial wood species etc caused massive damage (Nair 1991). With threats of different nature looming large over the forests of Western Ghats leading to its present scale of deforestation, insitu conservation of remnant forests is most desirable. This is possible if forest areas with minimum human interferences are set aside. It thus becomes imperative to make an assessment of the status of forests and their health. Such assessment is possible only if pristine stands of forests are available with periodically collected databases of the floral and faunal elements.

Though the floral and vertebrate faunal diversity found in the region are well documented, little is known of the litter insect distributional pattern in the different vegetation types of Western Ghats forests. Documentation of the insect fauna of the state was initiated with the establishment of the British rule. The results of these surveys were made in areas, which were easily accessible or in areas close to human settlements, many locations, particularly in formidable areas, have been either poorly covered or not covered at all. Also, the intensity of the sampling was low as indicated by data generated by subsequent workers especially of the ZSI, various universities and research institutions (Mathew 2004).

With the wettest and biologically diverse portion of Western Ghats, Kerala part of Western Ghats has landlocked Islands of biodiversity resulting in high endemism (Chatterjee & Sastry 2001). In terms of total extent, richness of habitat types, natural inaccessibility and low level of forestry operations, the Nilgiri tracts were amongst the most significant localities from the viewpoint of conservation of biological diversity in Western Ghats (Nair 1999). Biogeographically Wayanad region of Western Ghats is a transitional zone between the moist *Cullenia sp* dominated forests of South Western Ghats and dry dipterocarp forests of the northern region, harbouring habitat restricted, endemic species as well as disjunct populations of species that are found in both regions (Rodgers & Panwar 1988; Pascal 1988; Rawat et al. 2001). Low elevation evergreen forests dominated by dipterocarps constitute the most threatened habitat in the Wayanad region and its continuum along the Western Ghats has been fragmented (Nair 1991; Pascal 1991). These ecologically sensitive lowland forests along the foothills of the Western Ghats and on the hillocks in the mid lands were cleared in the early phases of deforestation (Nair 1991). A strong need exists for the documentation of litter insects of remaining evergreen forests of Wayanad to know about their ecological roles, succession patterns or how they respond to different seasons of the year. With this outlook, a low elevation wet evergreen forest in one of the biodiversity 'hotspot' region is selected for this work.

The view that tropical evergreen rain forests are static communities that function under consistently optimal moist and warm climatic conditions have changed with the recent recognition of a strong seasonality of leaf litter fall (Swamy & Proctor 1994; Clark et al. 2003; Wood et al. 2005) with moderate fluctuations in rainfall reported to impose a distinct seasonality (Ricklefs 1975; Jansen 1983). Accordingly the seasonal component of diversity must also be measured, since many tropical insects vary in abundance or may not be represented in samples taken at certain times of the year (Wolda 1987; Richardson et al. 1997). While it is clear that seasonal fluctuations in rainfall modify the physical environment (Holdridge 1967) and change resource availability (Fodgen 1972), data on seasonal patterns on insect abundance are scarce (Wolda 1988). Major peak in the number of leaves in the beginning of wet season and increase in dry and dead suspended leaves during dry season result in litter layers of different decomposition stages thus creating fluctuations in food and water availability to litter insects resulting in different patterns of litter insects in successive litter layers in evergreen forest. With favourable conditions of multilayered tree species providing shelter and moisture accumulation and litter fall remaining consistent through out the year, insect fauna present in the wet evergreen forest would be indicative of the influence of litter conditions in determining the habitat preference. The prime objective of the **second chapter** is to check out the seasonal and layerwise pattern in litter insect diversity and abundance influenced by precipitation in a selected tropical wet evergreen forest in Wayanad. This study provides a baseline that allows other more poorly known sites in Western Ghats to be assessed for richness, structure and endemism.

In 1988, Edward Wilson, noted rainforest ecologist described insects as "the little things that run the world". Among them, beetles represent the most spectacular and diverse group. In the evergreen study habitat also, Coleoptera is the most diverse and abundant group of insects. Within Coleoptera, the largest and most studied family is Scarabaeidae, the scarab beetles. They are functionally important taxa playing a crucial role in tropical and subtropical forests by recycling nutrients (Halffter & Matthews 1966; Mittal 1993), aerating soil (Mittal 1993), controlling vertebrate parasites (Bryan 1976), and dispersing seeds (Andresen & Feer 2005). In the family Scarabaeidae, Scarabaeinae and Aphodiinae are dung beetles (Baraud 1992). The first group is well adapted to warm conditions, whereas Aphodiinae is predominantly adapted to cold, temperate conditions (Hanski & Cambefort 1991). My study is limited to the Scarabaeidae, which is the common taxonomic group, found in India.

Choice of dung beetles as a study taxon in this work was due to the fact that they are coprophagous insects, which have a relatively well-known taxonomy and are known to be highly habitat specific (Halffter & Favila 1993; Scheffler 2002). Variation in height of vegetation, types of soil and amount of insolation have been associated with changes in species composition of dung beetles (Doube 1983; Lumaret & Kirk 1991). Subtle changes in the habitat have been shown to affect dung beetle communities (Galante et al. 1991; Halffter & Favila 1993; Nummelin & Hanski 1989). Because of the rapid rates at which tropical forest is being modified and destroyed, it is important to study forest species while intact forest is still relatively common. Degradation and disturbance of Western Ghats have implication for the biodiversity of dung beetles and other taxa, which depend on intact forest habitat. As habitat heterogeneity is thought to be one of the parameters determining their species diversity at a regional scale (Huston 1994; Rosenzweig 1995; Begon et al. 1996) and perhaps the most important one (Schoener 1974) similar studies, which provide information on species composition, behaviour and abundance, are needed in other unexplored vegetation types of Western Ghats.

Very little is known about dung beetles in the rainforests of India, especially from the rainforests of Western Ghats in India and Srilanka which is a recognized hot spot of biodiversity (Bossyut et al. 2004; Myers et al. 2000) except for checklists from Silent Valley National park (Biswas & Chatterjee 1986) and Nilgiri Biosphere Reserve (Biswas & Mulay 2001). The classic work of Arrow (1931) provides a catalogue and identification manual for the Indian region, but does not mention whether the collections have been from agriculture field or forest lands. High variability in precipitation and topographic diversity of Western Ghats has generated a wide variety of vegetation types, ranging from wet evergreen and semi-evergreen forests on the western side and at high altitudes to dry deciduous forests and scrub vegetation on the eastern slopes and lowlands (Jha et al. 2000). Since structure of the vegetation, soil type and physical structure of the forest appear to be an important factor in the structure and local distribution of dung beetle communities (Doube 1983; Nealis 1977; Jansen 1983; Davis 1993; Davis 1998;

Davis & Sutton 1998; Davis et al. 2000) cataloguing the dung beetle fauna from the remaining forest fragments and understanding the peculiarities of their phylogenetic structure would serve to recognize the regional variation in the dung beetle community structure across different forest vegetations of Western Ghats and will add to the general efforts towards the conservation of biodiversity in Western Ghats. In the **third chapter** a checklist of dung beetle fauna (Coleoptera: Scarabaeinae) from the evergreen forest in Wayanad region of Western Ghats along with a pictorial key for the species collected from the habitat is provided.

Forest litter acts as an input-output system of nutrients and the rates at which forest litter falls and subsequently decays, contribute to the regulation of nutrient cycling, as well as to soil fertility and primary productivity in forest ecosystems (Berg 2000). These tree/soil relationships are reflected in nutrient concentrations and biochemical constituents of leaves and litter that influence herbivory, litter quality, decomposition processes and hence the study of litter chemical qualities that feed back to plant production through nutrient availability (Stachurski & Zimka 1975; Bryant et al. 1983; Pastor et al. 1984; Zak et al. 1993; Aerts & Chapin 2000). Tree species on fertile soils tend to produce leaves and leaf litters with high nitrogen concentrations, low concentrations of carbon-based plant protection compounds such as tannins and lignin mainly associated with vascular tissues. The high quality litters decompose rapidly and support high plant production through fast turnover of the nutrient pools. Trees on soils of low inherent fertility generally produce leaf litters that decompose slower, reducing the rates nutrient turnover, because of low nitrogen, higher tannins and polyphenol concentrations, and greater lignification of leaf tissues often associated with longer leaf life spans (Sariyildiz et al. 2005; Cornelissen & Thompson 1997; Hättenschweiler et al. 2003). To maintain production and biomass, forest ecosystem requires stable nutrient cycles that form equilibrium between trees and soil (DeAngelis 1992). The concentration of nutrients at the time of leaf fall is also an important parameter because it influences the rate of decomposition and is the starting point for the measurement of the amount of nutrients recycled (Songwe et al.1997). In humid tropical forests with abundant moisture and warm annual temperatures, litter quality becomes the dominant control on decomposition rates (Lavelle et al. 1993; Aerts 1997; Loranger et al.2002).

The dynamic nature of tropical evergreen rain forests with strong seasonality of leaf litter fall, with the peak at the end of the dry season followed by a surge in nutrient availability in the forest floor (Swamy & Proctor 1994) results in a pulse of increased soil nutrient availability at the beginning of rainy season leading to high nutrient concentrations in live leaf tissue, often coinciding with the peak-growing season (Wood et al. 2005). Hence, litter fall rates and its quality may not be constant along the year and over the surface, so they may contribute to the creation of litter of different quality and quantity on the ground and therefore they may have an effect on decomposition of litter during different seasons and influence faunal diversity (Sundrapandian et al. 2005). Concentrations of nutrients in the litter determine the amount of returned nutrients and the decomposition rates of litter controls the speed at which bound nutrients are transformed into viable form ready for reuse by plant uptake. Given the low apparent intra year variability in mean temperature and solar radiation in tropical wet forests, seasonal changes in leaf litter nutrient concentrations could serve as a constraint on net primary productivity (Wood et al. 2005).

Despite this recent evidence indicating the influence of seasonality on patterns of nutrient cycling, litter fall nutrient measurements in evergreen forests are never considered in the tropical moist evergreen forests of southern moist Western Ghats. This gap in knowledge limits our understanding of overall nutrient cycling in these forests. In the **fourth chapter,** my aim is to evaluate the seasonal patterns of leaf litter nutrient variation in freshly fallen, fermentation and humus litter layers in the climax wet evergreen forests on the windward side of Western Ghats.

Though there is significant role of litter diversity for the composition and activity of litter communities and processes during decomposition has rarely been studied. This circumstance is surprising because litter quality as the overriding determinant for decomposition within a given climate (Co^uteaux et al. 1995) varies tremendously among species (Perez-Harguindeguy et al. 2000, Hättenschwiler 2005). Where low- quality plant litter decomposes slowly to form deep organic layers with complex structure, this structural heterogeneity in turn promotes the development of diverse surface living communities (Anderson 1978). Factors, such as plant species and structural diversity above ground, which are often related to diversity of above ground insect species (Southwood et al. 1979), therefore may have important implications for below ground insect diversity as well.

The dynamics of litter contributions and decomposition and subsequent bioelement release play a fundamental role in the biogeochemical cycle of organic matter and mineral elements thus becoming a key component in the functioning and stability of forest ecosystems (Waring & Schlesinger 1985; Keenan et al. 1996; Martin et al. 1996). Organic residues coming from vegetation and accumulated on ground together with providing energy resources and bioelements necessary for edaphic micro and mesofauna represent the main source of mineral return to the ground (Caritat et al. 1996; Martin et al. 1997). In terrestrial ecosystems, major part of the net primary production enters the detritus-based food web (Swift et al. 1979; Wardle & Lavelle 1997). Therefore, litter decomposition is an important process regulating energy flow, nutrient cycles, and structures of these ecosystems (Swift et al. 1979; Wachendorf et al. 1997). Decomposition of forest litter has been extensively studied in temperate forests, in relation to various factors such as fauna (Bocock 1964; Witkamp & Crossley 1966), species (Heath et al. 1966) and other environmental factors (Bocock & Gilbert 1957; Witkamp & Van Der Drift 1961) or with the purpose of estimating nutrient release. Among the first authors who studied the decomposition of the litter in tropical forests, Jenny et al. (1949) indicated the rapid disappearance of tropical forest litter, which was emphasized by Laudelout & Meyer (1954) and Bartholomew et al. (1953).

Several works on this subject have been carried out particularly in recent years, and many attempts have been made to compare the different results obtained (Hopkins 1978). In tropical ecosystems, maintenance of soil organic pool is achieved by the high and rapid circulation of nutrients through the fall and decomposition of litter. Standing crop of litter (total forest-floor material) acts as an input–output system of nutrients and the rates at which forest litter falls, and subsequently decays, regulate energy flow, primary productivity and nutrient cycling in forest ecosystems (Sundarapandian & Swamy 1999).

Many studies have shown that decomposition is influenced by litter quality, climatic factors and soil biota (Tian et al. 1997; Wachendorf et al. 1997; Wardle & Lavelle 1997; Heneghan et al. 1999; Gonzalez & Seastedt 2001). Nutrient concentrations of litter are always in a dynamic process. Some nutrients and compounds are withdrawn from senescing plant tissues and others show relative increase, the concentrations of some elements can increase while the others will decrease in decomposing litter (Berg & Cortina 1995). Some studies suggest that the soil/litter fauna may have a greater effect on decomposition in tropical forests than in temperate ones (Heneghan et al. 1999; Gonzalez & Seastedt, 2001). However, decomposition rates vary greatly even among tropical forests, depending on factors such as climate and litter quality. Microflora (bacteria and fungi) is the major group that decomposes litter directly (Vossbrinck et al. 1979; Wardle & Lavelle 1997). Micro invertebrates directly consume or indirectly regulate micro floral communities, thereby affecting decomposition rates (Vossbrinck et al. 1979; Reddy & Venkataiah

1989). Macro invertebrates influence decomposition through changing the abundance of micro decomposers (Lawrence & Wise 2000). Regarding the decomposition rate constant (k), greater faunal abundance and diversity correlated with increased mass loss in the experiments by Kaneko and Salamanca (1999). However, the role of litter fauna in decomposition process, however, has only recently begun to be addressed. (Irmler 2000; Heneghan et al. 1999; Zimmer et al. 2002; 2004). Active participation by litter fauna in decomposition contributes to spatial transfer of nutrients to sites of progressive degradation of litter, thus significantly altering the chemical environment, favoring enhanced rate of decomposition (Vogt et al. 1986). Physical factors like water availability affect rates of mass loss and nutrient release primarily through its effects upon the activity of decomposer community (Meetenmeyer 1978; Orchard & Cook 1983; Berg 1986). As the major factors that affect litter decomposition are on one hand litter biota activity (Martín et al.1994) and on the other hand, litter composition and quality (Heneghan et al. 1999; Gonza´lez & Seastedt 2001), in the **fifth chapter** an attempt has been made to study the decomposition rate of litter along with the patterns in biochemical profiles of the decomposing litter and in the **sixth chapter** successional patterns of faunal groups during decomposition is carried out in the wet evergreen forest using litter bags

Most of the vegetation change occurring today is very likely to cause a major shift in plant life and ecological strategy because it alters the proportion of woody and herbaceous plants (Jackson et al. 2000). This happens in tropical and sub-tropical regions experiencing de forestation and re-forestation. The sensitivity of above and below ground relationships to changes in species composition has important implications for prioritizing future research and management (Hooper et al.2000). There is a need for research networks and for setting up new experiments in poorly known but important habitats (e.g. Tropical forests). A proper understanding of both changing interactions between above – and below ground organisms and feed backs between atmosphere and biosphere that may occur through shifts in vegetation types will allow us to develop more reliable global change scenarios of ecosystem functioning that include biota and soil processes (Schimel & Gulledge 1998).

1.1 STUDY AREA

The research was carried out in the wet evergreen forests, at Chanthanathode covering an area of 85.12 sq km on western slope of North Wayanad Western Ghats ecoregion (11° 50′ N latitude and 75° 49′E longitude) (Plate.1 & 2). Entire area is a part of the Nilgiri Biosphere Reserve. The altitude range is 800–850 m. Though Teak and Eucalyptus plantations have wiped out most part of the natural vegetation in the region, study area is one of the best-preserved climax tropical forests in Wayanad part of Western Ghats and it is an isolated remnant of the original extensive natural ecosystem (Nair 1991).

Vegetation description

The study habitat exhibit characteristics of evergreen forests, which include multilayered forest structure; copious growth of fine feeder roots, slender and clear boles of trees with thin barks and presence of lianas and woody species. The forest has two tree layers and subordinate shrub and herb layers, as well as abundant epiphytes. The upper canopy of the forest is 18–25 m high and contains a number of tree species including *Artocarpus hirsutus, Terminalia bellirica, Lagerstroemia microcarpa, Schleichera oleosa, Mesua ferrea, Dalbergia latifolia, Xylia xylocarpa* and *Alstonia scholaris.* A variable second storey of small trees or tall shrubs includes *Macaranga peltata, Embilica officinalis, Olea diocia, Nemedra elaeagnoidea, Cinnamomum malabatrum, Flacourtia cataphracta* and *Diospyros bourdillonii.* Small shrubs in the study habitat include *Calamus sp.,* and *Costus speciosus* and prominent herbs are *Elephantopus scaber* and *Molineria trichocarpa*. The undergrowth consisted of canes, *Strobilanthes sp.* and ferns of *Allophylus sp.* The common climbers are *Entada scandens, Gnetum edule, Acacia intsia, Caesalpinia sp., Calycopteris floribunda, Celastrus paniculata* and *Butea parviflora*. Moss, ferns and lichens with much moss cover on tree boles and branches, exposed rock and dead wood. Information on phenological patterns in the area is lacking. Leaf flushing and new leaf production was observed prior to the rainy season or during the summer season is observed in many tree species. Some trees of deciduous character have not affected the evergreen nature of the forest as a whole (Forests and Wildlife Department working plan, 2001).

Physical parameters

The climate of the habitat is controlled by both southwest monsoon and northeast monsoon. Meteorological observations (2002–2003) at the regional rainfall stations (KSEB meteorological station), show annual precipitation of 3752 mm, of which 81% was received during southwest monsoon (Jun- Aug), 10% during northeast monsoon (Sep-Nov), 1% during pre-summer (Dec-Feb) and remaining 8% during summer (Mar-May) (Figure.1.1). Temperature ranges around 21-31°C. Natural disturbances commonly affecting forests in the Periya are strong winds during the monsoon seasons and the occasional dry spell in pre-summer and summer seasons. P^H of litter is acidic (4.9–5.6). A litter layer (4–7 cm thick) covers almost all the soil surface.

Human activity around the habitat

Timber requirements by the British army during Second World War and state sponsored developmental activities such as hydroelectric projects and human settlements during the late 1970s and 1980s wiped out most part of the natural vegetation in the region (Nair 1991) and only a few fragments of the old mature wet evergreen forest remains. Contiguity of Tholpetty and part of Brahmagiri with Kuttiadi region of Wayanad north is lost due to encroachment along the Kuttiadi-Mananthavadi road. Developmental programmes and encroachment have led to the degradation of forest in the lower areas and a large extent of the vested forest has been planted with eucalyptus and teak. Wood-based industries are located in and around the north Wayanad division. Human settlements within and adjoining the reserve forests and illegal woodcutting might damage the forest habitat.

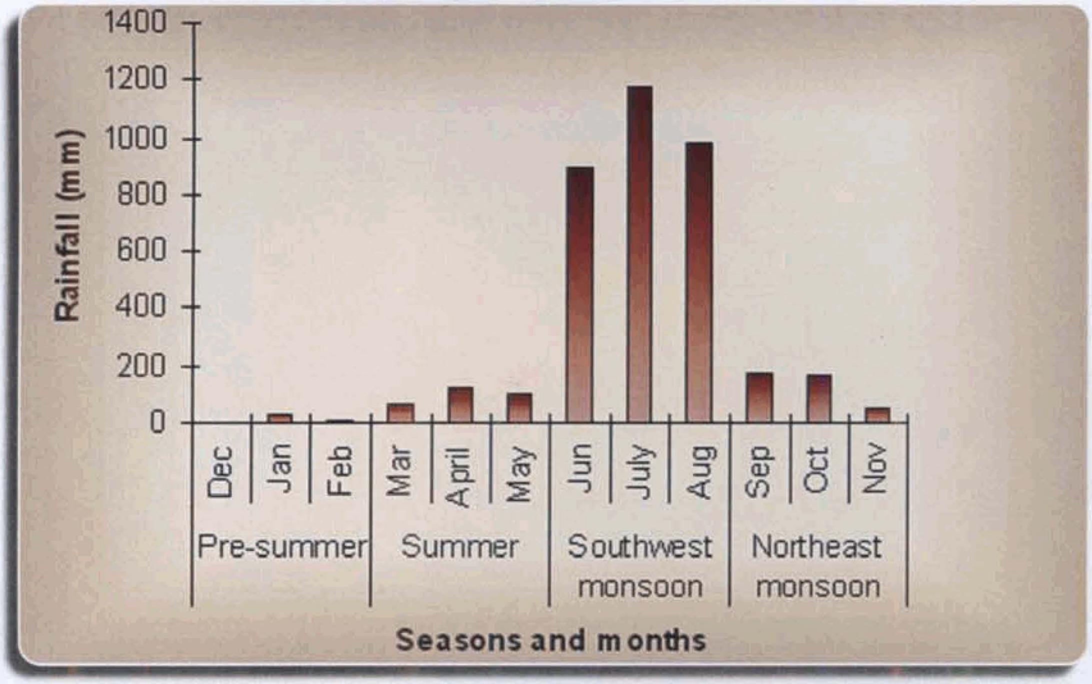
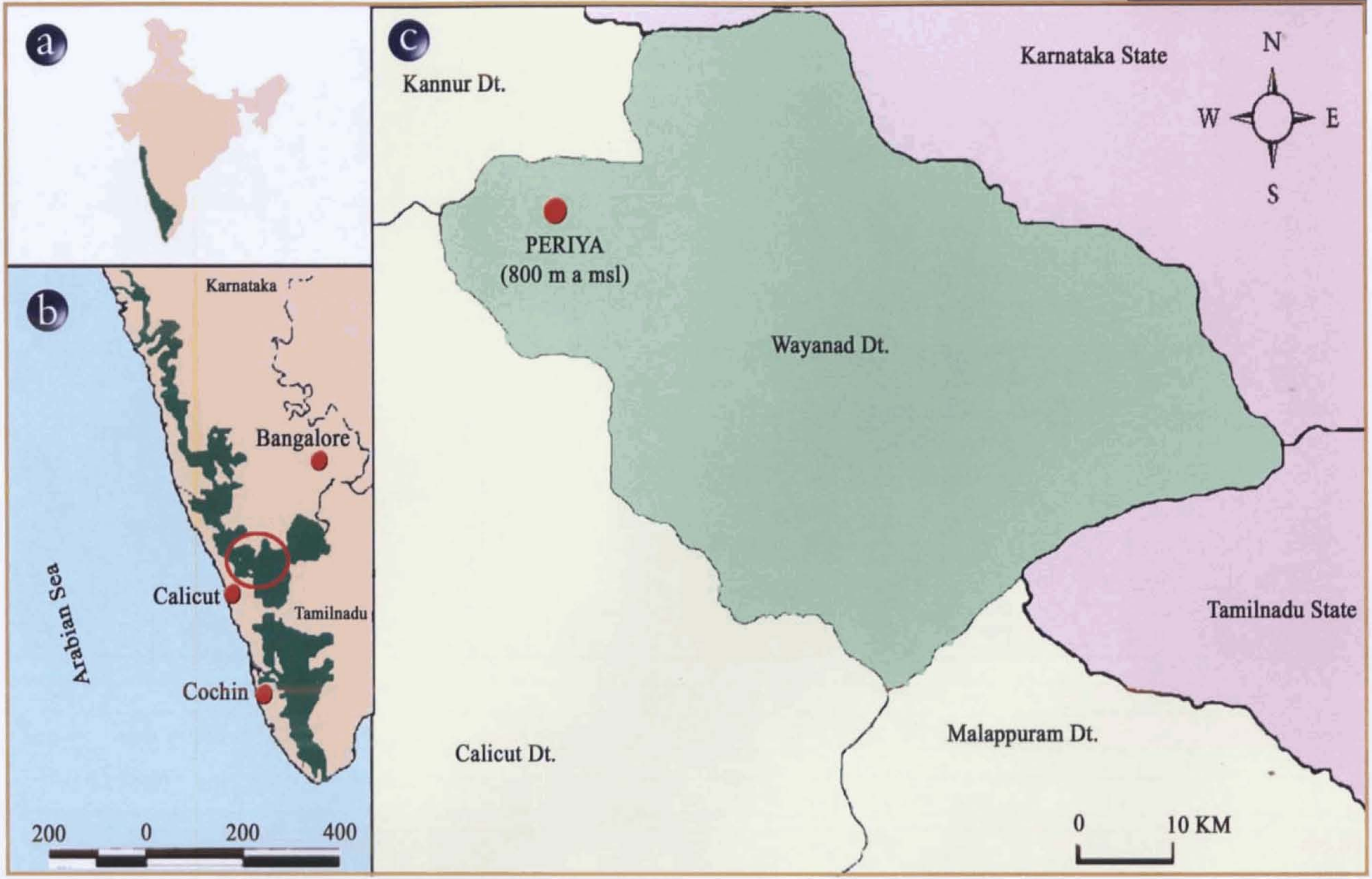


Figure 1.1. Rainfall received during different seasons and months in the wet evergreen forest study region during 2002-03.

PLATE.1



Map showing (a) India (b) The Western Ghats and (c) Study habitat

PLATE.2

Evergreen forest habitat

2. Seasonal variation in litter insect diversity and community structure

INTRODUCTION

Litter invertebrates provide a good indication of ecological conditions because they are highly diverse and functionally important and can integrate a variety of ecological processes, besides being sensitive to environmental change (Greenslade & Greenslade 1984; Brown 1997). Although insects may seem to be small and inconspicuous compared with vertebrates (Whitmore 1990) they are extremely important, arguably dominant elements within the ecosystems (Janzen 1987). A lesser interest in belowground invertebrate communities is obviously due to the fact that litter fauna are locally very numerous, with a wide range of mobility requiring enormous sampling efforts and are often difficult to identify. Insect communities in forest litter are heterogeneous and are represented by detritivores feeding on litter fragments as communitors and mycophagous species, taking part in important ecosystem functions such as decomposition and nutrient mobilization (Anderson 1988; Setälä & Huhta 1991; Laakso & Setälä 1999). Moreover, predatory fauna through predation regulate the populations of other faunal groups (Hyvönen & Persson 1996; Huhta et al. 1998) and thereby possibly influence decomposition processes. Complex natural forests harbour a wide variety of insects which can be directly correlated with the abundance of niche resources, contribute significantly to decomposition and nutrient cycling, (Seastedt 1984; Moore et al. 1988) influence the functioning of decomposer flora (Seastedt 1984) and increase overall soil fertility (Edwards & Bohlen 1995). In spite of their role in decomposition and the fact that litter/soil organisms make up a substantial part of the global biodiversity (Giller 1996: Adams & Wall 2000), many of these species remain poorly known.

The amount of present knowledge on the insects of tropical forests is comparatively sparse compared to that of the temperate forests. Although the insects form around 50% of the biota described from India, and it is clear that seasonal fluctuations in rainfall modify the physical environment (Holdridge 1967) and change resource availability (Fodgen 1972), data on seasonal patterns on arthropod abundance in the natural ecosystems are scarce (Wolda 1988). Temporal fluctuations in the abundance are an important manifestation of populations' response to the environmental conditions. Such seasonal fluctuations are especially prominent in the populations of lower organisms such as insects (Ezhoe 1995; Frith & Frith 1985; Kato et al. 1995). Insects are generally more sensitive to these environmental changes and the various distinct life-history stages of insects are adaptively timed according to the seasonal environmental conditions (Parker & Courtney 1983). Except for a few recent studies (Arun 2003), information on seasonality of insects is grossly lacking from the Western Ghats region, one of the two internationally recognized biodiversity hotspots of Indian region.

As the litter layer of the forest becomes deeper and as it undergoes an orderly and sequential breakdown, the insect faunal assemblages tend to succeed one another. Humid litter conditions in the evergreen forest all through the year supports wet litter preferring insect fauna indicative of the role of climatic variables in determining local distribution patterns. The prime objective of this work is to record the seasonal and layer wise patterns of litter insect diversity and abundance in a selected tropical wet evergreen forest in Wayanad. It is expected that at a conservation level this analysis may provide the decision makers and conservation organizations a powerful tool in maximizing the impact of policies for the conservation of the remaining evergreen forests in the region.

METHODOLOGY

Data collection

Six litter samples of one m^2 area, two each of freshly fallen (L), fermentation (F) and humus (H) layer were collected on a monthly basis during southwest monsoon season (June-August), northeast monsoon season (September-November), pre-summer season (December-February) and summer season (March-May) in 2002-03. Altogether 18 litter samples were collected during each season comprising L, F and H layer. The collected litter was transferred to 45 cm X 30 cm polythene bags with a clearly displayed label having information of the collection date and time. Mean values of bimonthly collection were taken to account for the abundance of individuals in each season.

Fauna was extracted with a series of 15-20 cm diameter Berlese funnel fitted with 4-6 mm mesh screens and a 60-watt bulb (Plate.3) for 1- 2 days until litter was dry (Ananthakrishnan 1996). Organisms living within the sample tend to move downward to escape desiccation and eventually fall into a container of alcohol beneath the funnel. The preserved faunal samples were emptied into a Petri dish with a grid drawn on its underside. The dish is then searched repeatedly under a stereo zoom trinocular microscope (Labomed-ZM45 TM) and collected fauna were sorted, counted, identified and assigned to trophic level according to whether the majority of members of the taxon were predatory, detritivorous or fungivorous (Borror et al. 1996). Once identified to this level, insects were removed and placed in small vials (Tarson, model no: 510000) containing 70 % ethyl alcohol and members of each category for each sample were lumped together. Fine (#8) Watchmaker's forceps were used for picking up insects from the dishes but occasionally a small hairbrush was substituted. Each vial contains a clearly displayed label having information of the site, location, number, collection date, taxon name and preservation date. Following the initial sorting, the whole set of vials from a particular sample were then bundled together using an elastic band. The count of each order/ category of insects was entered on a pre printed tally sheet, also having the date of collection, preservation, sorting and sample code.

Data Analysis

To understand the diversity patterns, alpha diversity indices (richness, evenness and diversity), rarefaction plot, rank abundance plot and Bray Curtis similarity index (Beta diversity index) were considered.

For analyzing taxa richness, **Margalef's index (d)** (Clifford & Stephenson 1975; Magurran 2004) was calculated by using the following formula.

$d = S - 1 / \log (N)$

S = total number of taxa

N = total number of individuals

Evenness expressed as **Pielou's evenness index (J')**, addresses equitability of the taxa (Pielou 1966).

$J' = H' / \log S$

H'= Shannon diversity index

S = Total number of taxa.

Among the diversity indices, **Shannon-Weaver diversity index** (Shannon & Weaver 1949) is the most commonly used because it incorporates both species richness and evenness components and can provide heterogeneity of information (Rosenstock 1998; Cheng 1999). Also, it is possible to test the differences between two communities using a Shannon *t*-test/ANOVA (Magurran 2004; Cheng 1999).

$H' = - \Sigma_i P_i (\log (P_i)$

where P_i is the proportion of the total count arising from the $_i{}^{th}$ species ($\log_e$ was used in its formulation).

Simpson's dominance index (λ) (Simpson 1949) gave the probability of any two individuals drawn at random from an infinitely large community belonging to the same species, its largest value correspond to assemblages whose total abundance is dominated by one, or a very few of the species present

$$\lambda = \Sigma p_i^2$$

where p_i is the proportion of the total count arising from the i th species

Bray-Curtis similarity coefficient (Bray & Curtis 1957) was used to quantify and compare the similarity of insect community composition among seasons or months. This index is calculated as

$$BC_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}\left(y_{ij} + y_{ik}\right)}\right\}$$

where BC_{jk} is the similarity between the jth and kth seasons/months and y_{ij} represents the abundance for the ith insect order in the jth season/month.

This method start from a triangular matrix of similarity coefficients computed between every pair of seasons/months. To measure the similarity coefficients between various seasons/months, a data matrix with p rows (insect groups) and n columns (seasons/months), filled with entries of abundance counts of each insect order for each season/month was first constructed. The similarity based on the Bray-Curtis coefficient was calculated between every pair of seasons/months, and an abundance similarity matrix was then constructed. The Bray-Curtis similarity coefficient was used because it is often a satisfactory coefficient for biological data on community structure (Clarke & Warwick 1994). Furthermore, to reduce the large disparities in counts between species and to validate statistical assumptions for parametric techniques, square root transformation were applied to the original abundance counts of insect order before computing the Bray-Curtis coefficient.

Although there are many classes of clustering methods (Johnson & Wichern 1992; Clarke & Warwick 1994), this study applies **hierarchical clustering** with group-average linking to achieve its purpose because the technique has proven useful in a number of ecological studies conducted during the last two decades (Clarke & Warwick 1994). Seasons were grouped and the groups themselves form clusters at the levels of similarity of insect abundance. These take a similarity matrix as their starting point and successively fuse the samples into groups and the groups into large clusters, starting with the highest mutual similarities then gradually lowering the similarity level at which groups are formed. The process ends with a single cluster containing all samples. The result of the hierarchical agglomerative clustering is represented by a dendrogram, with the X axis defining similarity level at which two samples or groups are considered to have fused and the Y axis representing the full set of samples (seasons/months).

All diversity analysis was done with PRIMER 5 software version 5.2.9 (Clarke & Gorley 2001).

Rarefaction plot, a method for intrapolating smaller samples and estimating taxa richness in the rising part of the taxon-sampling curve (Colwell & Gotelli 2001) was done using Biodiversity pro software (McAleece 1997). Expected numbers of order are plotted against number of individuals on the x-axis. Steeper curves indicate more diverse communities (Hurlbert 1971).

$ES_n = \Sigma^S{}_{i=1}[1-((N-Ni)!(N-n)!)/((N-Ni-n)!N!)]$

S = total species (in this case total insect order/groups)

N =number of individuals

ES_n= how many species/groups would have been expected had we observed a smaller number (n) of individuals

Rank/abundance plot was plotted with relative abundance of each order against rank of taxa/order for the study habitat as a whole and for different seasons (Whittaker 1965). Three abundance models (geometric, log-series and log normal) were fitted to log abundance data using PAST software package ver 1.43 (Hammer et al. 2001).

Most of the data derived from diversity analyses were not normally distributed. Consequently, non-parametric statistics (**Mann –Whitney U tests**) after multivariate comparison through **Kruskal –Wallis H tests** (Sachs 1992), were used for pair wise comparison of data sets during each season. Significance levels of the seasonal variations in Shannon diversity value (H') of each litter layer during each season and between the seasons were analysed with Kruskal Wallis H tests. As the data's of individual insect groups/orders were normally distributed, **one-way ANOVA** was applied to data to test for significant difference in the abundance of different insect groups in different layers (for e.g. abundance of Coleoptera in L, F, H layers)

The relationship between predators and other trophic categories *viz.*, detritivores, microdetritivores and fungivores were analysed with **Pearson's correlation**. Relation between insect diversity values and rainfall received was analysed using correlation analysis. For all analysis, significance was determined at $P<0.05$.Statistical analysis was done with GRETL open source software version 1.1 (Cottrell 2006).

RESULTS

Twelve litter insect faunal groups were collected during four sampling seasons of the study period (Table.1) (Plate.4) and their rank based on relative abundance is represented in (Figure.2.1). Coleopterans and ants were the most abundant taxa sampled, collectively accounting for 53 % of the total individuals captured. The abundance of Ptiliids (Coleoptera) during pre-summer season and Psocopterans during summer season was noticeable. List of family/species of insect orders and beetle families identified from the study habitat provided in table.2.2 and plate.5 respectively.

Seasonal abundance patterns

Coleopterans were the dominant group during all seasons. During pre-summer season, Coleopterans take up >50 % of the insect faunal abundance, chiefly due to the dominance of Ptiliids. Hymenopterans and Collembolans were the other dominant groups in pre-summer season occupying 13% and 11% respectively. Summer season showed the predominance of Coleoptera (20.4%) followed by Psocopterans (15.8%) and Thysanopterans (15.6 %). During the monsoon seasons (southwest and northeast) Coleopterans was the dominating insect order contributing 39% and 42% respectively. Hymenoptera (16%) and Collembola (15%) were abundant during southwest monsoon season while Coleopteran larvae (17%) and Hymenoptera (16%) dominated northeast monsoon season (Figure.2.3). Rank abundance plot showing dominance of insect groups during different seasons is shown in figure.2.2 a, b and c and patterns of insect abundance during different months of the study period provided in figure.2.4.

Layer wise abundance patterns

Thysanoptera dominated fresh litter during all seasons except during summer period, which was dominated by Psocopterans contributing about 60% of the total insect faunal abundance. In the F and H layer Coleoptera was the major insect fauna during all four seasons mostly due to the abundance of Ptiliids and Staphylinids (Figure.2.5).

Litter insect trophic structure

Predatory Staphylinids and ants belonging to *Tapinoma* sp., *Strumigenys* sp., fungivorous Ptiliids, Thysanopterans and microbidetritivorous Collembolans were the dominant trophic categories during different seasons of the study period. During all seasons except summer season, L layer was dominated by fungivorous thrips. During pre-summer season predatory Staphylinids and ants were abundant in F layer while fungivorous Ptiliids was dominant in the humus layer. In summer season preponderance of fungivorous Psocopterans was evident in the fresh litter whereas F and H layer was dominated by predatory ants belonging to *Tapinoma* sp. and Coleopteran Staphylinids respectively. During southwest monsoon season, F layer was dominated by predatory ants and H by fungivorous Ptiliids. Detritivorous larvae and Orthopterans dominated F layer during northeast monsoon period and H layer by fungivorous Ptiliids and predatory ants. (Figure.2.6 & 2.7; Table. 2.1).

Diversity and statistical analysis

The rank-abundance plot showed a shallower slope, implying that the litter insect faunal distribution is even during the study period, consistent with the lognormal model (Magurran 2004). Three models have been fitted for the order – log rank abundance data with log normal plotting the best fit (Geometric k = 0.29, P=6.122 e-13; Log series alpha=2.08, x=0.99, P =1.377 e-31; Log- normal –mean=1.43, variance=0.31, P=0.08) (Figure.2.8 a, b & c).

Rarefaction plot showed higher values of diversity during southwest monsoon period. The rarefaction curve for the pre-summer season reached an asymptote indicating sampling was satisfactory for the period, whereas the curve (Figure.2.9) for southwest monsoon period indicates further sampling is required for the period.

Kruskal Wallis test on abundance of insect faunal groups showed no significant difference with seasons (H=3.30,df= 3, P>0.05), while litter insect diversity (H') revealed significant effect of seasons in the evergreen forest study site (H= 16.69, df=3, P<0.05). Shannon diversity (H') recorded high values during southwest monsoon season (H'=1.972) and high evenness during summer season (J'= 1.77). All 12 insect orders were present during southwest monsoon season, showing high values (d= 2.76) for Margalef's richness index. Simpson's dominance index recorded high values during pre-summer period (0.34) (Table.2.3; Figure.2.10). Pair wise comparison of the diversity values between seasons showed significantly higher diversity values between summer and northeast monsoon season. During pre-summer season fresh litter showed significantly higher diversity value (H'= 2.00) over F and H layers (F=132.42, $P<0.05$). In summer, southwest and northeast monsoon seasons, diversity values were high for F layer but no significant difference with other layers was noted during summer (F=1.77, $P>0.05$) and northeast monsoon season (F=0.62, $P>0.05$) while significantly high values was noticed in southwest monsoon season (F= 20.46, $P<0.05$). When fresh litter of all seasons were analysed, significantly high diversity was recorded during pre-summer season (H'=2.01) (F=8.47, $P<0.05$) while F layer recorded significantly high diversity values during southwest monsoon season (H'=2.09) (F=15.35, $P<0.05$) and H layer during northeast monsoon season (H'=1.60) (F= 29.35, $P<0.05$).

All insect groups, showed significant difference in their abundance in different litter layers. Collembola and Coleoptera were abundant in H layer, ants in F layer and Psocopterans and thrips showed clear-cut preference towards fresh litter (Figure.2.5).

Pearson's correlation analysis revealed a highly significant positive relationship between predators with microbidetritivores ($R^2=0.850$, $P<0.01$) and detritivores ($R^2=0.824$, $P<0.01$) and a marginally insignificant positive relationship with the abundance of fungivores ($R^2=0.52$, $P=0.08$). Significant positive correlation was observed between rainfall and diversity of insect fauna in the study habitat ($R^2= 0.65$ $P<0.05$) (Fgure.2.11).

Bray Curtis similarity coefficient showed greatest similarity between southwest and northeast monsoon season, combined in the dendrogram at a similarity level of 83.96% (Figure.2.12a). To this group, pre-summer season joined with a similarity level of 77.75 % and the final merge of remaining sample (summer season) into the existing cluster to form a single group took place at a similarity level of 73.6 %.

The clustering analyses between various months are represented in figure 2.12b.Three major clusters were evident from the analysis. Highest similarity was observed between monsoon months June and August showing 97.37% similarity to which another monsoon month July got linked at 94.14% similarity. Summer months April and May showed a similarity percentage of 91.6 % and formed a cluster and got linked to southwest monsoon months at 85.02% similarity. Northeast monsoon months September and October observed a similarity percentage of 87.75 % to which February got linked at 83.29% similarity. Three of these minor clusters linked at 82.03 % similarity (Cluster 1). Pre-summer months December and January formed a cluster (Cluster 2) at 95.22% similarity. Insect fauna during dry month of March and wet northeast monsoon month of November showed least similarity, forming a cluster (Cluster 3) at 79.62%. Cluster 3 was linked to cluster 1 and 2 at 62.96% similarity.

DISCUSSION

Forest floor litter insect faunal community structure and abundance associated with an evergreen forest litter habitat in the Western Ghats is recorded for the first time. The existing data is from the moist and dry deciduous forests and plantation forests in the region (Ananthakrishnan et al. 1993). Significant differences were noticed in the insect faunal diversity (H') during different seasons in the study habitat where as abundance of insect fauna revealed no significant variation with seasons. Fluctuations in the amount of rainfall appeared to be the most important factor underlying seasonal fluctuation in insect diversity of tropical forests (Boinski & Fowler 1989; Wolda 1988). Insect fauna living within the relatively sheltered microenvironments provided by dead leaves is less affected by heavy rains (Boinski & Fowler 1989) as their diversity did not declined during monsoon seasons in the study habitat. Peaks of arthropod abundance in the dry season or in the transition from dry to wet season have been reported else where, where the dry season is relatively short (Janzen 1973; Buskirk & Buskirk, 1976). In this study during the middle part of the wet season detritivorous larvae and fungivorous ones were abundant in agreement with the same reported by Boinski & Fowler, 1989 in Costa Rican wet tropical rainforests.

Abundance of fungivorous Psocoptera during the summer and Ptiliidae during pre-summer season were noticed. Though Ptiliid abundance can be attributed to humidity in the wet evergreen tropical forests (Marinoni & Ganho 2003), their low abundance during the monsoon months might be due to the excessive wetness in the area. Staphylinid formed the next major Coleopteran family owing to the increase of mites that serves to them of food (Didham et al. 1998; Sabu 2005). The presence of Ptiliids as the dominant Coleopteran fauna is obvious in the study habitat whereas Staphylinids and Scarabaeids were the major Coleopteran families in the adjacent deciduous forests (Vineesh et al. 2003). This could be attributed to the lesser herbivore dung availability and extensive wetness in the evergreen forests in general. Moisture changes might also have affected the fungal community and thereby, have indirect effects on the fungivorous fauna (Hågvar 1998). During southwest monsoon period, Collembolan populations doubled compared to other months. This might be related to the preference of Collembolans towards wetness (Swift et al. 1979; Lensing et al. 2005). The Psocopterans showed a climb in pre-monsoon months and their abundance can be noticed in L layer alone. The presence of two wet rainforests preferring ant genera *Acropyga* sp. and *Paratrechina* sp. (Shattuck & Barnett 2001) exclusively in the evergreen forest is indicative of the influence of litter habitat conditions in determining the habitat preference of ants. Abundance of ants during southwest monsoon season could be related to the abundance of Collembolans serving as food to *Strumigenys* sp. abundant in the study habitat (Anu & Sabu *in press*). First record of Carabids *Perigona nigriceps* and *Clivina* spp. from the evergreen forest of Wayanad were made in this study. Scarcity of termites in the samples might be due to their better adaptability to environments with poor quality of organic resources, low quality of water and also they have very aggregated distributions (Decaens et al. 1994; Stork 1993). Several other studies (Madge 1965; Plowman 1979; Lasebikan 1988; Stork 1988) also report low numbers of termites in litter/ soil samples in tropical forests. Abundance of moisture loving Staphylinids, Ptiliids, Collembola and Psocoptera are indicative of the influence of moist wet litter floor on faunal distribution patterns (Didham et al. 1998).

Prominence of fungivorous thrips and Psocopterans in the fresh litter might be due to the abundance of fungal communities colonizing the fresh litter. Dominance of predatory and fungivorous insect fauna in the evergreen litter habitat indicates the high resource availability including fungal blooms and prey organisms. The parallel rise in predator groups *viz.*, ants and Staphylinids with detritivorous, microbidetritivorous and fungivorous groups suggests the significance of the latter in maintaining diversity and abundance of predator faunal community in natural forest litter stands. Abundance of insect fauna is often influenced by the initial chemistry of litter and changing chemical profile during litter break down influences the abundance and distribution of insect communities (Ananthakrishnan 1996; Maity & Joy 1999).

The rarefaction curve for the pre-summer season reached an asymptote indicating sampling is satisfactory for the period, whereas the rarefaction curve for southwest monsoon period shows further sampling is required for the period (Magurran, 2004). Even though the abundance values showed a peak during pre-summer season, the high diversity value during southwest monsoon season is due to the even distribution and high richness of litter insect fauna during the period. Evenness index showed a lower value during pre-summer season due to the dominance of Coleopterans and ants.

The fit of general log normal distribution with faunal abundance data is a feature of species rich communities (Whittaker 1965; Hughes 1986;

Magurran 2004). It could be asked whether anything is to be achieved by fitting models since agreement with such a model does not support any particular ecological hypothesis. Pielou (1975) answers the question by pointing out that fitting model leads to economy of description and facilitates comparison among different communities. These models are important ecological tool and their potential in elucidating empirical patterns of diversity has only just begun to be realized (Magurran 2004).

There are no comparative data from southwest Western Ghats forests on the effects of sampling season on diversity of insects captured. However, studies by Arun & Vijayan 2004 in Siruvani forests of Western Ghats have reported highest insect abundance during southwest monsoon period. High insect abundance recorded in this study during pre-summer season was due to the dominance of Ptiliids while diversity, evenness and richness were high during southwest monsoon period. As temperature influences seasonality in subtropics and temperate zones (Basset 1991), seasonality in litter invertebrates of tropics is influenced more by rainfall and relative humidity (Wolda 1988; Kai & Corlett 2002; Levings & Windsor 1985). Likely, a significant positive correlation was observed between rainfall and diversity of insect fauna in the study habitat. Many studies have roughly correlated peaks of insect abundance with plant phenology, with invertebrate abundance peaking during the period of maximum young leaf availability (Wolda 1988; Fodgen 1972; Buskirk & Buskirk 1976) As my study did not considered the phenological patterns a correlation between insect diversity and leaf/fruit production cannot be made with respect to the study habitat. Again separating the influences of temperature, rainfall and plant phenology is difficult because all three show basically similar seasonal pattern (Kai & Corlett 2002). Seasonal patterns were quantified only for single year in this study, but casual observations made in other years support the hypothesis that the patterns observed in this study are indeed seasonal and not primarily due to some other source of variation.

Bray Curtis similarity coefficient showed greatest similarity between 2 monsoon periods due to the similar pattern in insect abundance, again influenced by similar rainfall patterns. Summer months of April, May and pre-summer months of December and January clustered together showing similar insect abundance. Clustering between summer month of March and pre-summer month of November at 79% similarity owing to resemblance in insect abundance pattern in accordance with likeness in the amount of rainfall received during the 2 months.

The sampling technique might have resulted in under representation of large, active species, such as many Carabids, that were able to take evasive action during this approach. Again, many soft-bodied ones might have missed out from the collections and sources of error probably introduce a conservative bias in the richness and abundance counts. Still, it provides a glimpse of the insect faunal diversity enclosed within the wet evergreen litter ecosystem in the Wayanad forests. Some taxa *viz*., Psocopterans and many Coleopteran families were abundant in the samples and could not be as thoroughly sorted or precisely identified as others.

Interpretation of studies such as this is compromised by difficulties in identification of species due to the incomplete knowledge of species diversity within speciose but little known taxa, inability to identify larvae of many groups especially the Coleoptera at lower taxonomic level. Obviously, more information needs to be gathered about biologies of the component taxa at various life stages in order to gain a more complete picture of how these assemblages interact.

Table.2.1. Abundance of litter insects recorded from L-F-H litter layers during the various seasons from the evergreen forest at Periya

Order	Seasons															
	Pre-summer				Summer				Southwest monsoon				Northeast monsoon			
	L	F	H	Mean±Sd	L	F	H	Mean±Sd	L	F	H	Mean±Sd	L	F	H	Mean±Sd
Blattaria	2±1.4	3±1.5	4±1.8	3.0±1	0±0.4	1±0.8	3±1.5	2.5±1.52	2±1.4	3±1.7	4±1.7	3±1	0±0.2	2±1.4	2±1.4	1.3±1.2
Coleoptera	20±4.9	15±14.6	294±4.8	155±137	6±4.5	25±2.8	94±4.4	35.4±46.3	8±5.7	27±1.4	90±4.4	41.7±43	8±3.4	21±2.8	93±4.5	40.7±45
Ptiliidae	7±2	52±14	160±22.4	112.3±78.6	1±0.2	5±1.2	26±8	10.66±13.4	2±1.2	10±2.3	29±8.9	13.66±13.4	3±0.1	7±2.3	45±8.1	18.3±23.2
Staphylinidae	5±1	62±12	71±14.2	90.66±35.9	0	10±2.3	36±12	15.33±18.5	4±1.3	7±1.5	25±7.8	12±11.3	4±0.2	5±1.4	22±6.7	10.3±10.1
Hydrophylidae	1±0	10±2	22±6.3	18.33±10.5	0	2±0.1	8±2	3.33±4.1	0	1±0.1	7±2.1	2.66±3.5	0	1±0.3	14±2.3	5±7.8
Carabidae	1±0.2	5±1	8±2.3	8.66±3.5	1±0.3	4±0.2	2±1.2	2.33±1.5	1±0.3	1±0.4	2±0.9	1.33±0.5	0	0	1±0.1	0.3±0.7
Bostrichidae	0	2±1	2±0.4	2.66±1.5	0	0	5±1.3	1.66±2.8	0	0	0	0	0	0	0	0
Curculionidae	1±0.1	7±2.5	5±0.2	9.66±3.0	0	1±0.1	3±1	1.33±1.5	0	0	2±0.2	0.66±1.2	0	0	1±0.3	0.3±0.7
Scydmaenidae	0	8±2	2±0.1	8.66±4.2	4±0.2	0	4±1.2	2.66±2.30	0	0	1±0.3	0.33±0.5	0	0	0	0
Scolytidae	1±0.2	2±0.8	15±1.8	8±7.8	0	0	3±1.3	1±1.70	1±0.2	8±2.4	19±2.6	9.33±9.1	0	5±1.3	6±2.3	3.6±3.2
Trogossitidae	0	1±0.1	0	1±0.6	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomelidae	2±1	2±0	3±1.2	5±0.6	0	3±0.1	2±1.2	1.66±1.5	0	0	1±0.1	0.33±0.7	0	3±1.2	1±0.2	1.3±1.5
Elateridae	1±0.2	0	1±0.7	1.33±0.7	0	0	1±0	0.33±0.5	0	0	1±	0.33±0.7	0	0	0	0
Scarabaeidae	1±0.1	0	2±1.2	1.66±1	0	0	4±1.3	1.33±2.3	0	0	1±0.3	0.33±0.7	1±0.5	0	2±0.3	1±1
Histeridae	0	0	1±0.1	0.3±0.2	0	0	0		0	0	2±1	0.6±1.2	0	0	1±0.1	0.3±0.7
Tenebrionidae	0	0	2±0.8	0.6±1.1	0	0	0		0	0	0	0	0	0	0	0
Collembola	12±5.4	41±5.7	40±4.1	31±16.5	3±1.4	2±1.4	13±4.5	9.6±6.1	8±3.7	14±4.5	25±2.3	15.7±8.6	4±1.7	5±1.7	6±1.6	5±1
Entomobryidae	6±1.2	28±3.4	31±6.5	21.66±13.5	1±0.1	2±0.3	5±0.5	2.66±2.1	4±1.2	5±1.3	9±2.7	6±2.6	2±0.4	2±0.8	4±1.6	2.66±1.2
Hypogastruridae	6±1.5	10±2.1	8±1.6	8±2	2±0.8	2±0.2	6.5±1.6	3.5±2.5	3±1.1	6±1.8	12±3.1	7±4.6	1±0.2	3±1.2	2±1.2	2±1
Sminthuridae	0±	2±1	1±0	1±1	0	0	1±	0.33±0.5	1±0.5	2±0.3	3±0.9	2±1	1±0.3	0	0	0.33±0.7
Isotomidae	0±	1±	0	0.33±0.5	0	0	0	0	0	1±0.4	1±0.2	0.66±0.7	0	0	0	0±0
Dermaptera	0±0.4	0±0	1±0.9	0.3±0.6	0±0	0±	1±0.8	0.1±0.6	0±0.2	0±	1±0.8	0.3±0.7	0±0.2	0±	3±1.5	1±1.7
Diptera	2±1.4	2±1.4	2±1.4	2.0±0	0±0	1±0.6	2±1.4	2.4±1	0±0.2	6±1.6	2±1.4	2.7±3.1	3±2.3	1±0.9	2±1.4	2±1
Hemiptera	2±1.4	3±2	4±1.8	3.0±1	2±1.4	0±	4±1.7	3.8±2	1±0.9	2±1.4	2±1.5	1.7±0.6	0±0.2	1±0.9	6±1.7	2.3±3.2
Hymenoptera	13±2.5	77±13.4	21±2.7	37.0±35.6	2±1.1	11±1.9	35±1.6	13.5±17.1	6±1.2	13±0.7	31±3.7	16±12.6	6±1.9	3±1.7	40±5.0	16.0±20.4
Isoptera	14±1.4	14±4.6	0	9.3±8.1	11±2.6	11±1.4	0	22±6.3	6±3.1	13±4.5	0	6.3±6.5	0±0	0±	2±1.4	0.7±1.1
Larva,egg,pupa	3±4.6	31±1.7	18±2.6	17.3±14	4±2.8	18±3.4	2±1.4	23.4±8.1	0±0.1	3±1.7	22±2.3	8.3±11.9	1±0.6	12±1.4	38±5.6	17.0±19
Orthoptera	3±2.3	3±1.8	5±1.8	3.7±1.2	0±0.3	0	5±1.7	1.8±2.8	0±0.1	3±1.7	0	1±1.7	3±2.8	12±1.4	4±1.7	6.3±4.9
Psocoptera	0±0	0	0	0	77±9	0	0	25.6±44.4	2±1.41	0	0	0.7±1.1	0±0.2	0±	0	0.0
Thysanoptera	25±8.3	18±2.6	10±5.6	17.7±7.5	19±2.8	2±1.4	8±5.3	25.2±9.1	22±7.0	6±1.61	0	9.3±11.4	12±6.2	1±0.9	3±1.5	5.3±5.8

Table.2.2 List of family/species identified from the study habitat

Insect Order	Family	Species
COLEOPTERA	Carabidae	*Clivina* spp., *Perigona nigriceps*
	Curculionidae	*Rhadinomerus* sp.
	Histeridae	*Pachylister chinensis*, *Santalus orientalis*
	Ptiliidae	*Bambara* spp., *Storicricha* spp.
	Scarabaeidae	*Copris davisoni*, *Copris repertus*, *Onthophagus bronzeus*, *Onthophagus dama*
	Scydmaenidae	*Euconnus* spp.
	Tenebrionidae	*Gonocephalum bilineatum*, *Uloma* spp.
	Bostrichidae	
	Chrysomelidae	
	Elateridae	
	Hydrophylidae	
	Scolytidae	
	Staphylinidae	
	Trogossitidae	
COLLEMBOLA	Entomobryidae	
	Hypogastruridae	
	Isotomidae	
	Sminthuridae	
ORTHOPTERA		*Mecopoda* spp., *Gryllus* spp.
ISOPTERA		*Odontotermes obesus*
HEMIPTERA	Pyrrhocoridae	
THYSANOPTERA		*Stigmothrips limpidus*, *Bactothrips* spp.
HYMENOPTERA	Formicidae	*Acropyga* spp., *Camponotus angusticolis*, *Camponotus radiatus*, *Camponotus* sp.*1*, *Camponotus* sp.2, *Cardiocondyla* sp.1, *Crematogaster* sp., *Diacamma* sp.1, *Leptogenys* sp.1, *Leptogenys* sp.2, *Monomorium* spp., *Myrmicaria* sp.1, *Myrmicaria* sp.2, *Oduntomachus* spp., *Pachycondyla* sp., *Paratrechina* sp., *Ponera* sp., *Solenopsis* sp.1, *Solenopsis* sp.2, *Strumigenys* sp., *Tapinoma* sp., *Tetramorium* sp.1
	Chalcidae	*Aphanogmus* spp.

Table 2.3. Seasonal variations in the litter insect diversities at Periya

Seasons	**Number of insect orders (S)**	**Abundance (N)**	**Margalef's richness (d)**	**Pielou's evenness (j')**	**Shannon index (H')**	**Simpson's dominance (lambda)**
Pre-summer	11	279.33	1.949328	0.619468	1.53932	0.340039
Summer	12	165.27	2.219459	0.768288	1.97062	0.186871
Southwest	12	106.66	2.76036	0.747262	1.972067	0.200573
Northeast	11	97.66	2.380415	0.747459	1.857366	0.225016

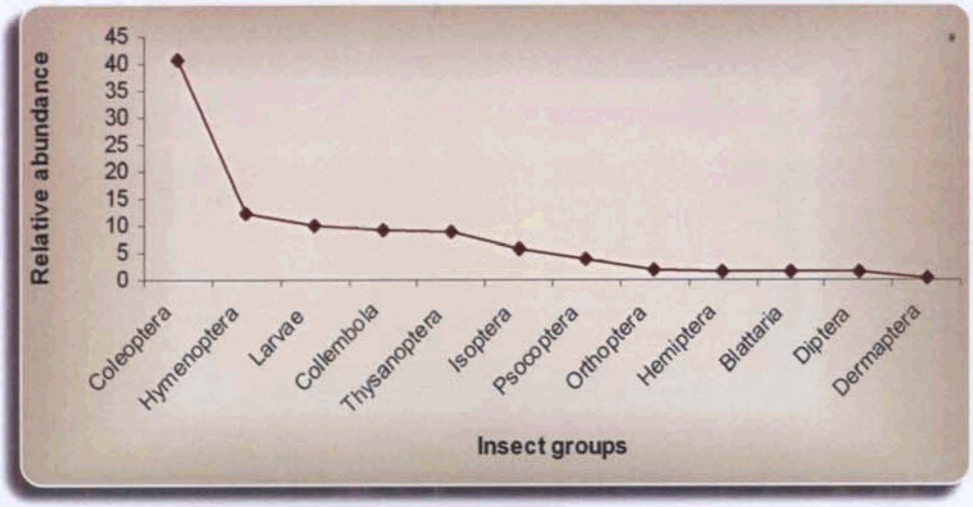


Figure.2.1 Rank abundance plot showing the dominance of insect groups in the evergreen habitat during the study period

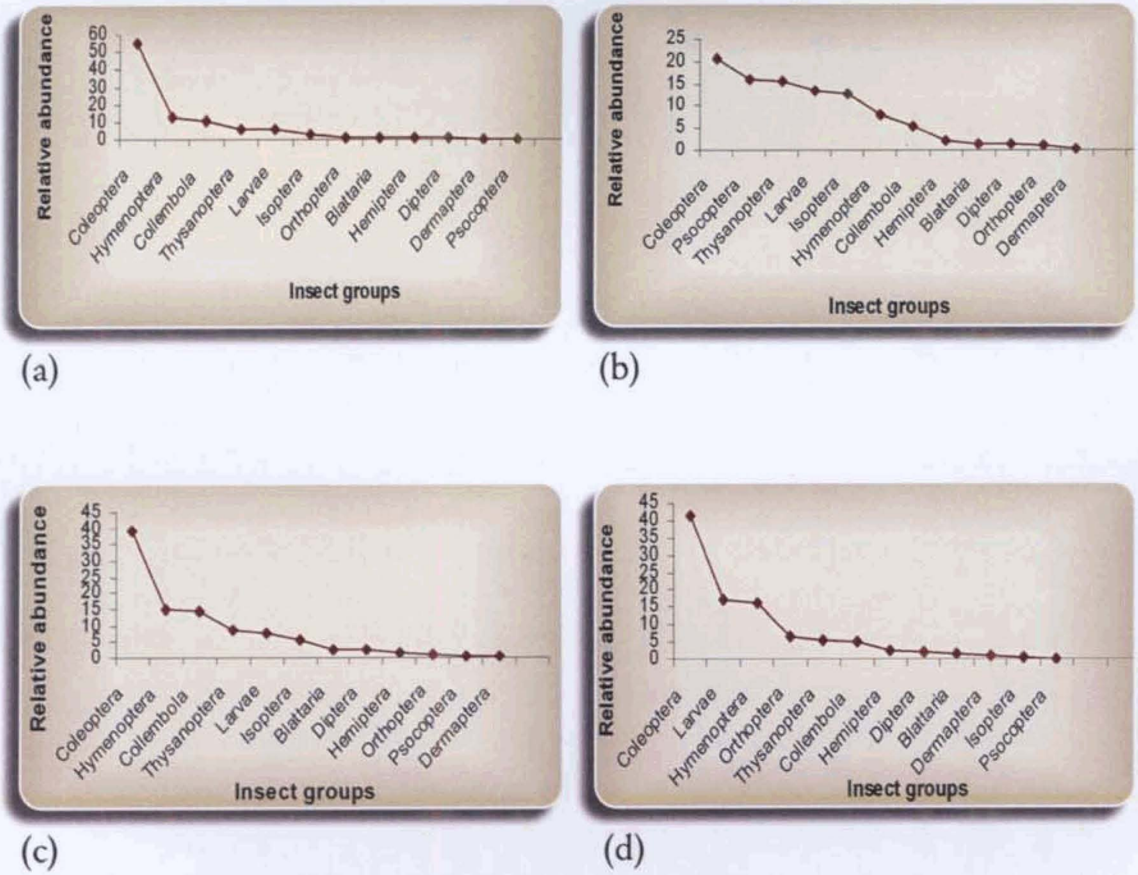


Figure.2.2 Rank abundance plot showing the dominance of insect groups during (a) pre-summer (b) summer (c) southwest monsoon and (d) northeast monsoon seasons

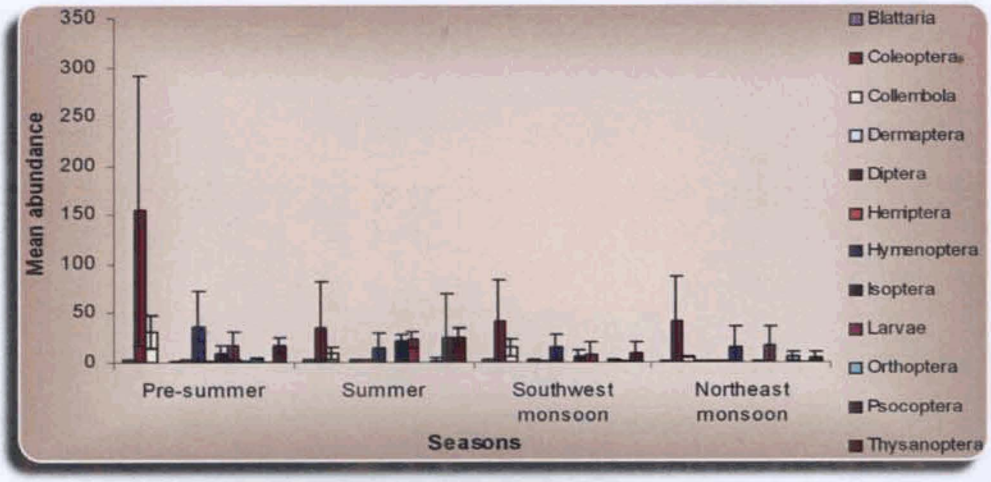
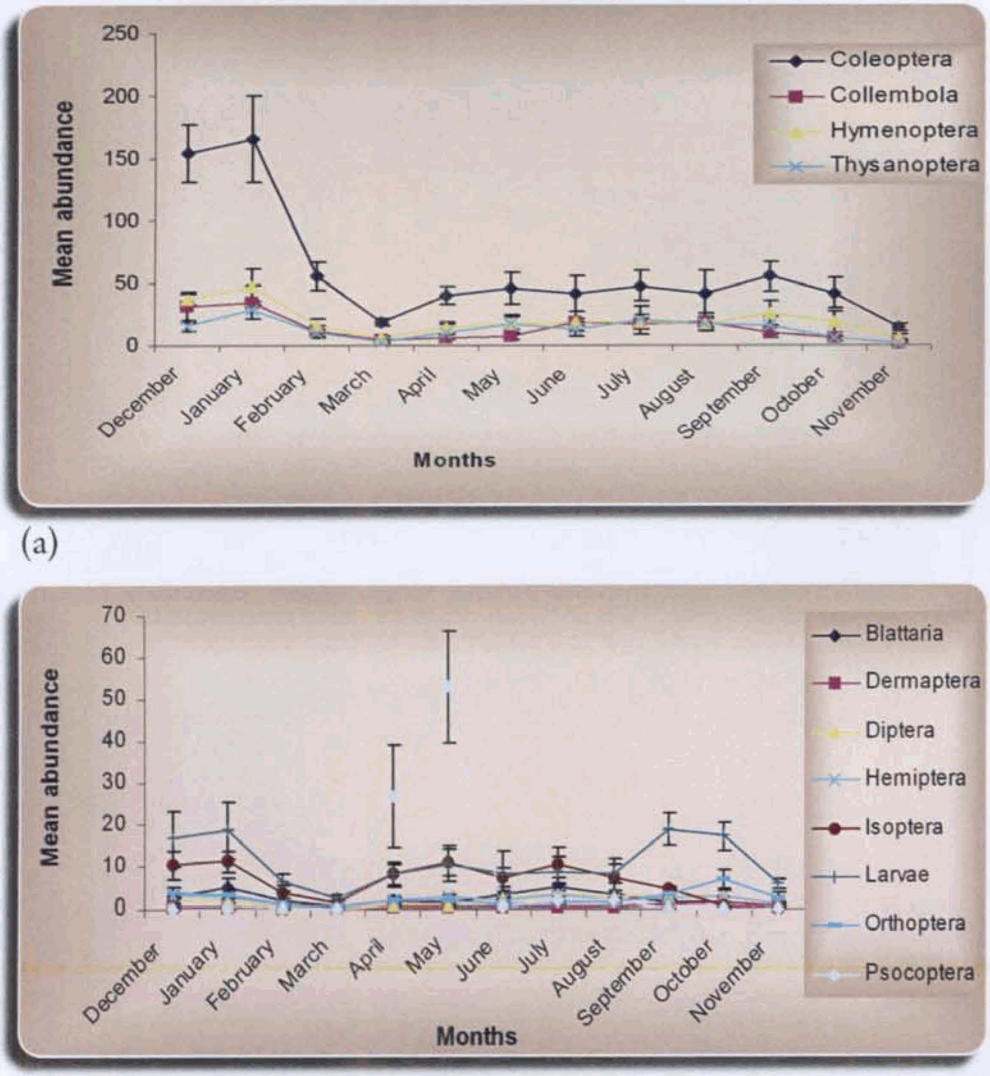


Figure.2.3 Seasonal distribution of litter insect fauna in the evergreen forest at Periya



(a)

(b)

Figure.2.4 Monthly variation in the faunal abundance of litter insects at Periya (a) Major groups and (b) Minor groups

A1C

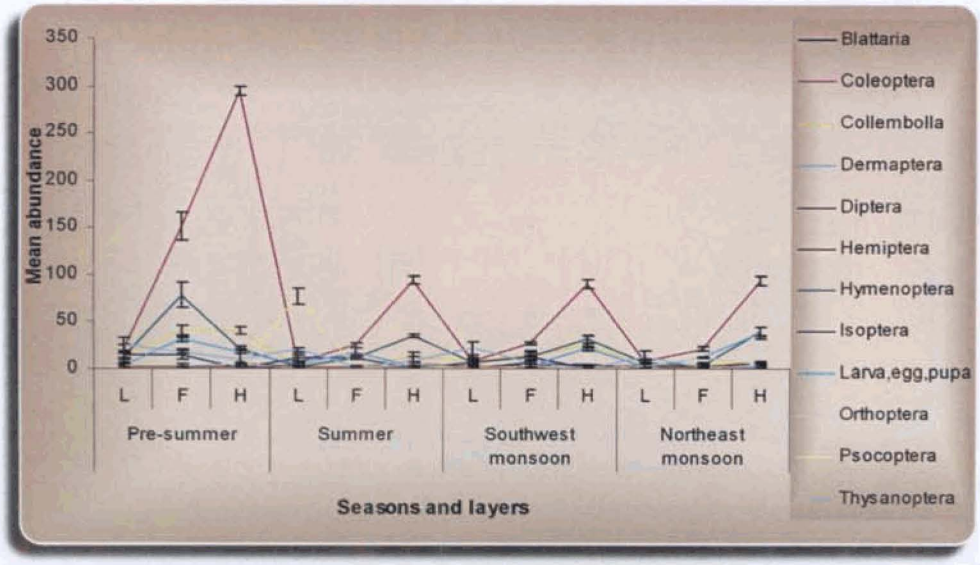


Figure.2.5 Seasonal and layer wise distribution of insect faunal groups in the evergreen habitat

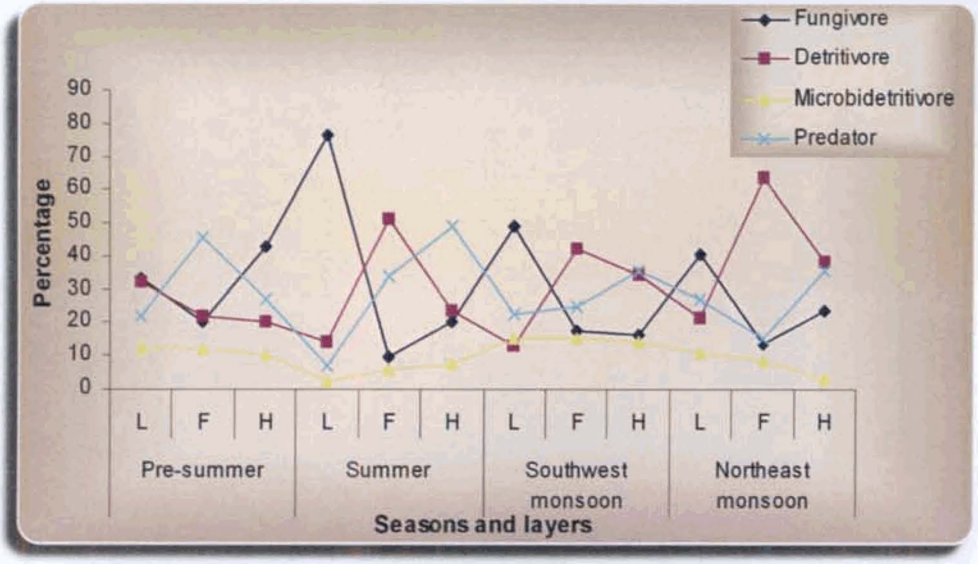


Figure.2.6 Seasonal variation in the abundance (%) of various trophic groups in the evergreen habitat

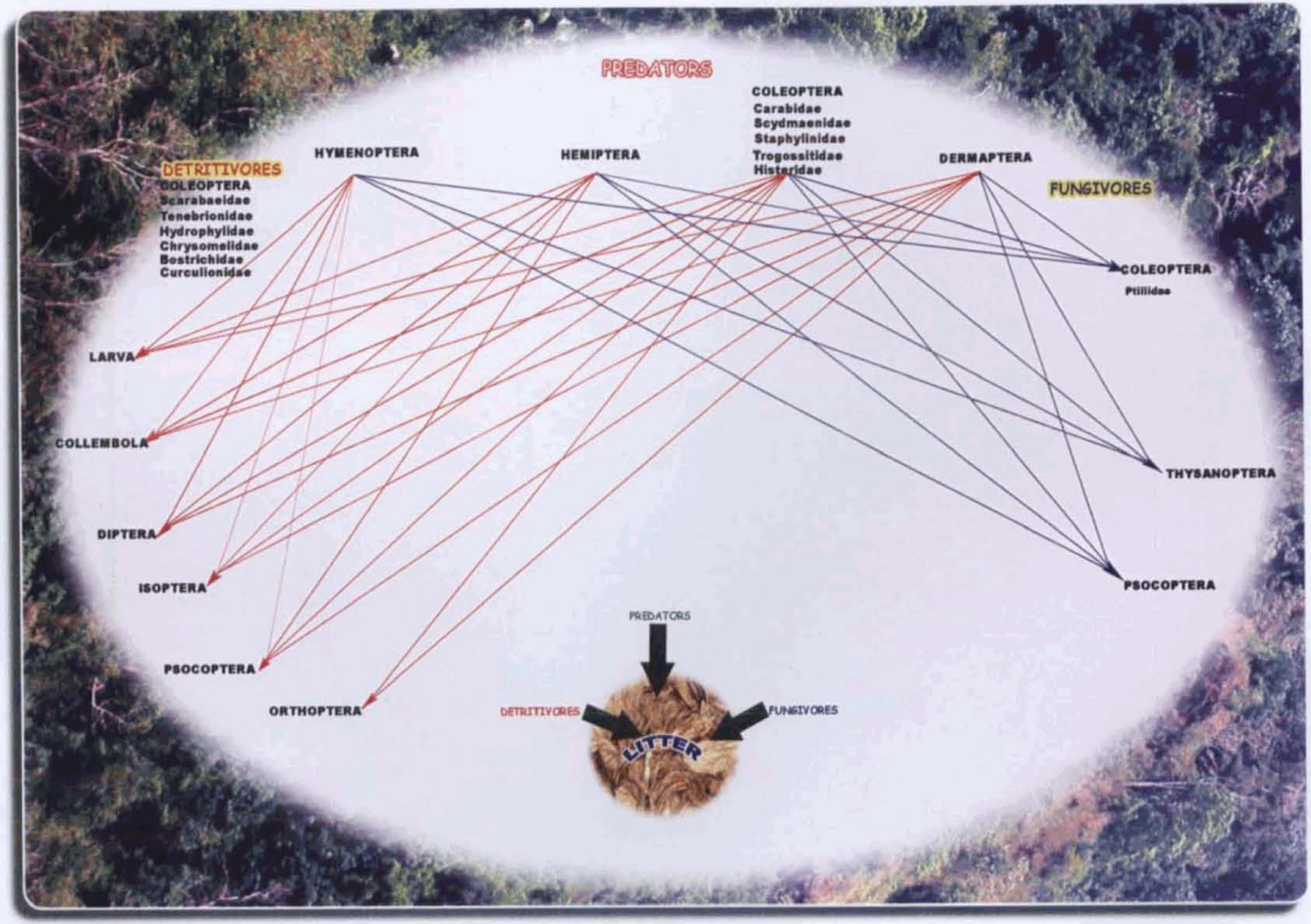


Figure. 2.7 Trophic web of insect orders collected from the study habitat

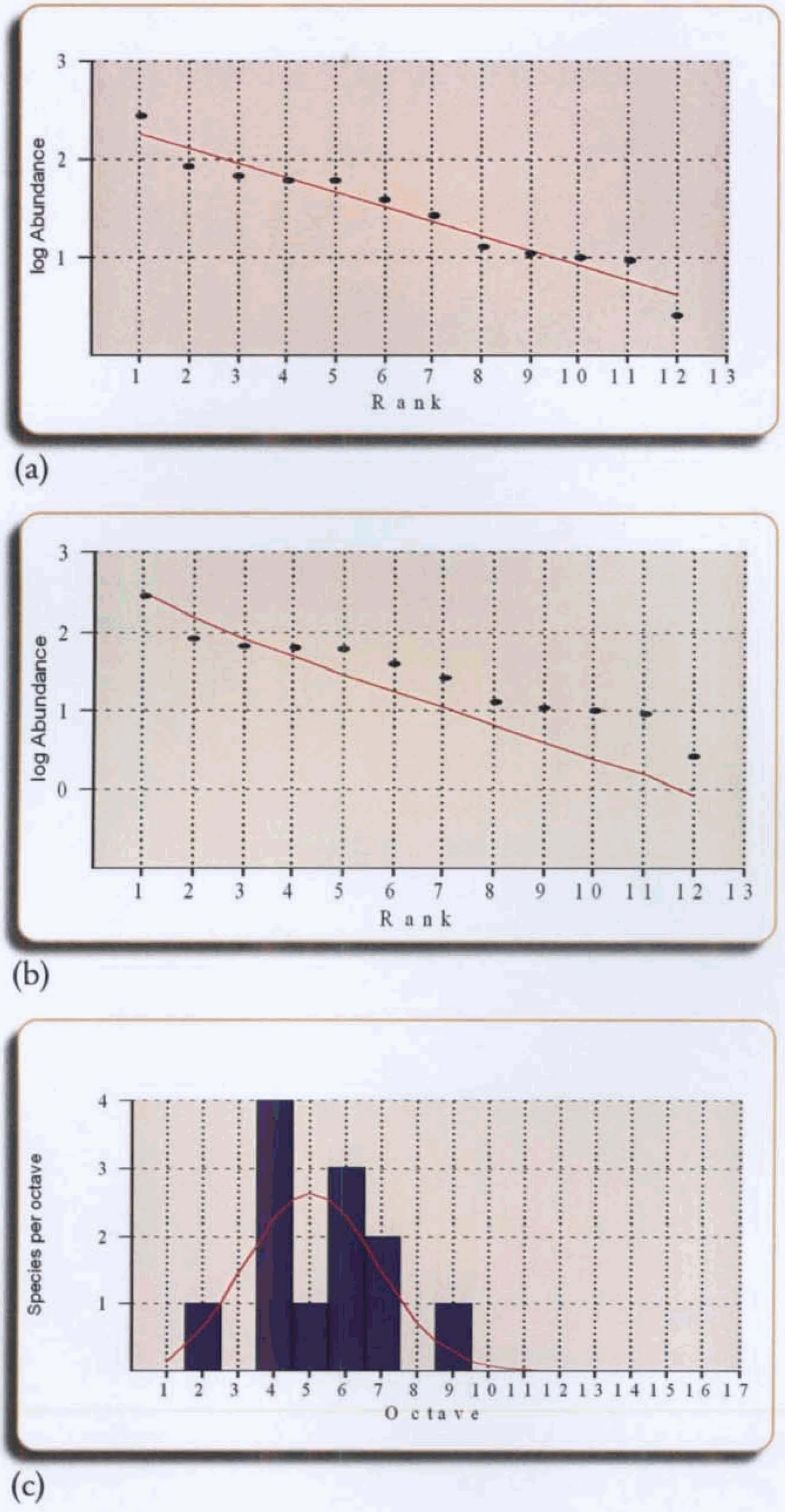


Figure. 2.8 Abundance models fitted to log abundance data of insect faunal abundance during the study period (a) Geometric (b) Log-series (c) Log normal

41F

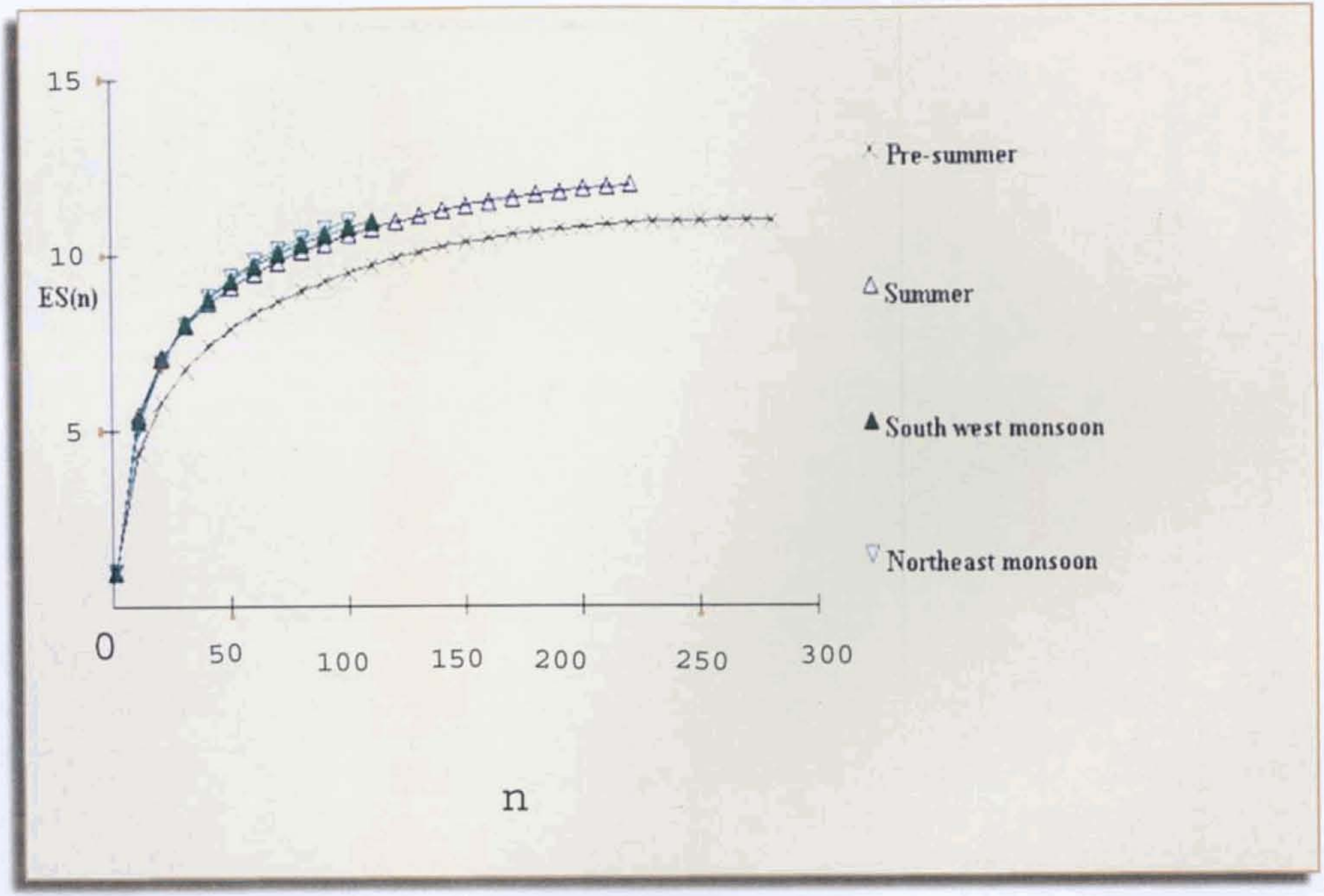


Figure. 2.9. Rarefaction plot with expected no of insect orders
Es (n) plotted on Y-axis against abundance of individuals (n) on X-axis

A1 G7

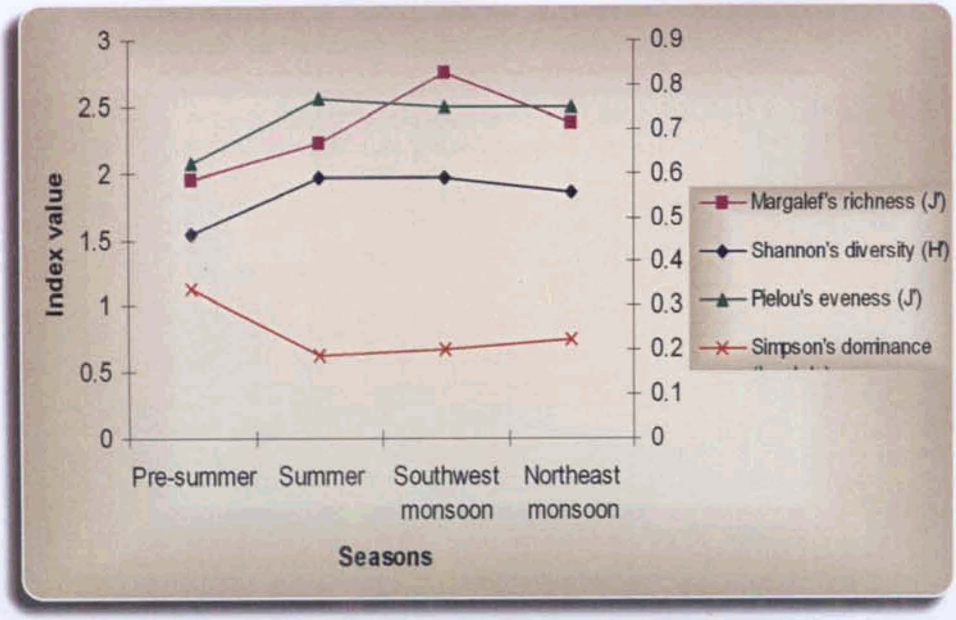


Figure.2.10 Seasonal variation of insect diversity during the study period

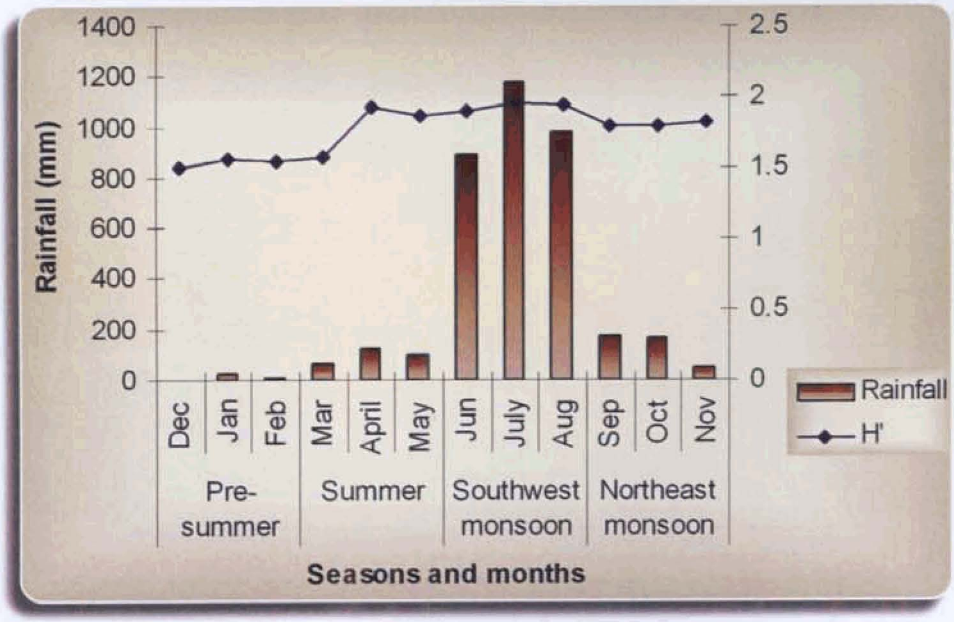


Figure.2.11 Relation between rainfall and litter insect diversity (H') during study period

A1 H

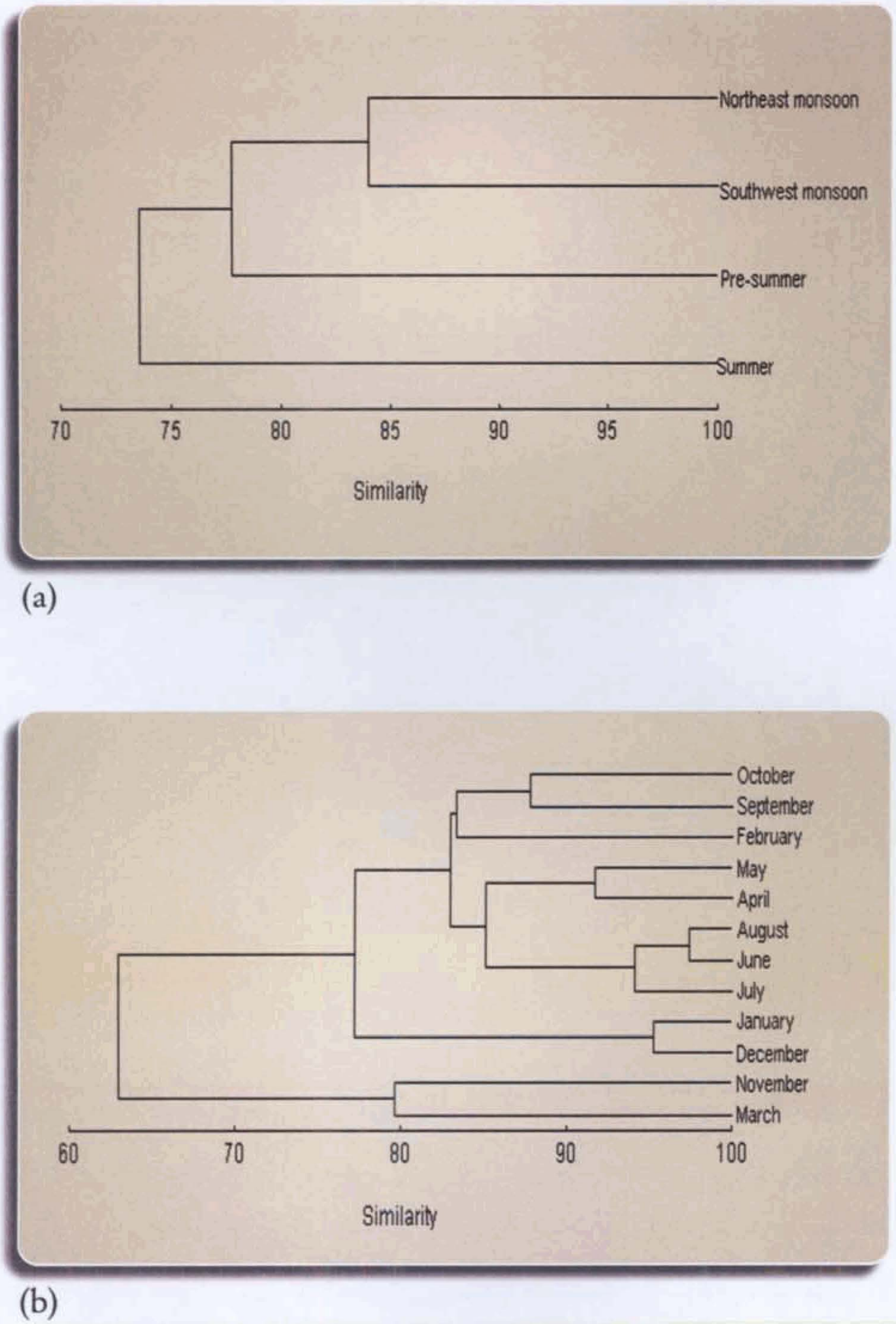


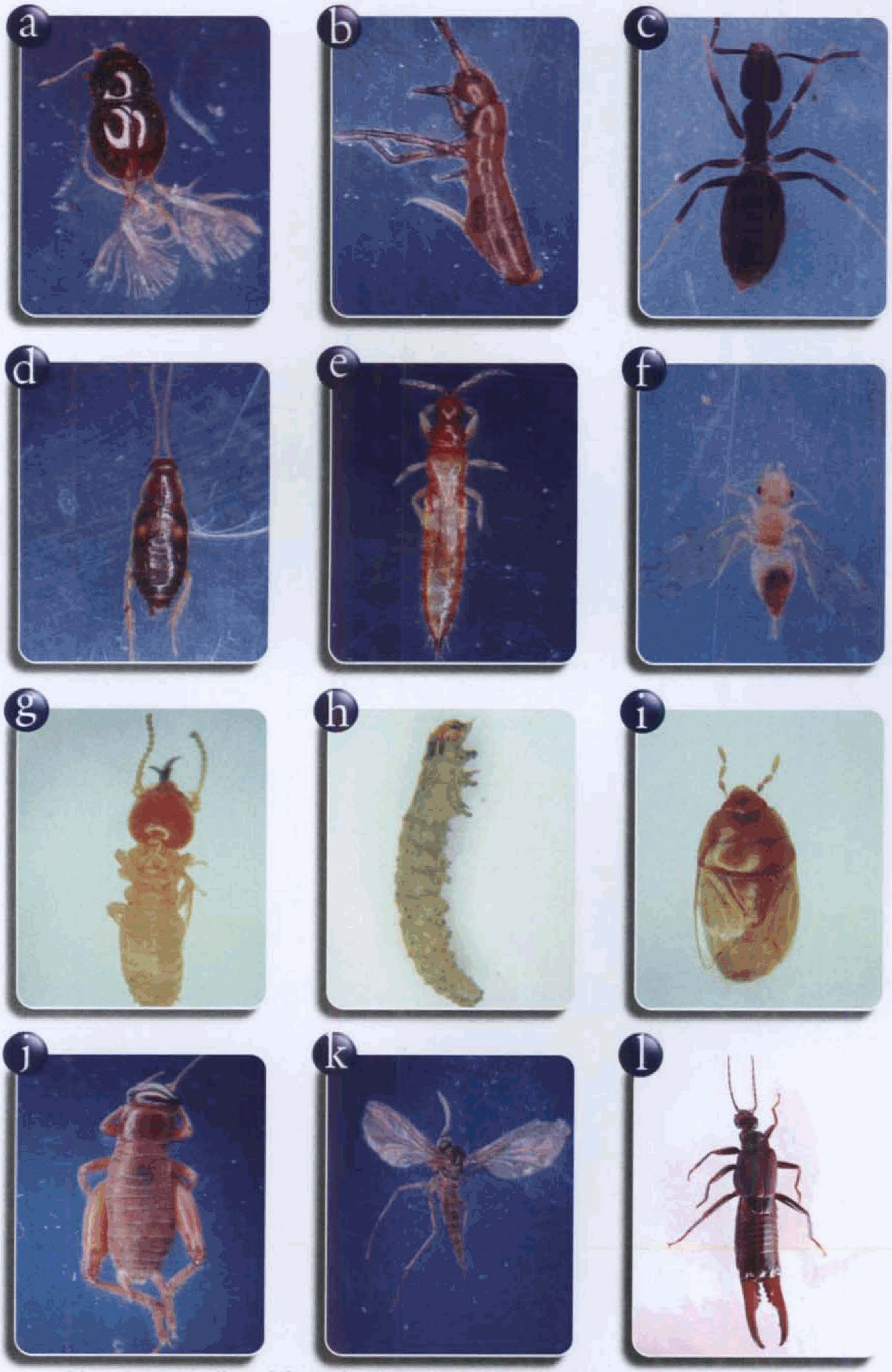
Figure.2.12 Dendrogram based on hierarchical agglomerative clustering (group-linking) of litter insect faunal assemblage during (a) seasons and (b) months

PLATE.3

(a) Series of Berlese funnels and (b) Forest leaf litter floor

4'J

PLATE.4



Litter insects collected from the evergreen habitat (a) Coleoptera (b) Collembola (c) Hymenoptera (d) Blattaria (e) Thysanoptera (f) Psocoptera (g) Isoptera (h) Larvae (i) Hemiptera (j) Orthoptera (k) Diptera (l) Dermaptera

41K

PLATE.5

Litter Coleoptera of evergreen forest (a) Staphylinidae (b) Ptiliidae (c) Scarabaeidae (d) Chrysomelidae (e) Carabidae (f) Bostrichidae (g) Curculionidae (h) Histeridae (i) Tenebrionidae (j) Trogossitidae (k) Scolytidae (l) Scydmaenidae

41 L

3. Checklist and pictorial key of dung beetles

INTRODUCTION

Structure of the vegetation, soil type and physical structure of the forest appear to be an important factor in the structure and local distribution of dung beetle communities (Doube 1983; Nealis 1977; Jansen 1983; Davis 1993; Davis 1998; Davis & Sutton 1998; Davis et al. 2000). Our knowledge about the composition and dynamics of forest dung beetle communities and their responses to destruction, fragmentation and isolation of rain forests are based on the records from Central and South America (Durães et al. 2005; Horgan 2002; Halffter et al. 1992; Peck & Forsyth 1982; Klein 1989; Scheffler 2005) and Malaysia in South east Asia (Davis 2000; Davis et al. 2001). Whereas, very little is known about the forest dung beetles in South Asian region especially from the Western Ghats which is a recognized global hot spot of biodiversity (Bossuyt et al. 2004; Myers et al. 2000) with distinct regional variation in topography, rainfall patterns and vegetation types.

Though, in his classic work Arrow (1931) has reported 48 species of dung beetles from the western slopes of South Western Ghats it is unable to decipher how many are from the forests, as habitat details are not provided along with site descriptions. An analysis of the sites indicated that his collections from the western slopes had been confined to lower elevations and gaps in the Western Ghats. No records of dung beetles from the midlands and highlands in Western Ghats, which were densely forested and remained inaccessible till Second World War. Timber requirements by the British army during Second World War and state sponsored developmental activities such as hydroelectric projects and human settlements during the late 1970s and 1980s wiped out most part of the natural vegetation in the region (Nair 1991) and only a few fragments of the old mature wet evergreen forests remains.

As per the records (Biswas & Chatterjee 1986; Biswas & Mulay 2001), only 19 species are known from the moist evergreen forests of Western Ghats against the 89 species recorded from the evergreen forests in Malaysia (Davis 1993) and 59 from the Amazon region (Andresen 2002). Collections made from the Shola and deciduous forests of Wayanad revealed the existence of 22 and 41 species of dung beetles respectively (unpublished data). In the current study a catalogue of dung beetles based on 1 year collections using bait surface grid pitfall traps exclusively from one of the best-preserved wet evergreen forest in the Wayanad region of Nilgiri biosphere in Kerala state, in Southern Western Ghats is provided.

METHODOLOGY

Most coprophagous beetles do not disperse long distances to find food as they are very sensitive to environmental changes and have a stenotopic distribution in relation to vegetation types (Cambefort & Hanski 1991, Klein 1989, Favila & Halffter 1997). Bait-surface-grid pitfall trap is the widely accepted standard method for the random collection of dung beetles (Lobo et al. 1988, Veiga et al. 1989) (Plate.6).

The collections were done during one-year period from November 2003 – 2004. 30 bait-surface-grid pitfall traps, made up of plastic basins (210 mm in diameter) were set in the ground in the study site at randomly selected spots separated by about 100 m using hand trowels. Traps were baited with fresh cow dung and the contents were collected at an interval of one week. The collected dung beetles were preserved in 70% ethanol prior to processing and were sorted from each sample. Species identification was done with the help of taxonomic keys available in the books of Arrow (1931), Balthasar (1963 a & b) and Baraud (1992) and confirmed with the assistance of specialists. After identification specimens were dried, pinned, labeled and temporarily kept in the insect collections of St. Joseph's College and would be transferred to the Zoological Survey of India, Western Ghats station, Calicut.

RESULTS

Current checklist on beetle fauna of evergreen forests of Wayanad region of Western Ghats reveals the existence of 29 species, all belonging to subfamily Coprinae comprising four tribes- Coprini, Onthophagini, Onitini and Oniticellini. Of the 29 species reported, four are first record from South India; six species are endemic to South India of which three are endemic to Western Ghats including the two, which are specific to Nilgiri Biosphere Reserve (Plate.7). This checklist may serve as baseline information on the dung beetle fauna in the western slopes of South Western Ghats and will be useful in future comparisons with faunal lists from other regions of Western Ghats. Synonymies (in italics) for genera and species are provided. Superscripts provided to species furnishes the following details * first report from South India, $^\#$ endemic to Nilgiri Biosphere reserve, $^+$ endemic to South India, $^\$$ endemic to Western Ghats.

SCARABAEIDAE
SCARABAEINAE
COPRINI

Copris GEOFF.

GEOFFROY, 1762, Ins. Env. De Paris I:87; BURMEISTER, 1846, Genera Ins. Heft 10, Col. No. 27; REITTER, 1892 (1893): 39, 93; PERINGUEY, 1900 (1901): 110, 342; BOUCOMONT et GILLET, 1921: 10; ARROW, 1931: 102; BALTHASAR, 1933: 263; BALTHASAR, 1935: 66; JANSSENS, 1939: 40; PAULIAN, 1945: 71; -subg. *Litocopris* WATERHOUSE, 1891, Ann. Mag. Nat. Hidt. (6) VIII: 53; -subg. *Paracopris* BALTHASAR, 1939, Redia XXV:2; PAULIAN, 1945: 72; -subg. *Microcopris* BALTHASAR, 1958, Acta. Ent. M.N. Prague 32: 474; -Ökologie: FABRE, 1922, souvenirs entom. V. Ed.def.: 109-157; ARROW, 1904, Trans. Ent. Soc. London: 722; KOLBE, 1906, Aus der Natur I: 678; KRAUSSE, 1907,Entom. BI. III: 105; LENGERKEN, 1952, Der Mondhornkafer und seine Verwandten. Neue Brehm-Bucherei, Bd. 58: 1-57; LENGERKEN, 1954, Die Brutfursorge und Brutpflegeinstinkten der Käfer. Leipzig, II. Aufl.:240-347.

Copris (Paracopris) davisoni WATERH.

WATERHOUSE, 1891, Ann. Mag. Nat. Hist. (6), VII: 520; ARROW, 1931: 132.

*Copris (Paracopris) furciceps** FELSCHE

FELSCHE, 1910, D. Ent. Ztschr.: 348; BOUCOMONT et GILLET, 1921: 12; ARROW, 1931: 130; BALTHASAR, 1933: 268; BALTHASAR, 1935: 73; PAULIAN, 1945: 73.

Copris (s.str.) *repertus* WALKER

WALKER, 1858, Ann.Mag.Nat.Hist. (3) II: 208; GILLET, 1911: 290; ARROW, 1931:116; BALTHASAR, 1933: 272; BALTHASAR, 1935: 78; -*claudius* HAROLD, 1877, Ann. Mus. Civ. Genova X:48; (sub *Catharsius*) -? *orientalis* FABRICIUS, 1792, Entom. Syst. I.:52.

Copris (Paracopris) signatus WALK.

WALKER, 1858, Ann. Mag. Nat. Hist. (3), 2: 208; BOUCOMONT et GILLET, 1921: 12; ARROW, 1931: 131; PAULIAN, 1945: 74.

Catharsius HOPE

HOPE, 1837, Col. Man. I: 21; BURMEISTER, 1846, Gen. Ins. X, No. 27; PERINGUEY, 1900 (1901): 109, 323; BOUCOMONT et GILLET, 1921:7; ARROW, 1931: 92; BALTHASAR, 1935:62; PAULIAN, 1945:68.-Subg. *Metacatharsius* PAULIAN (GILLET in litt.), 1939, Rev. Fr.Ent.VI:13.

Catharsius (s.str.) *sagax* (QUENS.)

QUENSTEDT, 1806, Schönh. Syn. Ins. I:43; BOUCOMONT et GILLET, 1921:8; ARROW, 1931:96; BALTHASAR, 1935:65.

Heliocopris HOPE

HOPE, 1837, Coleopt. Manual I: 23; BURMEISTER, 1846, Gen. Ins.Heft 10, Col. Nr.27; REITTER, 1892 (1893): 92; PERINGUEY, 1900 (1901): 109, 310; ARROW, 1931: 84; BALTHASAR, 1935: 58; JANSSENS, 1939; 47; PAULIAN, 1945:66.Ökologie: ARROW, 1904: 722; KOLBE, 1905, Zool. Jahrb. Suppl. VIII: 488; 1906, Aus der Natur I: 681.

Heliocopris bucephalus (FABR.)

FABRICIUS, 1775, Syst. Ent. I: 24 (sub *Copris*); CASTELNAU, 1840: 76; ARROW, 1931: 43; BALTHASAR, 1935: 61; PAULIAN, 1945: 68.-*cristatus* DEGEER, 1778, Mem. Ins. VII: 636 (sub *Copris*), - *tmolus* FISCHER, 1822, Entomogr. Russ. I: Tf. 13, Fg.2 female. Ökologie: GHOSH, 1923 (1924), Rept. Proc. 5th Meet. Pusa: 404.

ONTHOPHAGINI

Onthophagus LATR.

LATREILLE, 1802, Hist.Nat. Crust. Ins.III: 141; MULSANT, 1842: 102; ERICHSON, 1848. III: 762; LACORDAIRE, 1856. Gen. Col. III: 107; MULSANT-REY, 1871: 78; REITTER, 1892 (1893): 47; d'ORIBGNY, 1898: 132; d'ORIBGNY, 1900: 289; PERINGUEY, 1900 (1901): 168; PERINGUEY, 1908: 560;REITTER, 1909: 325; BEDEL, 1911; 25; d'ORIBGNY, 1913: 49;1915: 378 (Suppl.); BOUCOMONT, 1914: 238; BOUCOMONT et GILLET, 1921: 1; BOUCOMONT, 1924a: 669; ARROW 1930: 159; PORTEVIN, 1931:42; PORTA, 1932: 408; BALTHASAR, 1935d: 303 ; SAVCENKO, 1938; 46, 136; PAULIAN, 1941:66; PAULIAN, 1945: 85; ENDRÖDI, 1956:94; TESAŘ, 1957: 127; -*Monapus* ERICHSON, 1848, Naturg. Ins. Deutschl. Col. III: 763; -*Psilax* ERICHSON, 1848, l.c.; -*Matashia* MATSUMURA, 1938, Ins. Matsum. XII: 63; -subg. *Proagoderus* LANSBERGE, 1883, Not. Leyd. Mus. V: 14; d'ORIBGNY, 1913: 493; BOUCOMONT, 1914: 261; MARCUS, 1917,A (1919): 1; MARCUS, 1920, D. Ent. Zeitschr.: 177, 1921, ibid. 163; -*Tauronthophagus* SHIPP, 1895, Entomologist XXVIII: 179; - subg. *Diastellopalpus* LANSBERGE, 1886, Not. Leyd. Mus. VIII: 91; d' ORIBGNY, 1913: 577; MARCUS, 1920, 1921:1.c.; -subg. *Serrophorus* BALTHASAR, 1935, Fol. Zool. Hydrob. VIII: 306; PAULIAN, 1945: 86; -subg. *Micronthophagus* BALTHASAR, 1935, l.c: 306; PAULIAN, 1945: 86; -subg. *Strandius* BALTHASAR, 1935, l.c.:307; PAULIAN, 1945: 86;-*Gonocyphus* LANSBERGE, 1885. Ann. Mus. Civ.Genova. XXII: 382

(ex parte); -subg. *Phanaeomorphus* BALTHASAR, 1935, 1935,1.c.: 307; -*Gonocyphus* LANSBERGE, 1885,1.c. (ex parte); PAULIAN, 1945; 86; -subg. *Gibbonthophagus* BALTHASAR, 1935,1.c.: 308; -subg. *Onthophagiellus* BALTHASAR, 1935, 1.c.:308; PAULIAN 1945: 87; -subg. *Colobothophagus* BALTHASAR, 1935,1.c.: 308; PAULIAN, 1945, 87;-subg. *Parascatonomus* PAULIAN, 1932, Bull. Soc. Ent. Fr.; 205 (als selbst. Gattung); PAULIAN, 1945: 87; -subg. *Euonthophagus* BALTHASAR, 1959, Acta Ent. Mus. Nat. Prague 33: 467; -subg. *Digitonthophagus* BALTHASAR, 1959,1.c.:464; -subg. *Paraphanaeomorphus* BALTHASAR, 1959,1.c.:465; -subg. *Paronthophagus* BALTHASAR, 1959, 1.c.:466; -subg. *Endrödius* BALTHASAR, 1959;1.c; 465; -subg. *Indachorius* BALTHASAR, 1941, Zool. Anz. 133: 161;-*Onthoellus* BALTHASAR, 1959, 1.c.: 466; -subg. *Pseudonthophagus* BALTHASAR, 1959, 1.c: 466; -*Chalcoderus* ERICHSON, 1848, Naturg. Ins. Deutschl. Col. III: 763 nota (ex parte); BOUCOMONT, 1914: 272.

*Onthophagus (*s.str.) *amphinasus* #ARR.
ARROW, 1931, Fauna Brit. India, Lamell. III: 184, 195.

Onthophagus (s.str.) *andrewesi* +ARR.
ARROW, 1931, Fauna Brit. India, Lamell. III: 321, 324.

Onthophagus (Paraphanaeomorphus) bifasciatus (F.)
FABRICIUS, 1781, Spec. ins. I: 25 (*Scarabaeus*); ARROW, 1931; 327, 339;-*birmanicus* HAROLD, 1879, Col. Hefte XVI: 226;ARROW, 1931; 339.

Onthophagus (s.str.) *bronzeus* ARR.
ARROW, 1907, Ann. Mag. Nat. Hist. (7), XIX: 429;ARROW, 1931: 184, 192.

Onthophagus (s.str.) *dama* (F.)
FABRICIUS, 1798, Syst. Suppl.:32 *(Copris)* ;d'ORIBGNY, 1898: 217;ARROW, 1931: 279, 280;-*aeneus* OLIVIER, 1789, Ent. I.3: 131;-*zubači* BALTHASAR, 1932, Stett. Ent. Zeit., 93: 151;ARROW, 1933: 422.

Onthophagus (Digitonthophagus) *diabolicus* HAR.
HAROLD, 1877, Ann. Mus.Civ. Genova: 78; BOUCOMONT, 1914; 266; BOUCOMONT et GILLET, 1921: 40; BALTHASAR, 1935 d; 319; PAULIAN, 1945; 87,91; -*nilgirensis* GILLET, 1922, Ann. Soc. Sci. Brux. LI: 128; ARROW, 1931: 229, 242; BALTHASAR, 1935; 319.

Onthophagus (s.str.) *ensifer* + BOUC.

BOUCOMONT, 1914, Ann. Mus.Civ. Genova. XLVI: 220; ARROW, 1931: 327, 334.

Onthophagus (s.str.) *falsus* * GILL.
GILLET, 1925, Ann. Soc. Sci. Brux. XLIV: 236; ARROW, 1931: 328, 350; -*cervus* d'ORIBGNY (nec FABRICIUS), 1898, l'Abeille, XXIX: 214.

Onthophagus (s.str.) *fasciatus* BOUC.
BOUCOMONT, 1914, Ann. Mus. Civ. Genova, XLVI: 231; ARROW, 1931: 310, 311.

Onthophagus (s.str.) *furcillifer* BAT.
BATES, 1891, Entomologist XIV, Suppl.:11; ARROW, 1931: 270, 273.

Onthophagus (s.str.) *insignicollis** FREY
FREY, 1954, Arb. Mus. Frey, 5:744.

Onthophagus (s.str.) *laevis** HAR.
HAROLD, 1880, Not. Leyden Museum II: 194; HAROLD, 1886, apud RITSEMA, Col. Midden Sumatra;26;BOUCOMONT, 1914: 276; BOUCOMONT et GILLET, 1921; 51;ARROW, 1931; 171; PAULIAN, 1945: 89, 109; -ssp, *lampromelas* FAIRMAIRE, 1891, C.r. Soc. Ent. Belg. XXXV: 193; BOUCOMONT et GILLET, 1921:51; BALTHASAR, 1935d: 336; PAULIAN, 1945: 109; -ssp. *asiaticus* BOUCOMONT, 1919, Bull. Mus. Paris: 604; BOUCOMONT et GILLET, 1921; 51; ARROW, 1931: 172; BALTHASAR, 1935d: 336; PAULIAN, 1945: 110; -ssp. *stevensi* ARROW, 1931, Fauna Brit. India, Lamell. III: 172.

Onthophagus (s.str.) *madoqua* # ARR.
ARROW, 1931, Fauna Brit. India, Lamell. III: 252, 258.

Onthophagus (s.str.) *pacificus* LANSB.
LANSBERGE, 1885, not. Leyden Mus. VII; 17;BOUCOMONT, 1914: 280; BOUCOMONT et GILLET, 1921: 34, 53; ARROW, 1931: 171, 172;-var. *peguanus* BOUCOMONT, 1914, Ann. Mus. Civ. Genova XLVI: 215; BOUCOMONT et GILLET, 1921: 53; ARROW, 1931: 172; BALTHASAR, 1935d; 339; PAULIAN, 1945: 89, 112.

Onthophagus (Serrophorous) rectecornutus LANSB
LANSBERGE, 1883, Not. Leyden Mus. V: 49 (female); ARROW, 1907: 421 (male); BOUCOMONT, 1914: 293; BOUCOMONT, 1914a: 228; BOUCOMONT et GILLET, 1921: 55; ARROW, 1931: 229, 233; BALTHASAR, 1935 d; 342; PAULIAN, 1945: 90, 119; -*luridus*

ROTH, 1851, Arch. Naturg. XVII, I: 128; -*Cryptochirus* LESNE, 1900, apud Ch. Michel, Vers Fachoda: 499; -*Drepanochirus* PERINGUEY, 1900 (1901), Trans. S. Afr. Phil. Soc. XII: 17; BOUCOMONT, 1921b: 199.

Drepanocerus setosus (WIED.)
WIEDEMANN, 1823, Zool. Mag. II, 1: 19 (*Copris*); ARROW, 1931: 381; JANSSENS, 1953: 19, 31; -*setosa* MOTSCHULSKY, 1863, Bull. Soc. Nat. Moscou, XXXVI, II: 459 (*Ixodina*)

Tiniocellus PER.

BOUCOMONT, 1914, Ann. Mus.Civ. Genova. XLVI: 220; ARROW, 1931: 327, 334.

Onthophagus (s.str.) *falsus* * GILL.
GILLET, 1925, Ann. Soc. Sci. Brux. XLIV: 236; ARROW, 1931: 328, 350; -*cervus* d'ORIBGNY (nec FABRICIUS), 1898, l'Abeille, XXIX: 214.

Onthophagus (s.str.) *fasciatus* BOUC.
BOUCOMONT, 1914, Ann. Mus. Civ. Genova, XLVI: 231; ARROW, 1931: 310, 311.

Onthophagus (s.str.) *furcillifer* BAT.
BATES, 1891, Entomologist XIV, Suppl.:11; ARROW, 1931: 270, 273.

Onthophagus (s.str.) *insignicollis** FREY
FREY, 1954, Arb. Mus. Frey, 5:744.

Onthophagus (s.str.) *laevis** HAR.
HAROLD, 1880, Not. Leyden Museum II: 194; HAROLD, 1886, apud RITSEMA, Col. Midden Sumatra;26;BOUCOMONT, 1914: 276; BOUCOMONT et GILLET, 1921; 51;ARROW, 1931; 171; PAULIAN, 1945: 89, 109; -ssp, *lampromelas* FAIRMAIRE, 1891, C.r. Soc. Ent. Belg. XXXV: 193; BOUCOMONT et GILLET, 1921:51; BALTHASAR, 1935d: 336; PAULIAN, 1945: 109; -ssp. *asiaticus* BOUCOMONT, 1919, Bull. Mus. Paris: 604; BOUCOMONT et GILLET, 1921; 51; ARROW, 1931: 172; BALTHASAR, 1935d: 336; PAULIAN, 1945: 110; -ssp. s*tevensi* ARROW, 1931, Fauna Brit. India, Lamell. III: 172.

Onthophagus (s.str.) *madoqua* # ARR.
ARROW, 1931, Fauna Brit. India, Lamell. III: 252, 258.

Onthophagus (s.str.) *pacificus* LANSB.
LANSBERGE, 1885, not. Leyden Mus. VII; 17;BOUCOMONT, 1914: 280; BOUCOMONT et GILLET, 1921: 34, 53; ARROW, 1931: 171, 172;-var. *peguanus* BOUCOMONT, 1914, Ann. Mus. Civ. Genova XLVI: 215; BOUCOMONT et GILLET, 1921: 53; ARROW, 1931: 172; BALTHASAR, 1935d; 339; PAULIAN, 1945: 89, 112.

Onthophagus (Serrophorous) rectecornutus LANSB
LANSBERGE, 1883, Not. Leyden Mus. V: 49 (female); ARROW, 1907: 421 (male); BOUCOMONT, 1914: 293; BOUCOMONT, 1914a: 228; BOUCOMONT et GILLET, 1921: 55; ARROW, 1931: 229, 233; BALTHASAR, 1935 d; 342; PAULIAN, 1945: 90, 119; -*luridus*

PAULIAN, 1933, Bull. Soc. Zool. France LVII: 98; PAULIAN, 1945: 119.

Onthophagus (Proagoderus) vividus $^+$ARR.
ARROW, 1907, Ann.Mag. Nat. Hist. 7, XIX: 428; BOUCOMONT, 1914: 264; ARROW, 1931: 230, 245.

Caccobius THOMSON
THOMSON, 1863, Skand. Col.V: 34; HAROLD, 18667, Col. Hefte 1:5; HAROLD, 1867, l.c.II:1; MULSANT, 1871: 75; JEKEL, 1872, Rev. Mag. Zool.:405; WATERHOUSE, 1875, Trans. Ent. Soc. London: 73; REITTER, 1892 (1893): 39, 91;d'ORBIGNY, 1898; 127; PERINGUEY, 1900 (1901): 275; PERINGUEY, 1908:565;d'ORBIGNY, 1913: 17; BOUCOMONT et GILLET, 1921:27; ARROW, 1931:141;PORTEVIN, 1931:39; PORTA, 1932:412; MATSUMURA, 1936:61; PAULIAN, 1945:81; BALTHASAR, 1949:1; -*Onthophagus* (ex parte), div.auctores; -subg. *Caccophilus* JEKEL, 1872, l.c.:410; d'ORBIGNY, 1898: 130; d'ORBIGNY, 1913:21; BALTHASAR, 1935e:183; BALTHASAR, 1949:7; -subg. *Caccocnemus* JEKEL, 1872,1:c.:418; -subg. *Tomogonus* d'ORIBGNY, 1904, Ann.Mus. Civ. Gen. XLI: 284.

Caccobius (Caccophilus) meridionalis BOUC.
BOUCOMONT, 1914, Ann. Mus. Civ. Genova VI (XLVI): 239; ARROW, 1931: 142, 148; BALTHASAR, 1949: 8, 36.

ONITICELLINI

Liatongus REITT.
REITTER, 1892 (1893), Bestimmungstab.d. Lucaniden u. copr. Lamell.: 38, 45; d'ORIBGNY, 1898:222; BOUCOMONT, 1923; 53; ARROW, 1931: 79, 362; BALTHASAR, 1935: 26, 103; JANSSENS, 1953: 10, 62;- *Oniticellus* div.auct.;-subg. *Paraliatongus* BALTHASAR n.;- *Pseudoniticellus* PAULIAN (nec KRAATZ), 1945, Col. Scarab. Indochine: 136.

Liatongus (s.str.) *indicus* $^\$$ (ARROW)
ARROW, 1908, Ann. Mag.Nat. Hist. (8), 1: 180 (*Oniticellus*); ARROW, 1931: 363, 368; JANSSENS, 1953; 75, 95.

Drepanocerus Kirby
KIRBY, 1828, Zool. Journ. III: 521; CASTELNAU, 1840: 92; LACORDAIRE, 1856, Gen. Col. II: 105,III; PERINGUEY, 1900 (1901): 108, 110; BOUCOMONT et GILLET 1921: 19; BOUCOMONT, 1921b: 200; ARROW, 1931:380; BALTHASAR, 1935: 97; PAULIAN, 1945: 50, 137; JANSSENS, 1953: 9. 12; -*Ixodina*

ROTH, 1851, Arch. Naturg. XVII, I: 128: -*Cryptochirus* LESNE, 1900, apud Ch. Michel, Vers Fachoda: 499; -*Drepanochirus* PERINGUEY, 1900 (1901), Trans. S. Afr. Phil. Soc. XII: 17; BOUCOMONT, 1921b: 199.

Drepanocerus setosus (WIED.)

WIEDEMANN, 1823, Zool. Mag. II, 1: 19 (*Copris*); ARROW, 1931: 381; JANSSENS, 1953: 19, 31; -*setosa* MOTSCHULSKY, 1863, Bull. Soc. Nat. Moscou, XXXVI, II: 459 (*Ixodina*)

Tiniocellus PER.

PERINGUEY, 1900 (1901), Trans S. Afr. Phil. Soc. XII: 116; PERINGUEY, 1908, l.c.XIII: 693; ARROW, 1908: 183; d'ORIBGNY, 1916, Voy. G. Babault Afr. Or. Angl., 1912-13:29; BOUCOMONT, 1923: 53;-*Oniticellus* div. auct.

Tiniocellus spinipes (ROTH)

ROTH, 1851, Arch.f. Naturg. XVII, 1: 128 (*Oniticellus*); BOUCOMONT, 1921: 211; ARROW, 1931: 378 (= *modestus* ARR.); BALTHASAR, 1935: 102; JANSSENS, 1939, Parc Nat. Alb., mission Witte, fasc. 25; 12, 16; MÜLLER G, 1940, Miss. Biol. Borana, Zool.II: 97 (bei allen Autoren sub *Oniticellus*); sub *Tiniocellus*: PERINGUEY, 1900 (1901); 116; d'ORIBGNY, 1916, Voy. G. Babult Afr. Or. Angl.: 29; JANSSENS, 1953: 58, 60;-*variegatus* FÅHRAEUS, 1857, apud BOHEMAN, Ins. Caffr. II: 320;-*humilis* GERSTAECKER, 1871, Arch. Naturg. XXXVI, 1:52;-*imbellis* BATES. 1891, Entomologist XXVI, Suppl.: 13; -*setifer* KRAATZ, 1895, D.Ent. Zeitschr.: 143.

ONITINI

Onitis FABR.

FABRICIUS, 1798, Suppl. Ent. Syst.:2; FABRICIUS, 1801, Syst. Eleuth. I:26; CASTELNAU, 1840: 88; LACORDAIRE, 1856, Gen. Coleopt.III: 103; LANSBERGE, 1875: 14, 49; BEDEL, 1892, Abeille XXVII: 251; REITTER, 1892(1893): 96; PERINGUEY, 1900 (1901): 108, 118; ARROW, 1931: 386; BALTHASAR, 1935: 87;JANSSENS, 1937:15; PAULIAN, 1945: 140.

Onitis falcatus (WULFEN)

WULFEN, 1786, Descrip. Cap. Ins.: 14, Tf.2, Fg. 17 m# (*sub Scarabaeus*); LANSBERGE, 1875: 126; BOUCOMONT et GILLET, 1921: 17, 19; ARROW, 1931: 392; BALTHASAR, 1935: 93; JANSSENS, 1937: 44; PAULIAN, 1945: 142; *Onitis hymalajicus* REDTENBACHER, 1848, apud Hügel, Kashmir, IV, 2: 518;*Onitis sphinx* HERBST (nec FABRICIUS), 1789, Käfer II: 186.

Onitis subopacus ARROW

ARROW, 1931, Fauna Brit. India. Copr.:395: BALTHASAR, 1935: 94; JANSSENS, 1937: 51; *Onitis philemon* LANSBERGE (nec FABRICIUS), 1875, Ann. Soc. Ent. Belg.XVIII: 133; BOUCOMONT, 1914: 336; BOUCOMONT et GILLET, 1921: 19.

Onitis virens LANSB.

LANSBERGE, 1975, Ann. Soc. Ent. Belg. XVIII: 135; BOUCOMONT et GILLET, 1921: 19; ARROW, 1931: 396; BALTHASAR, 1935: 52; PAULIAN, 1945: 144;*Onitis amplectens* LANSBERGE, l.c.: 136.

DISCUSSION

First report of *Copris furciceps*, *O. insignicollis*, *O. falsus* and *O. laevis* from South India and the presence of 6 endemic species of South India highlight the chance of revealing several endemic species from Wayanad regional forests, which is a localized center of many endemic species in the Western Ghats (Nair 1991; Pascal 1991).

The present checklist of species of dung beetle fauna cannot be considered as a final picture and it seems that many species still remain to be described for which more surveys are needed. Whatever be the explanation for these observations, the new reports of species in an area where they were previously not recorded highlight the necessity for long-term studies in forest interiors. Vegetation type analysis of dung beetles as done here would be helpful in analyzing the influence of physical structure of forest in determining the composition and distribution of dung beetle assemblages.

51A

Dung baited pitfall trap

PLATE.7

Endemic dung beetles collected from the evergreen forest at Wayanad
(a) *O.amphinasus* (b) *O. madoqua* (c) *L. indicus* (d) *O. ensifer*
(e) *O. vividus* (f) *O. andrewesi*

3.1 PICTORIAL KEY

The purpose of this work is to provide practical pictorial guide to the identification of dung beetles collected from wet evergreen forest of Western Ghats. Photographs were taken using Nikon D50 digital camera. The images were finalized in JPEG format using Photoshop 7.0 (Adobe Co., Sanjose, CA). The pictorial key to the species is purposely designed for use by non-specialists in dung beetle taxonomy. Morphological characters were selected from Arrow (1931) and Balthasar (1965 a & b) for easy recognition as possible and for accurate diagnosis. Again many discriminating features of dung beetles *viz.,* distribution of punctures/granules, nature of elytra -shinning/opaque and pronotal declivity can be clearly distinguished using pictorial key.

KEY TO THE GENERA OF SUBFAMILY SCARABAEINAE IN AN EVERGREEN FOREST AT WAYANAD

1(16) Pronotum without 2 basal impressions near the middle

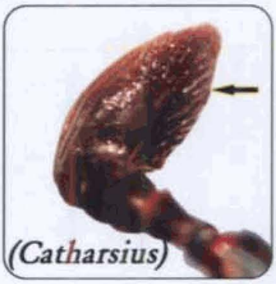
2 (11) Scutellum wanting

3 (6) Elytra with 2 lateral carina

4 (5) First joint of antennal club shinning

(Heliocopris)

5 (4) Antennal club entirely pubescent



(Catharsius)

52 B

6 (3) Elytra with one lateral carina

7 (8) Prontoum with a strong basal groove

(Copris)

8 (7) Pronotum without a strong basal groove

9 (10) Terminal margin of the front tibia at right angles to the inner margin and anterior angles of the prothorax hollowed beneath

(Caccobius)

10 (9) These characters not both, and usually neither present

(Onthophagus)

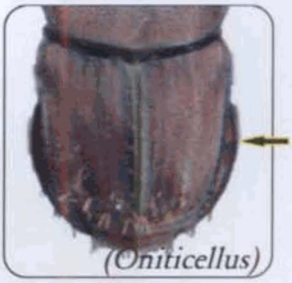
11 (2) Scutellum present

12 (13) Elytra not fringed before the hind margin

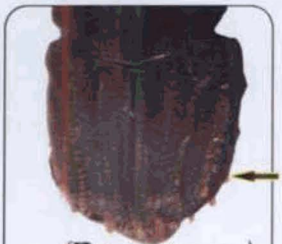

(Liatongus)

13 (12) Elytra fringed before the hind margin

14 (15) Sides of abdomen exposed above


(Oniticellus)

15 (14) Sides of abdomen not exposed above


(Drepanocerus)

16 (1) Pronotum with 2 basal impressions near the middle


(Onitis)

52 D

KEY TO THE SPECIES OF SUBFAMILY SCARABAEINAE IN AN EVERGREEN FOREST AT WAYANAD

Heliocopris

single species recorded

(bucephalus)

Catharsius

single species recorded

(sagax)

Copris

1 (2) Pronotum with sharply defined anterior declivity

(repertus)

2 (1) Pronotum without sharply defined anterior declivity

3 (4) Metasternal sheath not smooth behind

(furciceps)

52 E

3)

4 (3) Metasternal shield smoother behind

5 (6) Metasternal shield unpunctured

(signatus)

6 (5) Metatsernal shield unpunctured infront

(davisoni)

Caccobius

single species recorded

(meridionalis)

Onthophagus

1 (4) Hind tibia extremely short, triangular, as broad at the end as metatarsus is long

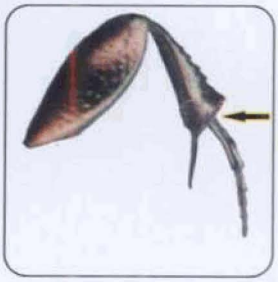
2 (3) Pronotum grooved, vertex bearing a median tubercle

(laevis)

3 (2) Pronotum not grooved, vertex without a median tubercle

(pacificus)

4 (1) Hind tibia not extremely short, not as broad at the end as metatarsus is long



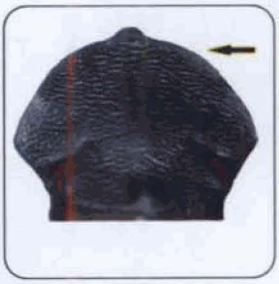
5 (16) Pronotum wholly or partly granular or rugose

6 (9) Pronotum with closely packed granules or rugose without distinct punctures

7 (8) Head gently rounded at the sides

(bronzeus)

8 (7) Head very strongly rounded or angular at the sides

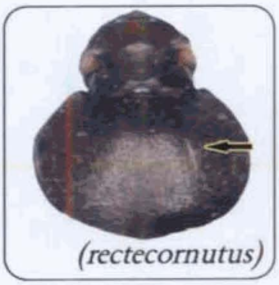


9 (6) Pronotum partly or rugose with some punctures
(or smooth areas)

(amphinasus)

10 (15) Elytra more or less opaque

11 (12) Pronotum not shinning



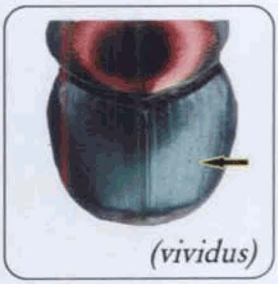
(rectecornutus)

12 (11) Pronotum shinning

13 (14) Elytra unpunctured

(diabolicus)

14 (13) Elytra punctured



(vividus)

15 (10) Elytra very shinning

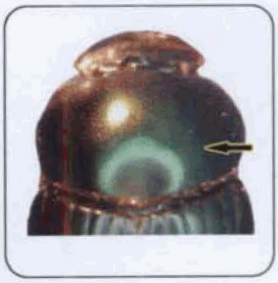
(madoqua)

16 (5) Pronotum punctured, without granules, asperities or rugosity

17 (18) Punctures of pronotum large, close, umbilicate

(furcillifer)

18 (19) Punctures of pronotum not large, close, umbilicate



19 (20) Upper surface, without hair, smooth, or with only very minute, scanty and inconspicous setae

(dama)

20 (19) Upper surface distincly hairy or setose

21 (22) Pronotum pale at the sides

(fasciatus)

22 (21) Pronotum uniformly coloured

23 (30) Pygidium with a basal ridge

24 (29) Pronotum evenly and uniformly punctured

25 (26) Uniformly dark above


(ensifer)

26 (25) Not uniformly dark above

52k

27 (28) Pronotum with longitudinal groove

(bifasciatus)

28 (27) Pronotum without longitudinal groove

(insignicollis)

29 (24) Pronotum unevenly and unequally punctured

(falsus)

30 (23) Pygidium without a basal ridge

(andrewesi)

Liatongus

single species recorded

(indicus)

Oniticellus

single species recorded


(spinipes)

Drepanocerus

single species recorded


(setosus)

Onitis

1 (2) Narrow; pronotum very feebly punctured


(falcatus)

2 (1) Broader; pronotum well punctured

3 (4) Clypeofrontal carina broadly interrupted


(subopacus)

4 (3) Clypeofrontal carina narrowly interrupted


(virens)

52M

4.

Seasonal variation in the chemical quality of litter

INTRODUCTION

Litter fall is the most important way of energy and organic matter transfer from the forest canopy to decomposer organisms of the soil surface (Hirabuki 1991). Major factors that affect litter decomposition are on one hand temperature, humidity and aeration, which affect litter biota activity (Martín et al. 1994) and on the other hand, litter composition and quality (Heneghan et al. 1999; Gonza´lez & Seastedt 2001). High quality litter encourages rapid initial breakdown of litter, resulting in faster decomposition and nutrient cycling, enhancing the site quality, whilst for low- quality litter, the effects of invertebrates increases with time (Scha¨dler & Brandl 2005; Vitousek 1982). Therefore, litter quality analysis based on various ratios of C, N, lignin and polyphenols is a significant step in assessing the nutrient cycling of vast forest ecosystems (Vanlauwe et al. 1997; Seneviratne 2000). Litter with high resource quality tends to be higher in nitrogen content, lower in lignin content, have greater moisture content and low C: N ratio (Berg 2000). Knowledge of C: N ratio of the litter is important as detritus with low C: N ratios lead to a greater amount of decomposition (Schlesinger 1997) and litter with low lignin: N ratios decompose most quickly (Chapin et al. 2002). Nutrient content of litter is also determined by mineral content of litter as higher levels of Ca, Mg, and K make litter more palatable, favouring microorganism's activity and litter decomposition. As the concept of 'substrate quality' varies among litter species (Berg 2000), assessing the initial litter quality of different types of forests helps to draw a conclusion about the variation in decomposition rates of the forest types.

A variety of mechanisms have been proposed to explain the seasonal variation in leaf litter nutrient concentrations in evergreen forests. One such potential mechanism is the rainfall mediated leaching of nutrients from live and senescent leaves (Aerts & Chapin 2000; Chuyong et al. 2000) and decomposing litter in forests (Aerts & Chapin 2000; Schuur & Matson 2001). Contrasting to this low nutrient and high rainfall hypothesis, strong winds during high precipitation would lead to increased nutrient rich green litter fall in tropical rainforests (Cuevas & Lugo 1998). Since, strong winds and increased green leaf fall during southwest monsoon period are common in the windward region of Western Ghats forests (personal observations), these events may be resulting in higher concentrations during the period. Another probable mechanism contributing to low litter nutrient levels during rainy periods is the lower photosynthetic rates resulting from the persistent cloud cover and reduced insolation reaching the canopy during rainy seasons in wet tropical forests (Graham et al. 2003; Santiago et al. 2004). Contrastingly leaf litter nutrient concentrations could be lower during early summer periods when the trees are flushing new leaves (Boinski & Fowler 1989), due to the source sink interactions taking place during flushing of new leaves and fruit production. Therefore, translocation of mobile nutrients from old tissue (source) to new (sink) occurs during this period (Nambiar & Fife 1991; Newbery et al. 1997). Another probability is the premature senescence of leaves due to water stress during non-rainy periods in tropical wet forests (Wright & Cornejo 1990; del Arco et al. 1991; Wieder & Wright 1995).

In the current study, the variation in leaf litter nutrient levels of freshly fallen, fermentation and humus litter present in a wet evergreen forest during the four seasons is analysed. It is expected that the results will invite more attention towards the assessment of seasonality of leaf litter nutrient variation in the windward region of Western Ghats.

METHODOLOGY

Data collection

Litter layer on the forest floor was sampled in randomly located plots of 20m x 80m, three times during a season covering all four seasons, southwest monsoon (Jun-Sep), northeast monsoon (Oct-Nov), pre- summer (Dec-Feb) and summer season (Mar-May) in 2002-03. Two samples of fresh fallen litter (L layer) were collected using a 50 X 50 cm net tied over the forest floor thrice in every season. Two composite samples (made of two sub samples) of litter sorted into fermentation (F) and humus (H) layers were also collected thrice a season from the forest floor. At each time the collected litter was dried at 30°C in the laboratory to constant weight. All dried litter sub-samples were ground and passed through a 1 mm mesh screen before chemical analysis. Thereafter required amount of sub-samples of litters were taken for nutrient analysis. Average of six samples of L layer contributed to the value of a chemical variable during a particular season.

Total phenols were quantified by Folin Ciocalteu method (Anderson & Ingram 1993) and Carbon determined by Walkley and Black method (Walkley & Black 1934). Nitrogen levels were determined by micro-Kjeldahl digestion (Jackson 1958) followed by distillation and titration. Na, Ca and K levels were determined by acid digestion of samples and flame photometry (Barrows & Simpson 1962). Lignin concentration in the litter was measured using acetyl-bromide extraction procedure (Iiyama & Wallis 1990), because of its greater sensitivity, the totality of an analysis achieved on the whole sample and reproducibility (Monties 1989). Values of ratios of lignin to N, carbon to N were derived from the above measurements. All chemical analyses were carried out in triplicates on the same sub sample. Mean values of the triplicates were taken as the value of the sub sample.

Data analysis

Data derived from chemical analyses were not normally distributed. Consequently, non-parametric statistics (Mann –Whitney U tests) after multivariate comparison through Kruskal –Wallis H tests (Sachs 1992), were used for pair wise comparison of data sets. Significance levels of the seasonal variations in chemical variables of each litter layer during each season and between the seasons were analysed with Kruskal Wallis H tests. All data analysis was performed using GRETL open source software version 1.1. Cottrell (2006).

RESULTS

Seasonal Variations in the biochemical parameters in fresh litter layer

Distinct seasonal variation in the levels of most litter chemical variables was evident with a peak in rainy season and low values in dry periods (Table.4.1& Figure.4.1). High levels of total phenols were noticed during pre-summer season. Phenolic concentration declined significantly during summer season but with the beginning of southwest monsoon a significant increase was noted. N levels peaked during northeast monsoon thereafter a significant fall was noted in pre-summer, which continued till summer season. Carbon, lignin, L:N and C:N values were high during summer season. Lignin and L:N values showed a steep rise during summer from the low levels in pre-summer season. C: N values were <25 during all seasons except in summer while the lowest C:N values were observed during northeast monsoon season. High amount of cations were recorded during monsoon seasons. Sodium levels were high in southwest monsoon and significantly low during summer season. Calcium and potassium levels peaked during northeast monsoon and recorded lowest in the driest pre-summer season (Figure.4.1).

Variations in the biochemical parameters in different layers of litter during different seasons

Levels of all litter chemical variables except lignin decreased during pre-summer season from L to H layer (Table.4.1). Lignin values in F and H layer were high during pre-summer season leading to rise in L:N ratios whereas a fall in lignin values was recorded during monsoon and summer periods. Nitrogen values decreased from L to H layers during all the seasons leading to high C:N ratios in H layer especially during northeast monsoon and summer seasons. Ca, Na and K levels declined steeply from L to H layers during all seasons except summer.

Statistical analysis

All litter chemical parameters in freshly fallen litter varied significantly between the seasons ($P<0.05$) (Table.4.2). Except lignin:N ($P>0.05$, H= 3.56), other biochemical parameters varied significantly between the seasons in F layer ($P<0.05$) and except calcium in H layer ($P>0.05$, H= 2.47). Excluding potassium and L: N values, all other variables varied significantly from L to H layers during all seasons (Table.4.3 & 4.4). C: N values increased significantly from L to H layer ($P<0.05$) except during pre-summer season ($P>0.05$). Potassium levels showed no significant layer wise variation during pre-summer period ($P>0.05$). Significant variation was absent for lignin:N values from L to H layers during summer and southwest monsoon season ($P>0.05$) (Table.4.3).

DISCUSSION

Nutrient quality of fresh litter varies seasonally in the aseasonal evergreen forests of the region all along the year, leading to the formation of litter of varying chemical quality during different seasons. It may have an effect on the decomposition rates of litter shed during different seasons and on the faunal community dynamics as litter chemistry and the activities of invertebrate decomposers are linked because chemistry is considered to be one of the major determinants of invertebrate colonization and comminution of litter (Anderson 1973; Maity & Joy 1999; Zimmer & Topp 2000). As per the litter quality indices *viz.*, C: N and cation levels, litter of high resource quality is shed during the monsoon seasons (northeast and southwest) and low quality during summer and presummer season. Elevated quality levels are suggested to be related either to the pulse of increased soil nutrient availability at the beginning of rainy seasons in evergreen forests (Swamy & Proctor 1994; Wieder & Wright 1995; Lodge et al. 1991; Mc Grath et al. 2000) or to the wind mediated green fall deposition by branch breaking and the thrashing action of branches on leaves (Fonte & Schowalter 2004) during the monsoon seasons which is common in the region. It implies that leaf litter added to the evergreen forest floor during the wet warm rainy season are richer in nutrients and are more palatable to detritivores than that produced during the drier months. Significant seasonal variation in chemical quality is also evident in the fermentation and humus litter layers in accordance with the variation in fresh litter.

Though, significant seasonal differences in litter quality was evident, on the basis of the threshold value of 25 (for mineralisation) for C: N (Regina et al. 2004; Myers et al. 1995), it can be stated that the litter of the study habitat was not N limited except during summer season signifying that litter of high quality was available for decomposition. Plant litter is considered as high quality when C: N < 25 and of low quality when C: N> 25 (Regina et al. 2004) and lower the C: N in fresh litter, the more organic matter is left for decomposition (Berg 2000). CN ratio by itself merely describes the proportion of C to N, without revealing how these elements are distributed among the important chemical classes of the plant cell (Cromack & Monk 1975).

Regardless of this simplification, the CN ratio has been shown to be a valuable predictive tool in numerous studies of litter decomposition at local, regional, and global scales (Flanagan & Van Cleve 1983; Fog 1988; Taylor et al. 1989; Aerts 1996).

Significantly high values of C: N and L: N during summer are resulting primarily by low nitrogen concentration as C levels did not vary much during the period. It may be related with the suggested source–sink interactions related to peak fruit production and leaf flushing in tropical rainforests (Sundarapandian et al. 2005; Pragasan & Parthasarathy 2005; Murali & Sukumar 1993; Wood et al. 2005) and also to the initiation of flowering and fruit production in the region (personal observations). As per source-sink interactions, when new plant tissue (fruits) is produced, greater translocation of mobile nutrients from old tissue (senescent leaf/source) to new (sink) occurs (Nambiar & Fife 1991; Newbery et al. 1997). Therefore, lower leaf litter nutrient concentrations in summer and presummer periods could be related to the fruit production in the region (Sundarapandian et al. 2005). Sharp decline in C: N values during southwest monsoon are attributed to rise in N levels. Green leaves have significantly higher nitrogen concentrations and lower lignin to nitrogen ratios compared to senescent leaves (Fonte & Schowalter 2004). Prior to the fall of senescent mature leaves, plants reallocate mobile nutrients especially N (Aerts & Chapin 2000), but when leaves are lost by unexpected hazards like wind mediated fall, where the plant does not have the opportunity to withdraw nutrients, foliar nutrient withdrawal is more-or-less zero and leading to a seasonal rise in litter nutrient pool (Wright & Cannon 2001) as observed in the region during southwest monsoon. CN ratios rose rapidly from L to H layers owing to the rapid loss of N from litter. Decrease in N concentrations from L-F-H layers without net accumulation suggest that either N immobilization is not taking place at significant detectable levels or this stage might be missed out which is distinct in litter bag studies, where a more steady step by step nutrient release is observable. Absence of a rise in N levels in F and H layers indicate that N may not have been a limiting factor for microorganisms during various seasons (Melillo et al. 1982; Lavelle et al. 1993) as fresh litter with high N levels was available round the year in the studied evergreen forest. Soil and humus CN ratios 22-24 are suggested as a critical threshold for the onset of nitrification and nitrate leaching (Ollinger et al. 2002). Hence, lower CN ratios (< 22) in H layer during pre-summer indicate higher net production of nitrates and higher CN values (>41) during summer indicate lower nitrification rates.

Explanations for increase in phenol levels during southwest monsoon might be due to the addition of green leaf fall already explained above. Pre-summer rise in phenol levels could be related to the rise in herbivore and pathogen pressure in humid forests succeeding the long wet monsoon periods (Wolda 1988). Seasonality in abiotic factors and food quality are suggested to be responsible for the abundance of larval herbivores in habitats dominated by evergreen plants, such as tropical rainforests (Lawrence et al. 1997; Wolda 1978 & 1988). Rise in phenol levels possibly with other secondary metabolites after monsoon periods might be a structural defence mechanism linked to the earlier experiences from herbivory to defend against the herbivores active after rainy season. Sudden changes in photosynthetic productivity of canopy trees linked to the solar insolation availability after cloud covered monsoon periods (Westoby et al. 2002) lead to variation in foliar nutrient levels (Graham et al. 2003; Wright & Westoby 2002). However, how far the differences in the seasonal average daily light availability during rainy seasons contributed to the observed patterns of litter nutrient variability and abundance of herbivore in the study region is to be studied.

Higher lignin: nitrogen ratios during summer and southwest monsoon seasons were observed in the evergreen habitat. High leaf lignin concentrations reflect relatively low nutritional content because lignin is indigestible to most insects and is negatively correlated with herbivory (Coley 1983) thus an interfering factor in the decomposition of cellulose and other primary metabolites (Gallardo & Merino 1992). High lignin levels during summer and southwest monsoon might also be a structural defense mechanism against herbivory during leaf expansion period facilitated by the low water stress in the region. High availability of rainfall and low water stress increase allocation to carbon rich compounds such as lignin (Austin & Vitousek 2000) and possibly other phenolic and primary metabolites in mature leaves. But such antiherbivore defenses mediated by lignin levels may continue to function against decomposers during decomposition (Grime et al. 1996). Hence, it is reasonable to expect that litter with high initial lignin shed during summer and southwest monsoon would remain in the humus pool of the region as accumulated recalcitrant materials for prolonged period (Berg & McClaugherty 1987) than litter of other seasons.

Seasonal variation in L:N and C:N values of fresh litter indicate that litter of variable quality are produced during different seasons and hence the limit value (the stage at which litter becomes the humus pool without further decomposition, Berg 2000) of the litter produced during each season might be varying unless the other two major factors, climate and fauna (Swift et al. 1979; Berg et al. 1995) very strongly influence litter decomposition. High L:N in H layer during presummer and summer and high C: N in summer means high immobilization of N during presummer and summer seasons indicating probably less N loss by leaching and denitrification from the H litter layer in the succeeding rainy seasons. These observations highlight the need to conduct litter decomposition studies in the moist evergreen forests in Western Ghats, employing litter shed during different seasons as against the general practice of employing single season litter in litter decomposition and faunal succession studies as it would potentially miss the influence of seasonal variations of litter quality on these processes.

High levels of all major cations *viz.*, Ca, Na and K during rainy periods in the newly added litter as if, leaching loss is not an important source of variation in the dynamics of major cations. However, physical leaching is a major driver of short-term variation in leaf litter cation concentrations and physical leaching as a process dominating the dynamics of K in many ecosystems is well known (Wood et al 2005; Dziadowiec 1987; Rapp & Leonardi 1988). Results of this study suggest that cation leaching is taking place during rainy days, but the higher cation values in samples during monsoon period are related to the wind mediated green leaf deposition and probably high nutrient reabsorption from soil during rainy seasons. Higher level of K which is highly soluble and not bound to any known organic compounds during southwest-northeast periods in the study region (Epstein 1972; Veneklaas 1991; Schlesinger 1997) substantiates the observations. Low Ca, K and Na levels during presummer and summer indicate nutrient sink absorption correlated to the fruiting-flushing events as well as retrieval by plants prior to leaf fall. However, what leads to high levels of Ca during summer season is not understood. Rapid loss of Ca-Na-K levels from L to F layers and a subsequent slow release from F to H except in summer season suggests utilization by decomposers along with rainfall mediated leaching loss.

Present study highlights the seasonal variation in the substrate quality of litter shed during different seasons in the evergreen forests of the region. This seasonal variation in litter quality must be leading to variation in the decomposition rates of litter present during different seasons, feeding activities and distribution pattern of detritivore community and nutrient availability in the forest floor. High levels of litter nutrients during rainy days indicate increased nutrient reabsorption from soil and it necessititates further research on seasonal changes in forest floor soil nutrient availability in the evergreen forests of moist Western Ghats, which will broaden our understanding of how seasonal variation in soil nutrient availability affects canopy leaf traits as well. Patterns observed in the present study from the transitional Wayanad forests may vary from the patterns in other evergreen forests as forests in Western Ghats differs from each other due to the local variations in climate and vegetations in different regions of Western Ghats would be leading to regional variations in litter shedding patterns.

Table.4.1 Seasonal variations in the biochemical profile of LFH litter layers during southwest monsoon, northeast monsoon, pre-summer and summer season in the wet evergreen forest

Biochemical parameters (mg/gm)	Southwest monsoon			Northeast monsoon			Pre-summer			Summer		
	L	F	H	L	F	H	L	F	H	L	F	H
Carbon	240 ± 48.64	210±17.2	147±27.1	298±18.5	245±14.7	218±16.8	295±20.54	280.5±8.19	121.5±13.8	300±29.8	255±22.7	210±44.75
Nitrogen	12.8 ± 0.80	10.6±1.74	6.7±0.73	16.8±2.27	7±1.06	6.4±1.97	12.33±0.58	10.08±1.2	7.28±0.84	11.2±0.71	7.28±0.81	5.04±0.08
Lignin	78±3.43	71.5±21.1	48.9±4.27	61.5±4.59	50±3.14	48±1.16	48±4.99	94.5±36.95	119±26.99	100.6±8.5	49±11.72	46±11.60
Lignin:N	5.8±0.37	6.66±2.85	6.73±1.84	4.93±0.76	7.36±0.79	8±2.22	3.88±0.41	9.35±3.19	16.34±1.87	8.15±0.98	5.59±2.33	8.72±4.08
C:N	18.75±4.72	19.81±3.6	21.94±4.9	17.74±2.3	35±4.49	34.06±9.6	23.93±1.54	27.83±4.49	16.69±2.24	26.79±2.7	35.03±4.7	41.67±6.91
Calcium	9.6±0.9	4.78±1.18	1.67±0.09	13.03±1.0	8.2±0.92	3.01±2.33	7.82±1.05	5.94±1.65	1.71±0.45	11.2±3.40	8.9±0.08	2.71±1.69
Sodium	0.39±0.06	0.27±0.06	0.22±0.02	0.34±0.09	0.21±0.06	0.18±0.11	0.27±0.08	0.15±0.04	0.02±0.004	0.21±0.08	0.12±0.04	0.08±0.008
Potassium	2.2±0.43	1.43±0.18	1.31±0.11	2.9±0.26	1.62±0.18	1.23±0.59	0.32±0.277	0.2±0.09	0.13±0.03	1.38±0.54	1.2±0.12	0.08±0.019
Total Phenols	7.01±0.91	3.2±1.44	0.8±0.21	4.87±0.53	2.6±0.01	0.49±0.16	8.41±0.50	3.2±1.13	0.49±0.20	4.3±0.82	1.2±0.53	0.9±0.31

Table.4.2. Results of Kruskal Wallis and Mann Whitney tests on the seasonal variation of biochemical parameters in (a) L (b) F and (c) H litter layers in the wet evergreen forest (s.w-southwest monsoon, n.e -northeast monsoon, p.s -pre-summer and s -summer)

Biochemical parameters	(a) *P*	H	Differences found (Mann whitney at 5%)	(b) *P*	H	Differences found (Mann Whitney at 5%)	(c) *P*	H	Differences found (Mann Whitney at 5%)
Carbon	<0.05	8.65	s.w<p.s ;s>s.w<n.e	<0.05	15.79	n.e>s.w<p.s>n.e;s.w<s	<0.05	17.37	n.e>s.w<s>p.s<n.e;s.w<p.s
Nitrogen	<0.05	14.15	p.s<n.e>s.w>s:n.e>s	<0.05	15.89	p.s>n.e<s.w>s<p.s	<0.05	11.65	s.w>p.s>s
C: N	<0.05	15.61	n.e<p.s>s.w>s>n.e	<0.05	16.35	p.s<n.e>s.w<p.s<s	<0.05	17.35	n.e>s.w<s>p.s<n.e;s.w>p.s
Lignin	<0.05	21.63	p.s<s.w<s>p.s<n.e<s	<0.05	11.58	n.e<p.s>s	<0.05	13.66	s<p.s>n.e;p.s>s.w
Lignin:N	<0.05	19.73	s.w>p.s<s>s.w>n.e:p.s<n.e	>0.05	3.56	n.e=s.w=p.s=s	<0.05	13.22	s<p.s>n.e;p.s>s.w
Sodium	<0.05	14.00	p.s<s.w. s.w>s<n.e	<0.05	13.33	s<n.e>p.s>s<s.w>p.s	<0.05	17.13	n.e>p.s<s.w>s>p.s
Calcium	<0.05	15.86	s.w<n.e>p.s<s	<0.05	17.68	n.e>p.s<s>s.w>n.e	>0.05	2.47	n.e=s.w=s=p.s
Potassium	<0.05	19.78	n.e>p.s<s.w>	<0.05	18.38	n.e<p.s<s.w<n.e;s.w>s>p.s	<0.05	19.2	s<s.w>p.s;s<n.e>p.s>s
Total phenols	<0.05	19.50	n.e<p.s>s.w:p.s>s<s.w>n.e	<0.05	10.33	p.s>s<s.w;n.e>s	<0.05	12.01	n.e<s.w>p.s<s>n.e

Table.4.3. Values of significance from Kruskal Wallis and Mann Whitney test on the seasonal variation of biochemical parameters in LFH litter layers in the wet evergreen forest (L= L layer, F= F layer, H= H layer; s.w-southwest monsoon, n.e-northeast monsoon, p.s-pre-summer and s-summer)

Biochemical parameters	Southwest monsoon			Northeast monsoon			Pre-summer			Summer		
	P	H	Difference found	*P*	H	Difference found	*P*	H	Difference found	*P*	H	Difference found (Mann
Carbon	<0.05	10.84	H<L=F>H	<0.05	13.39	H<L>F>H	<0.05	12.81	F>H>L=F	<0.05	12.26	H<L>F>H
Nitrogen	<0.05	14.72	L>F>H=F	<0.05	12.03	H<L>F=H	<0.05	14.38	H<L>F>H	<0.05	15.35	H<L>F>H
C:N	>0.05	1.51	L=F=H	<0.05	10.89	H>L<F=H	<0.05	14.00	F=L>H<F	<0.05	11.29	F>L<H>F
Lignin	<0.05	7.99	F=L>H=F	<0.05	12.05	H<L>F=H	<0.05	12.34	H>L<F=H	<0.05	11.44	H<L>F=H
Lignin:N	>0.05	1.21	L=F=H	<0.05	9.72	F>L>H=F	<0.05	14.75	F>L<H>F	<0.05	2.37	L>F=H
Sodium	<0.05	12.21	H<L>F=H	<0.05	7.04	F<L>H=F	<0.05	14.13	H<L>F>H	<0.05	13.37	H<L>F>H
Calcium	<0.05	15.19	H<L>F>H	<0.05	14.78	H<L>F>H	<0.05	13.35	H<L>F>H	<0.05	13.20	F=L>H<F
Potassium	<0.05	11.98	H<L>F=H	<0.05	11.95	H<L>F=H	>0.05	5.13	L=F=H<L	<0.05	11.62	F=L>H<F
Total phenols	<0.05	15.16	H<L>F>H	<0.05	15.27	H<L>F>H	<0.05	15.17	F<L>H<F	<0.05	11.92	F<L>H=F

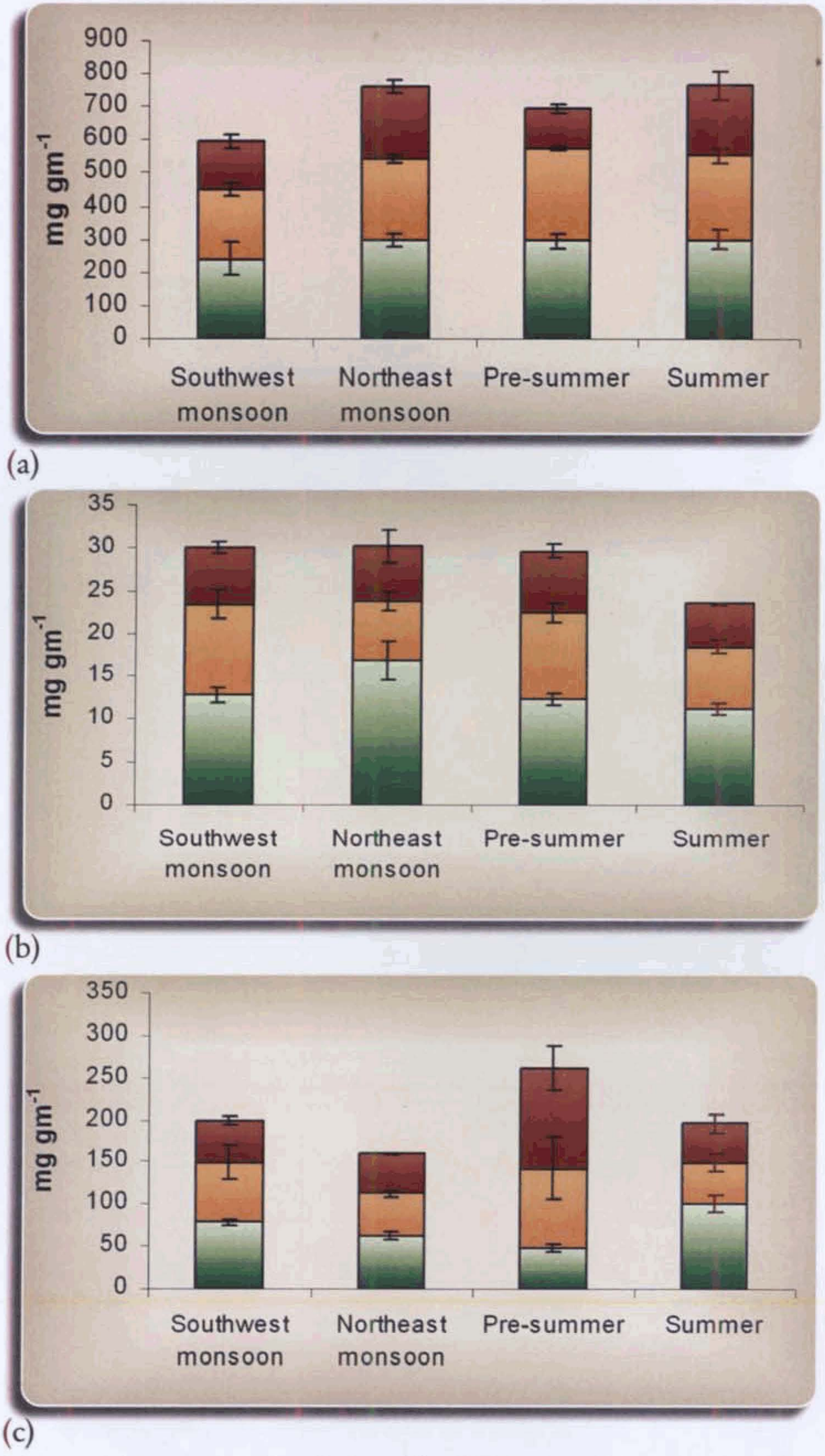


Figure.4.1 Biochemical profile of (a) Carbon (b) Nitrogen (c) Lignin in the litter layers of evergreen forest 🟩L 🟧F 🟥H

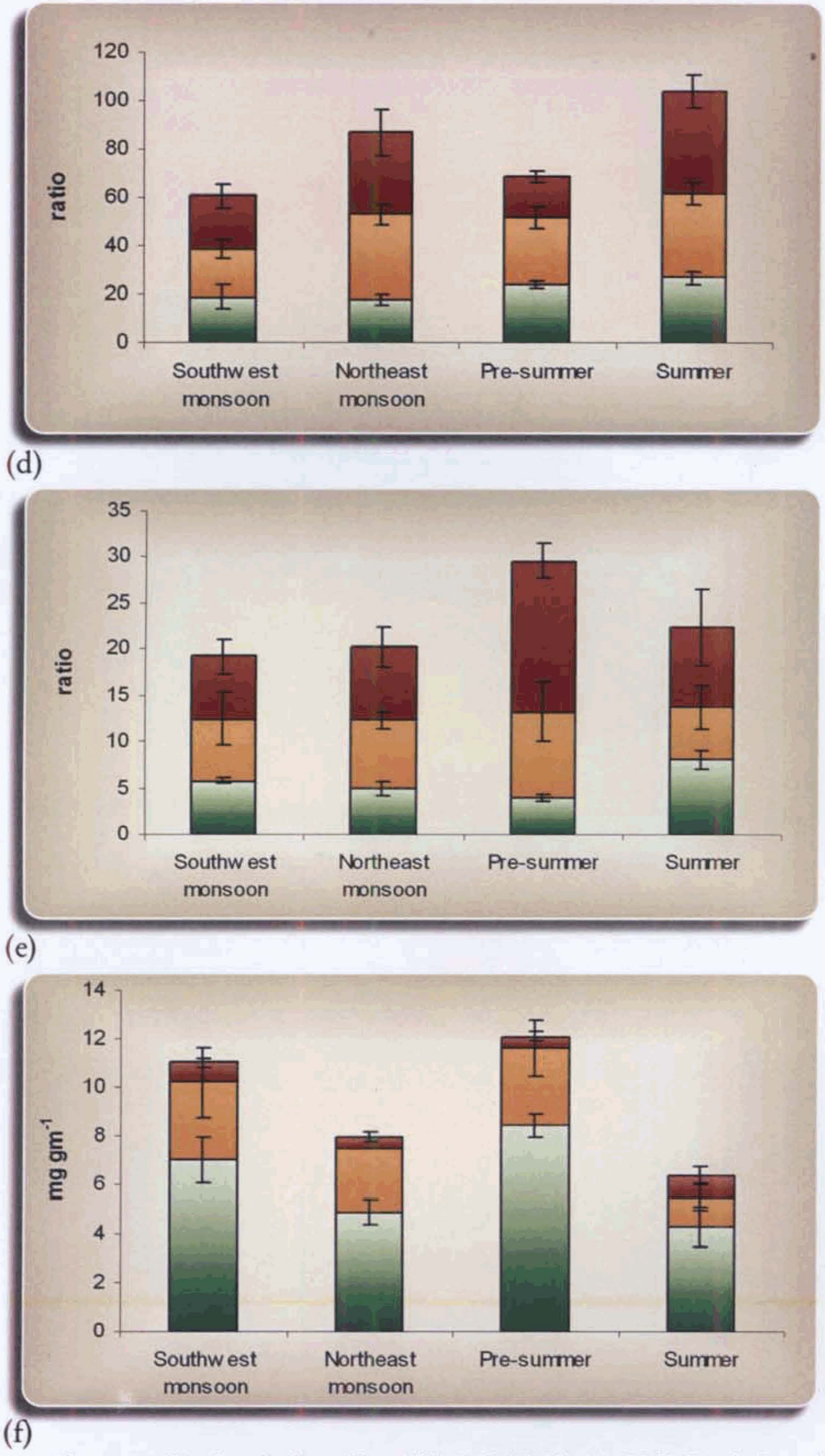


Figure.4.1 Biochemical profile of (d) C:N (e) Lignin: N (f) Total phenols in the litter layers of evergreen forest 🟩L 🟧F 🟥H

68C

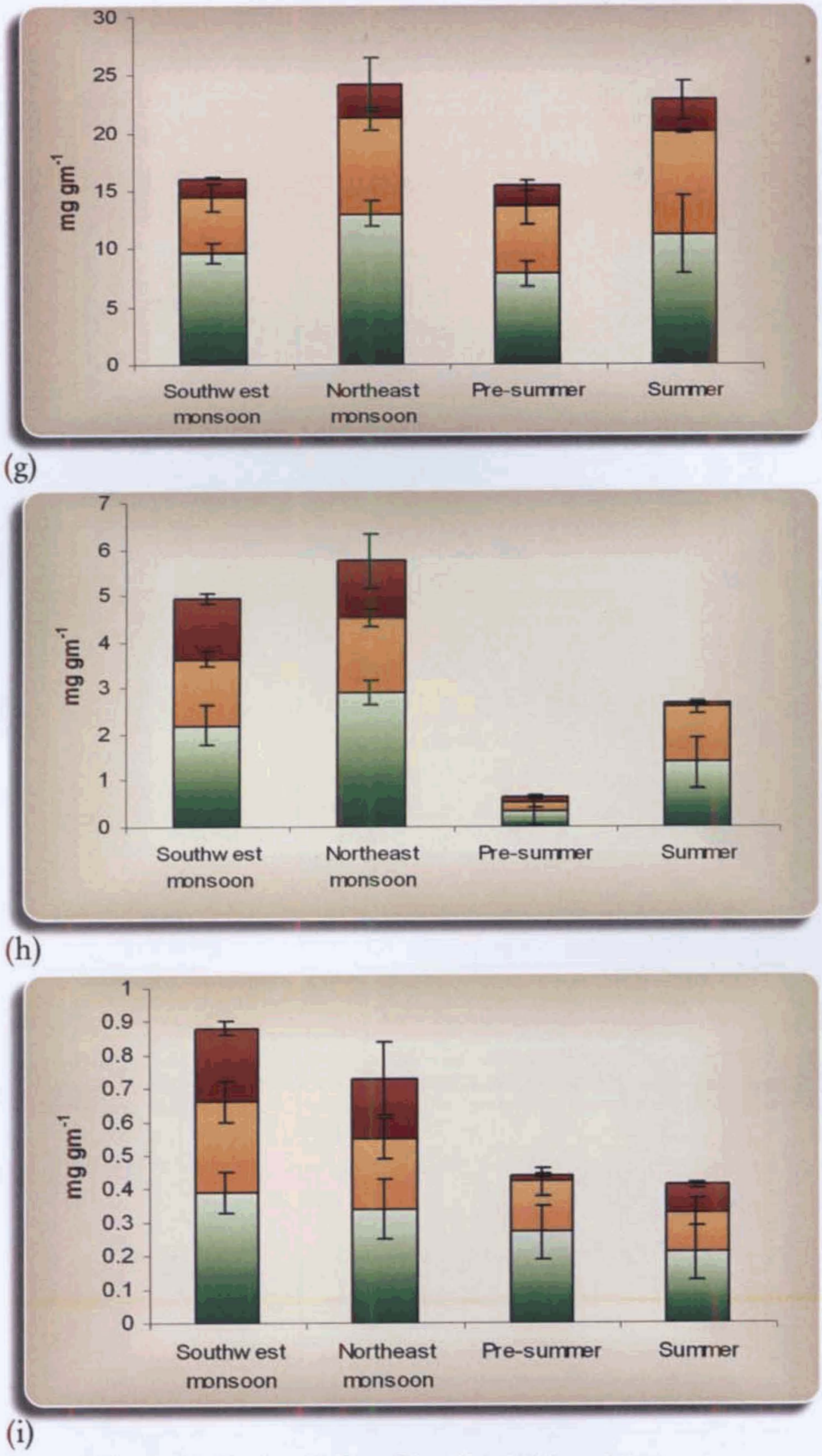


Figure.4.1 Biochemical profile of (g) Calcium (h) Potassium (i) Sodium in the litter layers of evergreen forest 🟩L 🟧F 🟥H

5.

Litter decomposition in relation to substrate chemical quality

INTRODUCTION

The decomposition of plant litter plays a significant role in the structure and function of natural ecosystems by acting as an energy source for soil organisms and as a nutrient reservoir for intra-system cycling processes (Kantarcõ 1978; Swift et al. 1979; Karaöz 1991, 1993) and is one of the ecological processes critical to the functioning of forest ecosystems. The rate at which decomposition occurs is an indicator of the functionality of biogenic belowground ecosystem processes of nutrient cycling in which soil organisms play a central role (Tian et al. 1997; Lavelle et al. 1997, 2001; Tian & Badejo 2001). It is estimated that the nutrients released during litter decomposition can account for 69-87% of the total annual requirement of essential elements for forest plants (Waring & Schlesinger 1985). This is particularly important in the nutrient budget of tropical forest ecosystems (Waring & Schlesinger 1985) as nutrient poor soils, where vegetation depends upon recycling of nutrients contained in the plant detritus (Singh 1968). Understanding these interactions is essential, since leaf litters do not segregate neatly into individual species types in ecosystems, and the composition of plant communities can show considerable intraspecific variations in the decay rates and nutrient release in relation to differences in the forest floor types (Prescott 1996) or soil conditions (Berg et al. 1995).

Decomposition has been widely studied (Anderson & Swift 1983; Golley 1983; Swift & Anderson 1989) and the fastest decomposition rates have been found in undisturbed tropical rain forests (Olson 1963). These studies have led to a better understanding of the factors that influence litter decay. A hierarchy of 3 main interacting factors influences rates of litter decomposition: physical (climate and microenvironment surrounding the litter), chemical (the chemical composition of the litter) and biotic (the nature of the micro-organisms and soil fauna active in the litter decomposition) (Swift et al. 1979). But variability of decomposition rates is high in tropical forest ecosystems, strongly related to the decomposer faunal community effects of seasonality on biochemical constituents of litter (Anderson & Swift 1983).

Availability of nutrients influences the crucial decomposer phase of decomposition that lasts for a year (Valiela et al. 1985), therefore, litter quality analysis based on various ratios of C, N and polyphenols is a significant step in assessing the nutrient cycling of vast forest ecosystems (Vanlauwe et al. 1997; Seneviratne 2000; Tian et al. 1992, Melillo et al. 1982). Plant litter is considered as high quality when C: N < 25 and of low quality when C: N> 25 (Regina et al. 2004) and lower the polyphenols make litter more palatable, favouring microorganisms activity and litter decomposition. Strong positive relationship between the initial concentration of nitrogen and rate of release of nutrients during the initial stages of decay has been reported in several studies (Yavitt & Fahey 1986: Stohlgren 1988). High quality litter encourages rapid initial breakdown of litter, resulting in faster decomposition and nutrient cycling, enhancing the site quality, whilst for low- quality litter the effects of invertebrates increases with time (Scha¨dler & Brandl 2005; Vitousek 1982).

As precipitation can control the physical process of leaching with greater rainfall accelerating the breakdown of surface litter (Swift et al. 1979). litter decomposability and quality changes with precipitation in tropical ecosystem (Austin & Vitousek 2000; Schuur 2001). With highly humid microenvironment surrounding the litter, the evergreen study habitat strongly influences the activity of microorganisms, which in turn affects the rate of decomposition of litter. Although there have been several studies on litter dynamics in tropical forest ecosystem in India (Rai & Proctor 1986; Kumar & Deepu 1992; Visalakshi 1993; Khiewtam & Ramakrishnan 1993) information on litter decomposition in natural forest ecosystems in Western Ghats is limited except for studies on selected tree species by Sundarapandian & Swamy 1999. In view of the relative importance of litter quality and site characteristics in determining decomposition in tropical forests (Vitousek et al. 1994) nutrient cycling rate in the evergreen forest is studied using litterbags. This study focuses on the decomposer phase of decomposition that lasts for one year and my objectives in this study is to (1) document the pattern of annual rate of leaf litter decomposition in a wet evergreen forest and to (2) determine the variation in the litter substrate quality during decomposition.

METHODOLOGY

The core of methodology regarding litter decomposition studies is the creation of a time series with litters of different degrees of decomposition. This was done with mass loss experiments using the litterbag method of Bocock (1964) modified by Rustad and Cronan (1988) (Plate.8). Although the litterbag method has a number of drawbacks (Witkamp & Olson 1963; Edwards et al. 1970; St John 1980), and may underestimate actual decomposition rates, it is assumed that biases are standard and allow direct comparisons to be made with other works (Wieder & Lang 1982).

Only yellow or brown leaves with a fully formed abscission zone were collected in the middle of 2004. Partially green leaves or those firmly attached to the branches were not used. The standard litterbag technique was employed for charactering litter decomposition dynamics (Bocock & Gilbert 1957). Litter was thoroughly mixed; air-dried and approximately 20 gm of dry litter was placed in litterbags of 20 x 20 cm constructed of single layer of 4mm mesh of nylon. This mesh size was sufficiently small to prevent losses of litter due to breakage, but sufficient enough for the access of micro, meso and macro fauna (Wise & Schaefer 1994). 56 litterbags were pinned to randomly selected surface of the forest floor in Aug 2004. Bags were placed in suitable gaps in the vegetation, incorporated into litter layer without causing excessive disturbance. Collections of litterbags were completed at 7, 15, 30, 60, 90,120,150,180, 210,240,270,300,330 and 365 days intervals selecting 4 bags at random at each date. After collection, any mineral soil or debris was carefully removed from the litter or wooden dowels and the samples were air dried for the determination of dry mass. There was very little or no mineral soil attached to the litter, and thus litter was not analysed for percentage ash. Decomposition was assessed in terms of percent mass loss based on air-dry weights at the beginning and end of the experimental periods.

All air-dried litter sub-samples were ground and passed through a 1 mm mesh screen before chemical analysis. Thereafter required amount of sub-samples of litters were taken for nutrient analysis. Nitrogen levels were determined by micro-Kjeldahl digestion (Jackson 1958) followed by distillation and titration and carbon determined by Walkley and Black method (1934). Values of ratio of carbon to N were derived from the above measurements. Total Phenols were quantified by Folin Ciocalteu method (Anderson & Ingram 1993). All chemical analyses were carried out in triplicates on the same sub sample.

Data analysis

Decay rate coefficient

To obtain decay rate coefficient (k) from exponential model, mass loss over time was approximated by regressing the log of the fraction of the mass remaining against time, using $\ln (M_t/M_o) = y\text{-}kt$ (Olson 1963). Changes in the percent initial litter dry weight over time were fitted to a single exponential model of litter decomposition (Jenny et al. 1949; Olson 1963; Wieder & Lang 1982) and also to linear and quadratic models. Linear model was fitted with $M_t = y\text{-} kt$ and quadratic model using the formula $M_t = y\text{-}kt + b{*}{*}t$ with M_t =mass at time t, M_o = initial mass of the litter, y is the intercept, b is the constant, k is the decomposition constant and t the duration of exposure of the litter bags in the field in days.

Time to 50% litter decomposition (litter turnover time) (t_{50}) was estimated from k values using the following equation (Bockheim et al. 1991).

$$t_{50} = {}^{0.693}/_{k}$$

For 99% decay (t_{99}).

$$t_{99} = {}^{4.605}/_{k}$$

Exponential, quadratic and linear models were also fitted to weight loss of carbon, nitrogen and total phenols obtained from litter analysis.

Regression analysis of effect of age of decomposition on the nutrient variables of litterbags (C, N, C: N and total phenols) was done. All data analysis was performed using GRETL open source software version 1.1 (Cottrell 2006). Significance was determined at $P<0.05$.

RESULTS

Weight loss during decomposition

For single exponential model the leaf-litter decomposition rate, *k* (days), was -0.007 after 365 days of decomposition. Only 4.5 % of the litter was remaining after 1-year decomposition studies (Figure.5.1). *k* value recorded was -0.005 after 3, 6 and 9 months interval whereas following 12 months; rate of decomposition was faster with a *k* value of -0.007, which estimated 99% mineralization of litter after 542 days. Approximately, 50 % of decomposition was completed after 120 days of deposition of litter. Quadratic model produced exceptionally good fits to mass loss data when compared with exponential and linear models (Figure. 5.2, Table.5.1).

Carbon and nitrogen dynamics in decomposing litter

Carbon concentration decreased till 1 month of decomposition. marginal increase was noticed during 3-month period, steadily decreasing till the end of decomposition (Figure.5.3a). After 1 year of litterbag study 63% loss was noted from the initial concentration. Significant decrease was noted for carbon values with age of decomposition ($r^2 = 82\%$, $F = 54.76$, $P < 0.05$).

Nitrogen values showed a peak during the 2nd week of litterbag study, thereafter significant decline was noticed (Figure.5.3b) with the course of litterbag experiment ($r^2 = 91\%$, $F = 123.91$, $P < 0.05$). A decrease of 63.5% was noted after 12-month decomposition study.

C:N ratio pattern in decomposing litter

A fluctuating pattern was noticed for C:N ratio during decomposition with values ranging between 16.6 and 21. Fall in C:N values was noted with lowest values during the 2nd month of decomposition followed by a gradual rise during the 3rd month again decreasing upto 6 months (figure.5.3c). During the 9th month of litterbag study C: N values showed highest value (21).

Total phenol levels with decomposing litter

Total phenol concentration noticed a sharp fall of 86% during the 2nd week of litterbag study thereafter decreasing gradually with significant decrease ($r^2 = 0.2\%$, $F = 4.67$, $P = 0.05$) (Figure.5.3d).

All chemical factors showed good statistical fits to quadratic model (Table.5.1).

DISCUSSION

An exponential litter decomposition rate of -2.55 k/year was reported after 365 days of litterbag study in the evergreen forest habitat. An initial rapid loss of litter weight followed by a slower rate of loss was observed with 50%

weight loss of litter noticed after 4 months of decomposition and further 46% of decomposition requiring 8 months period. Nutrient concentrations also varied during the decomposing period, due to the utilization of carbon and nitrogen by heterotrophic microbial and animal populations and also through leaching loss (Bubb et al. 1998; Jamaludheen & Kumar 1999; Palm & Sanchez 1990). The initial faster rate of disappearance of litter obtained in the current study is in agreement with the results reported by others (Anderson et al. 1983; Seastedt 1984; Swift & Anderson 1989; Kumar & Deepu 1992; Sundarapandian & Swamy 1999). This could be due to higher initial content of water-soluble materials, simple substrates and the breakdown of litter by decomposers, especially the micro flora (Songwe et al. 1995). The higher loss in the initial stages must also be due to the added effect of high precipitation received during the initial days of litter bag deposition, with conducive physical determinants such as soil moisture content, temperature and evapotranspiration for the activity of decomposers (Facelli & Pickett 1991) and also due to the leaching of soluble litter materials that occurs in the presence or absence of micro flora and fauna (Witkamp & Crossley 1966; Vossbrinck et al. 1979).

In this study negative exponential model is considered to explain the results. Although negative exponential model is an oversimplification of the decomposition process, it gave good estimates of decomposition rates. Alvarez-Sanchez and Becerra Enríque (1996) fitted an exponential model, a double exponential model and a negative exponential model through their leaf decay data at Mexico. They concluded that the double and negative exponential model yielded the best results. Decomposition rate of –2.55k/yr reported in the present study is equivalent to reported decomposition rates of natural leaf-litter in evergreen forest in Central Amazonia -1.3 *k*/year Klinge (1977); 0.58±5.00 *k*/year Cuevas & Medina (1988) and to average values for other tropical forests (-1±4 *k*/year) (Olson 1963). Thus, exponential litter decomposition rate measured in this study is to some extent a good measure of decomposition rate in wet evergreen forests. However, statistical fits to single exponential model were poor, as it overestimated initial litter decomposition rates.

Quadratic model fitted better than negative exponential model to the experimental data and it estimated a *k* value of -0.07/day showing faster decomposition rates than the exponential model. Overestimate of decomposition by experimental method might be due to the compaction of the leaves resulting in a better conservation of water during the dry periods, hence better conditions for the micro flora. But the decomposition rates obtained from experimental method are largely dependent on the experimental conditions and are generally not possible to compare results from different authors and countries (Torreta & Takeda 1999). Though, decay functions, such as linear or quadratic, produce better statistical fits to the data, but do not have a strong biological basis for describing litter decomposition (Wieder & Lang 1982).

Concentrations of C, N and total phenols in the leaves decreased in the course of litterbag experiment. Among chemical parameters, total phenols had the most rapid rate of release. Of the initial amount, 99.97 % was lost during 1-year decomposition compared with a weight loss of 96.5%. This indicated initial leaching loss of 84% because of its solubility. Studies conducted indicate that phenolics are removed rapidly from the leaf litter through leaching (Schofield et al. 1998). Positive effect of rainfall on nutrient release has been reported by Meetenmeyer (1978); Anderson (1991); Berg et al (1993) and Austin & Vitousek (2000).

Carbon and nitrogen also decreased over time, but at a constant rate. During decomposition processes in the study habitat, nitrogen dynamics showed leaching, immobilization and mobilization phases (Berg & Staaf 1981). The increase in N concentration followed by decline overtime as observed in this study is similar to the patterns found in other studies (Bubb et al. 1998; Singh et al. 1999; Palm & Sanchez 1990). A short leaching phase was evident during the start of decomposition up to 15 days probably due to heavy rains received, thereafter a short immobilization phase showing peak in nitrogen values, afterward continuous mobilization phase was recorded. Though phenols are lost rapidly through leaching, nitrogenous compounds are lost slowly through leaching (Khanna & Ulrich 1991), resulting in a relative increase in nitrogen content. Because it is immobilized in microbial biomass, N is further accumulated in decomposing leaf litter (Swift et al. 1979). The increasing N concentration during the 2nd week of decomposition indicates a short phase of N storage by microorganisms (Aber & Melillo 1982; Bosatta & Staaf 1982). A higher release of N could be observed during the last phase. Release of N without net N accumulation, suggesting that N was not a limiting factor for microorganisms because the initial N concentration in the litters of study habitat was relatively high compared to other studies (Aerts 1997: Melillo et al. 1982; Singh et al. 1999).

C and N dynamics are related to the relative availability of C and N to the litter faunal population. In many decomposition studies, nitrogen mobilization commences at the critical C/N ratio of about 20-30 in many species and about 30-40 in tropical species (Regina et al. 2004). As expected lower C:N ratio in the evergreen habitat suggests that nutrients are not limiting. As the C:N values reported in this study are <22 showing N mobilization through out the experiment with decreasing N concentration (64 % drop in N concentration). The decrease in N content and increase in C/N ratio of litter exposed to detritivores and fungivores is more readily explained by the selective removal of N rich litter and associated micro arthropods. Storage by microorganisms was not evident as N was continually decreasing after 2 weeks of study and C concentration also was decreasing (Aber & Mellilo 1982; Bosatta & Staaf 1982).

Loss of nutrients in the initial stage is correspondent to the leaching phase during which soluble substances leach for a month (Valiela et al. 1985). Continued decrease of litter in the evergreen habitat after the loss of soluble components is primarily the result of biotic processes (Vossbrink et al. 1979). Quadratic pattern was noticed for nutrient release characterized by slow release during initial phase and a subsequent rapid release phase, not agreement with results reported by Jamaludheen & Kumar 1999. Delay in initial nutrient release could possibly due to the fresh leaves of evergreen forest with high leaf toughness (Wolda 1988; Wright 1992).

Studies on the dynamics of nutrient release from litter report somewhat diverse results, even for litters of similar type (Berg 1986; Rashid & Schaefer 1988). Because different patterns were observed for the dynamics of particular chemical elements in various forest ecosystems, it was hypothesized that nutrient dynamics is determined to a large extent by the nutrient availability of decomposers (Swift et al. 1979). In this study, release of nutrients from the initial stage of decomposition highlights the fact that nutrients exceeding the needs of decomposers are released from the litter from the very start of decomposition while limiting nutrients occurring in suboptimal amounts would be accumulated during the initial stages of decomposition (Laskowski et al. 1995). The mechanism determining the dynamics of nutrients during litter decomposition are however still poorly understood. The decomposition constants *k* obtained in this study were typical of tropical forests (Olson 1963). Thus, the patterns of chemical element dynamics observed during decomposition are probably valid for a broad range of forest ecosystems in these climatic conditions.

Table.5.1. Regression models (linear, quadratic and exponential) fitted for changes in mass loss and biochemical parameters (dependant factor) with age of decomposition (independent factor)

Dependent Factors	Linear						Quadratic							Exponential					
	R^2	d.f	*F*	*P*	*y*	*k*	R^2	d.f	*F*	*P*	*y*	*k*	b	R^2	d.f	*F*	*P*	*y*	*k*
Mass loss	0.96	12	350.40	<0.05	17.69	-0.049	0.993	11	790.11	<0.05	19.16	-0.078	0.000083	0.922	12	141.2	<0.05	23.19	-0.008
Carbon	0.82	12	54.76	<0.05	246.79	-0.39	0.88	11	42.19	<0.05	226.75	0.005	-.011	0.754	12	36.70	<0.05	264.88	-0.003
Nitrogen	0.91	12	123.91	<0.05	13.06	-0.0221	0.94	11	79.94	<0.05	12.41	-0.0091	-0.000004	0.848	12	67.2	<0.05	13.99	-0.003
Total phenols	0.28	12	4.67	=0.05	1.05	-0.0035	0.440	11	4.33	<0.05	1.5390	-0.0132	0.000027	12	12	27.3	<0.05	0.73	-0.006

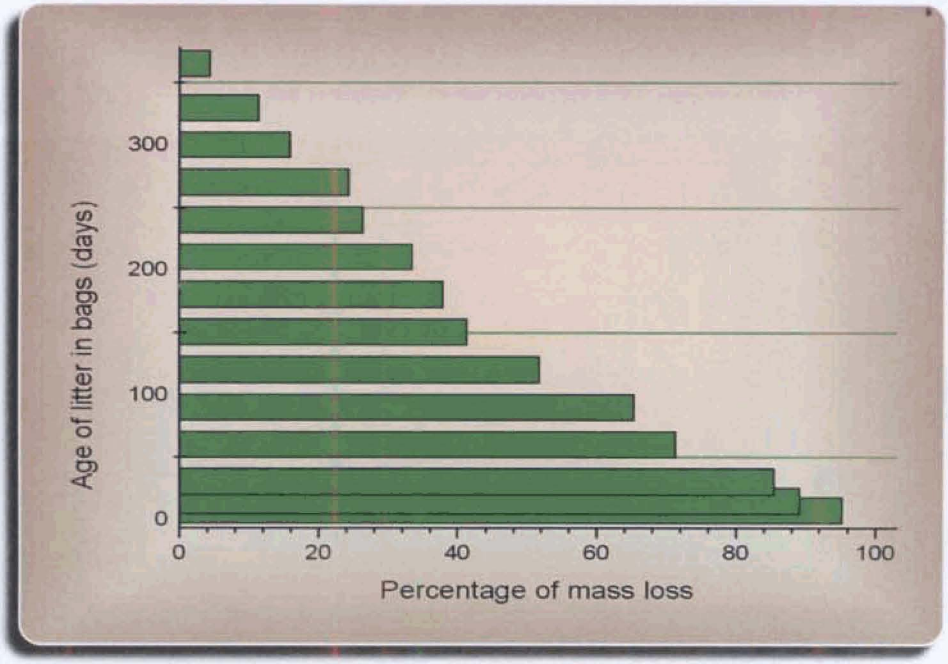


Figure.5.1 Percentage of leaf mass in the litter bags with increasing age of decomposition at the evergreen forest of Periya

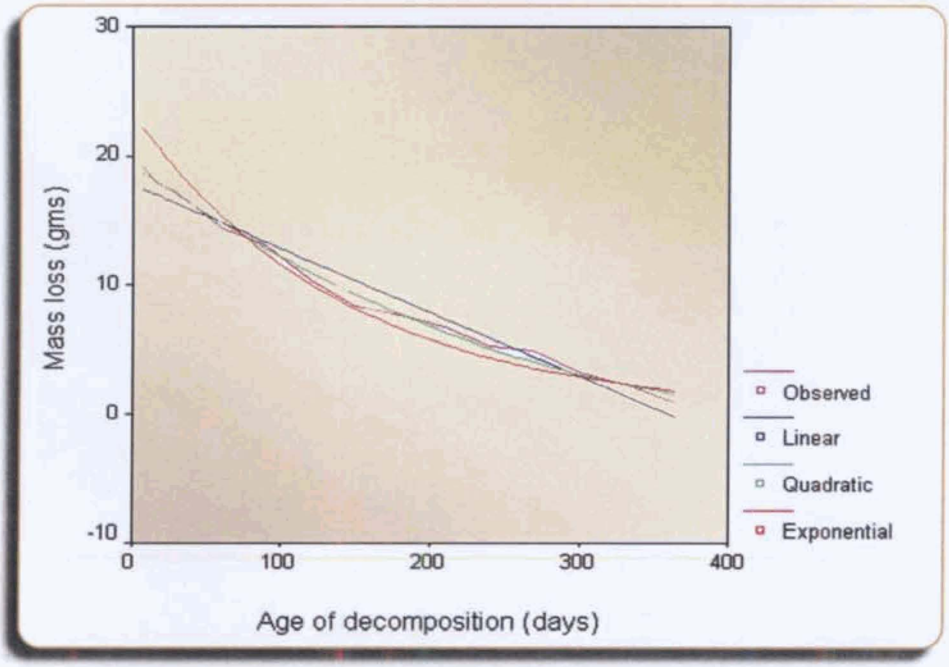
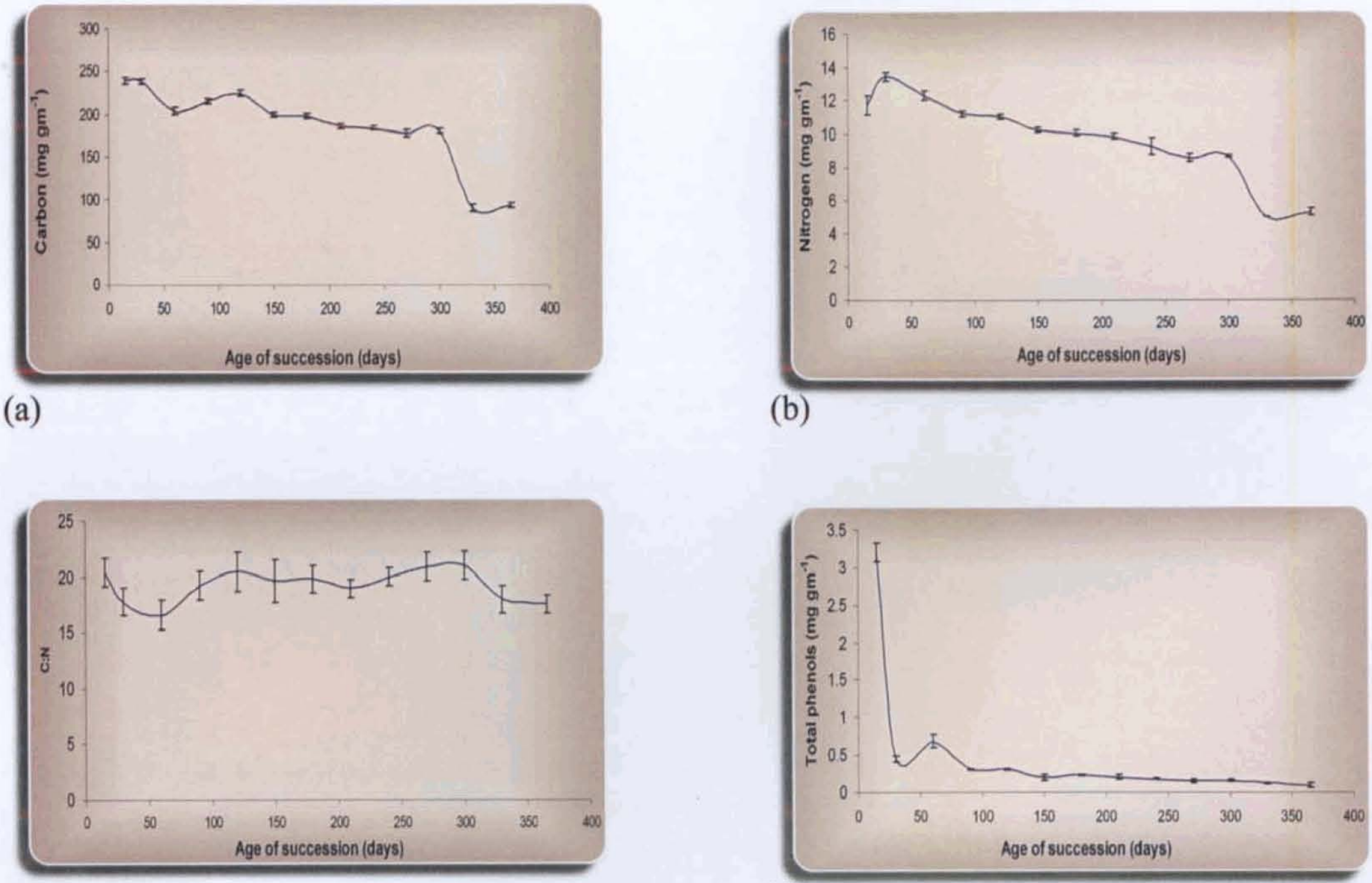


Figure.5.2 Fitted linear, quadratic and exponential models for litter mass loss during the study period

8113



(a) (b) (c) (d)

Figure . 5.3 Amount of (a) Carbon, (b) Nitrogen (c) C:N and (d) total phenols associated with decomposing litter of the study habitat

81 C

PLATE.8

Field placed litterbags employed for faunal succession analysis

6.

Litter arthropod faunal succession

INTRODUCTION

Through the related process of decomposition and mineralization. which includes leaching, mechanical breakdown and digestion by saprophagous animals and enzymatic degradation of chemical compounds by saprotrophic biota (Facelli & Pickett 1991), litter is broken down and the nutrients within the litter are released into the forest floor where the nutrients are available for plant uptake. Recent studies of litter decomposition have emphasized the effects of communition by fauna and microbial interactions in determining decomposition (Vossbrink et al. 1979; Wachendorf et al. 1997; Gonzalez & Seastedt 2001; Irmler 2000). Influence of these litter invertebrates in decomposition is due to the communition of litter and the resulting increase in surface area of the substrate for microbial colonization (Seastedt 1984). In the presence of microarthropods (free living Acari and Collembola), which are prevalent components of decomposer fauna, mass loss of newly senesced litter increases, amounts of inorganic nitrogen may be greater and primary productivity can be enhanced (Seastedt 1984; Seta¨la¨ & Huhta 1991). Adopting an experimental approach to reduce arthropod populations has shown them to be influential in determining mass loss from litterbags (Seastedt 1984).

Although a diverse fauna and micro biota are involved in the degradation of leaf litter, little is known about the significance of their diversity in the corresponding processes of nutrient cycling (Cragg & Bardgett 2001). The composition of the litter fauna successively changes during decomposition reflecting structural, chemical, biological changes in the litter (Hasegawa &

Takeda 1995). Furthermore, some species of fauna disappear during decomposition or change their feeding behaviour, which alters the food web involved in the decomposition process (Dilly & Irmler 1998). Microarthropods occupy all possible food webs within the detritivore food web and are primarily based on dead plant materials (Swift et al. 1979). In decomposition food webs fungi and bacteria provide most of the energy and nutrition to microarthropods (Moore et al. 1988). Most Oribatids, Collembolans and free living Astigmatid mites have well developed mouth parts capable of fragmenting organic matter while feeding on micro flora adhering to this detritus. These processes have very important consequences to decomposition and mineralization processes by creating new surfaces for microbial colonization (Elkins & Whitford 1982). In conclusion, the trophic structure of the detrital food web proves to affect the intensity of belowground processes and consequently, plant growth (Setälä 2002).

Availability of nutrients is an important factor in controlling the faunal succession processes in the decomposer phase, which lasts for one year (Valiela et al. 1985). Mechanical breakdown of litter by saprophagous arthropods and biochemical degradation of leaf litter compounds through enzymes originating from animals and microbiota, strongly depend on the physicochemical characteristics of leaf litter (Swift et al. 1979; Melillo et al. 1982). Effects of initial chemistry of litter has strong influence on subsequent trajectory of decomposition are based in part upon interactions with detritivores (Valiela et al. 1984; Lagerloef & Andren 1985; Pereira et al. 1998).

Assessment of nutrients during leaf breakdown provides important information on the function of faunal activity in particular during leaf breakdown (Robinson & Gessner 2003). Several studies have demonstrated that the chemistry of leaf litter represented by polyphenols and C:N influences subsequent colonization by, and activity of invertebrate decomposers (Maity & Joy 1999; Zimmer & Topp 2000). Low C:N ratios and low concentration of polyphenolics favour consumption by, and population growth of, some invertebrate decomposers (Maity & Joy 1999; Zimmer & Topp 2000).

Reports of successional changing of litter arthropods using litterbags in temperate forests dates back to 40 years (Bocock & Gilbert, 1957). While studies that assess the role of litter quality (Melillo et al. 1982; Taylor et al. 1989; Aerts 1997) or litter fauna (Heneghan et al. 1999) as determinants of decomposition rates are common, studies that investigate interaction between these two variables are not. The warmer and moister soils of the tropics provide optimal conditions for microbial growth and for the development of strong interactions between the microbes and the fauna, which feed on them (Heneghan et al. 1999). The patterns of the litter faunal succession in relation to the litter biochemical changes during decomposition using litterbag methodology differ widely from the patterns seen in temperate succession studies. As the relative importance of invertebrates differs from site to site (Swift et al. 1979; Seastedt 1984; Heneghan et al. 1998) and varies between litter types and specific litter mixtures, the objective of the present study is to analyse the faunal succession pattern with increasing age of decomposition of litter along with the influence of the variation in litter chemical quality in determining the abundance of various trophic groups of litter fauna in a wet evergreen forest.

METHODOLOGY

Freshly produced litter was collected from the study habitat during August 2004. Litter was thoroughly mixed; air-dried and approximately 20 gm of dry litter was placed in litterbags of 20 x 20 cm constructed of single layer of six mm mesh of nylon. This mesh size allows for the movement of most soil fauna into the litterbag (Edwards & Heath 1963) facilitating decomposition. 56 litterbags were pinned to randomly selected surface of the forest floor in the middle of August 2004. Bags were placed in suitable gaps in the vegetation, incorporated into litter layer without causing excessive disturbance. Four bags were collected at 7, 15, 30, 60, 90,120,150,180, 210,240,270,300,330 and 365 days intervals. Collections of litterbags made during first four months constitutes first phase of faunal succession, succeeding four months in second phase and last four months of succession forming 3rd phase of faunal succession.

Macroscopic litter-dwelling arthropod fauna were collected by hand from litterbags. Meso and micro fauna were extracted with a 15-20 cm diameter Berlese funnel fitted with 4-6 mm mesh screen and a 60-watt bulb for 2-4 days until the litter was dry (Ananthakrishnan 1996) and the fauna collected in 70 % alcohol. All fauna were counted and sorted to the taxonomic level required to establish adult trophic level when possible. For some common taxa this was established by identification up to order. Beetles were assigned to trophic level based on family and mites based on sub order. Categorization of soil/litter fauna into well-defined trophic groups or feeding guilds is difficult, mostly because of the limiting amount of experimental evidence of dietary requirements of most soil/ litter fauna (Hunt et al. 1987; Lee & Pankhurst 1992). However the collected litter arthropods were classified into the following guilds/ feeding groups *viz.*, predators, detritivores and fungivores. Collembolans were classified as microbidetritivores, because of a broad diet and lack of information about their trophic category; these were excluded from diversity analysis, instead their abundance considered.

(Methodology of chemicals discussed in chapter.5)

Data analysis

Differences in the abundance of arthropod assemblages during different phases of succession in litterbags were done using ANOSIM (Analysis of Similarities, with a maximum of 999 permutations)(Clarke 1993) in the program PRIMER. The program constructs a similarity matrix between samples using the Bray-Curtis similarity measure that is not affected by joint absences. This similarity measure also gives more weight to abundant than to rare species (Field et al.1982). Shannon diversity index was calculated for estimating trophic group diversity.

The following statistical analyses were performed using GRETL open source software version 1.1 Cottrell (2006). Regression analysis was carried out to assess the effect of age of succession on the diversity and abundance of trophic groups. Multiple regression on the abundance of each trophic group as a function of nutrient variables (C: N and total phenols) were carried out for different stages of succession. For all analysis, significance was determined at $P<0.05$.

RESULTS

Changes in litter fauna with succession

Oribatid mites, Collembolans, Coleopterans and Isopods were the most abundant groups during different days of succession. Proportion of mites in all litterbag samples were high, ranging from 10-48 % forming largest functional component of the fauna during all stages of succession, represented by four sub orders (Astigmatids, Prostigmatids, Mesostigmatids and Oribatids) (Figure.6.1 & 6.2). During the initial phase fungivorous Oribatids occurred in the litterbags with relatively high abundance. During the later phases, predatory (Mesostigmatids) and detritivorous (Oribatids) dominated (Figure.6.3). In contrast, Collembola and Isopods were slightly less abundant during the beginning of the experiment, but showed a steady increase in the 4-6 month period of succession; thereafter a declining trend was noted. Larval abundance towards the last days of succession can be observed, whereas fungivorous thrips were abundant in the first phase of succession. Hymenopterans dominated the faunal assemblage during the second week of succession (Figure.6.1 & 6.2). Seven Coleopteran families were reported from succession studies with predatory Staphylinids and fungivorous Ptiliids dominating the assemblages (Figure.6.4).

Assemblages of arthropods were not significantly different between the litterbags during different phases of succession (ANOSIM always with *P*>0.05) (Table.6.1). Using percent similarity as the measure, species composition within consecutive stages clustered together. Highest similarity was observed between arthropod groups in the litterbags of seven and fifteen days (100%) (Figure 6.5).

Diversity and abundance of trophic groups during succession

Fungivores recorded highest abundance during the litterbag study followed by detritivores, predators and microbidetritivores. Highest detritivore and predator abundance was noted during the 3rd month of succession, thereafter significant decrease was noted for predators (r^2=60%, *F*=17.89, *P*<0.05) while detritivores also showed a declining trend but not a significant one (r^2=0.9%, *F*=0.11, *P*>0.05). Fungivore abundance was noticed during the first week of succession study; thereafter a fluctuating pattern in abundance was noticed with no significant change (r^2=13%, *F*=1.82, *P*>0.05). Abundance of microbidetritivores was in the peak during the 6th month of succession, recording no significant change with succession (r^2=2%, *F*=0.25, *P*>0.05). Detritivore abundance was contributed mainly by Oribatids during first and last phase and Isopods during the middle phase of succession. Ants and Staphylinids were the major predators during first phase of succession followed by Mesostigmatids in the second and last phase. Oribatids dominated fungivores during the first and second phase and by Prostigmatids and Ptiliids in the last phase of succession. Microbidetritivorous Collembola was dominant in the second phase of succession (Figure. 6.7 a. b c & d).

During the initial phase of succession (up to one month) diversity of arthropod fauna was low thereafter H' value increased showing a peak during the 3rd month (H'=2.05) afterwards declining till the end of study. Predators too recorded highest H' value (1.90) in the 3rd month of succession. Fungivore diversity was high during the 6th month of succession showing a value of 1.50. Diversity of detritivores was high in the 1st month of succession and thereafter a significant loss in the diversity was noted in the litterbags (r^2 =30.8%, F= 5.34, P<0.05) (Figure.6.6).

Multiple regression analysis of abundance of detritivores as a function of litter biochemical variables (C:N and Total phenols) showed significant variation (r^2 =71%, F=6.34, P<0.05) (Table.6.2).

DISCUSSION

Low incidences of Collembola during the early phases of succession, dominance of mites throughout the litterbags and preponderance of Isopods in the middle phase of litterbag succession were noted in the one year faunal succession studies in the wet evergreen forest. Significant decrease was noted in the abundance of decomposer fauna (detritivores) with decreasing litter quality of the litterbags. There was little evidence of a trophic category being confined to a particular successional stage.

Oribatid mites were the abundant group through out the litterbag study. The dominance of these species in decomposing leaf litter was already demonstrated in the litter of temperate and tropical forests (Luxton 1982;

Heneghan et al. 1999). As the availability of food controls the survival of mites, their abundance in litterbags suggests lush of fungal and detrital materials in the litter layers. But their participation in the decomposing process is still unclear (Ribeiro & Schubart 1989). In accordance with studies in temperate deciduous forests abundance of Oribatid mites increased as decomposition proceeds (Seastedt et al. 1983; Anderson 1975) and further more, high litter quality through out the study period might have exerted influence on their community (Heneghan et al. 1999). It has been suggested recently that several species of putative litter-feeding Oribatid mites are not primary decomposers but mainly feed on fungi or are predatory or necrophagous (Schneider et al. 2004), and similar results have been obtained for Collembolans (Chahartaghi et al. 2005). Indirect evidence from litterbag studies showed that mesofauna (Acari and Collembola) might be more important in mobilizing nutrients than in contributing to mass loss, and that they act principally as "grazing arthropods" (Hanlon & Anderson 1979). The high moisture and warm temperatures favoring fungal growth (Hassal et al. 1986), might have lead to the preponderance of fungal grazers in the evergreen tropical system and these arthropods tend to have the greatest effect on decomposition in systems dominated by fungi (Moore et al. 1988).

In contrast to the findings in the temperate forests where Collembola was always earlier in succession than Oribatid assemblages (Irmler 2000), in the evergreen study habitat Oribatids dominated in the beginning and Collembola in the middle phase of experiment. It may be that competition between Collembola and Oribatids also influences the different period of occurrences of Collembolan. Kaneko et al. (1995) found that at least some species of Collembola and Oribatids compete for the same microbial food. Decrease in Collembolans might also be due to their increased rates of migration from litterbags to humus layers (Greenslade & Greenslade 1973; Filser & Fromm 1995) apparently searching for favourable microclimates (Usher 1970; Hijii 1987; Sgardelis et al. 1993). Furthermore, abundance of Oribatids increased with the increasing age of the litter, which indicates greater niche separation by Oribatids and reflects a higher efficiency of food exploitation. Decreasing microbial food availability and more efficient food exploitation by Oribatids may also be responsible for the low abundance of Collembola at the late breakdown phase. Abundance of mites in the litterbags can also be attributed to their "K –selected" nature as they live through several annual cycles of their habitat's renewal and decomposition exhibiting its dominance throughout the stages of decomposition (Hansen 2000; Hågvar & KjØndal 1981) whereas shorter dominance of Collembola in the litterbags indicates their "R-selection" behaviour which favours sudden boom- bust prosper in favourable conditions in which they take advantage of flushes of microbial growth.

In concordance with the results recorded by Zimmer (2002), Isopods formed the next dominant saprophagous group in the litterbags particularly during the last month of first phase. Abundance of Isopods was noted during phases of low phenol and C:N concentration as high amount of these adversely affected consumption by them (Cameron & Lapoint 1978; Swift & Boddy 1984). During the litterbag experiment other saprophagous groups (Oribatids, Isopterans, Larvae, Dipterans etc) were found to be less abundant in the Isopod dominated stages (end of first phase) of decomposition as Isopods compete with organisms of same guild for 'high quality food' (Zimmer 2002) in addition to the reduced fungal mass by Isopod feeding (Kayang et al. 1994,1996). Isopods could play a significant role in decomposition by enzymatic cellulolysis resulting in mechanical breakdown (Zimmer & Topp 1998; Swift & Boddy 1984).

During the 3rd month of succession (first phase), Coleoptera was the second dominating group contributing (22%) of litterbag fauna primarily due to Ptiliid and Staphylinid dominance. Staphylinid abundance can be attributed to the abundance of mites that serves as prey resources to them (Didham et al. 1998). Profusion of Ptiliids can be explained by the excessive humidity in the area with consequent proliferation of fungus (Marinoni & Ganho 2003). Humidity and high moisture levels in litterbags affect the foraging ability of smaller sized ant groups leading to the lower abundance of ants in litterbags (Brühl et al. 1998; Janzen 1973). Abundance of arthropods was lower in the litterbags through out the study period confirming the observations made by many researchers as the abundance fauna will be less in tropical forests (Anderson et al. 1983; Collins 1980; Pfeiffer 1996). In this study seasonal influence on faunal succession could not be factored out and dealt singly, however low abundance of Collembolans and ants were noted during periods of high precipitation.

Studies conducted by Smith & Bradford (2003) observed strong interactive effects of litter quality and faunal community on decomposition. Litter of the study habitat is having C: N ratio below 25, with high quality litter in the litterbags, N is mineralized readily from organic materials (Regina et al. 2004; Myers et al.1995) and this initial breakdown is due to the effect of invertebrates (Schädler & Brandl 2005). Wachendorf et al. 1997 has showed about 40% carbon loss in wet alder forest litter, attributed to the activity of fauna on the breakdown process. During the one year decomposition study in the study habitat, 60% loss of carbon was noticed which should be mainly credited to the faunal activity. The decreasing nitrogen and carbon concentrations indicate that there is no storage by micro-organisms (Aber & Melillo 1982; Bosatta & Staaf 1982). Increase in C: N ratio was noted in the litter bags (though not a significant positive one) exposed to detritivores and fungivores which can be more readily explained by the selective removal of N rich litter associated with micro fauna. It is well established that decomposer organisms more readily utilize herbaceous material because it has a higher N content and lower content of structural polysaccharides (Sah 1990; Meiwes & Beese 1988; Ellenberg et al. 1986). Phenolic compounds can directly affect the composition and activity of decomposer communities, thus showing a significant negative relation between detritivores abundance (Hättenschwiler & Vitousek 2000). However, direct effects of polyphenols on litter fauna are difficult to demonstrate because of the covariability of other compounds and the complexity of soil food webs. Field studies by Lavelle et al. 1993 also confirm that micro arthropod community has disproportionate effect on the nutrient cycling processes in humid tropical systems compared to temperate ecosystems.

In accordance with the high quality litter in the litterbags through out the experimental period, successional changing of species during decomposition was negligible with litterbags in the same phase clustering together except for litterbags during first month. Each bag is a very small sample of assemblage, including only 5-10% of the species that have collected from the habitat. Even with this daunting potential for variation in species composition, a consistent pattern of greater similarity was evident probably due to unchanging high quality of litter through out the study period.

In forests, up to 90% of aboveground net primary production may enter primarily detritus-based food webs (Swift et al. 1979; Peterson & Luxton 1982; Coleman et al. 1983). In this study detritivores were dominant members of the arthropod assemblage recovered from litterbags suggesting that decomposer mediated effects upon decomposition may have been most significant. My results are limited to the first 12 months of decomposition, as early changes in the chemistry of litter are known to influence a range of subsequent ecological processes including colonization of litter by microarthropods (Anderson 1973; Pereira et al. 1998). A parallel rise in relation with fungivores is evident in the predator fauna utilizing this high resource availability.

Litterbag sampling is just an indicator of the dynamics of the entire assemblage, reflecting as it does, only the activity of minority of insect groups at a part of its life stage (Hansen & Coleman 1998). But the relative ease with which large numbers of replicate treatments can be established for long succession studies improve our understanding of control processes in terrestrial decomposition processes. Future work must assess how litter faunal community composition, manipulated in a more realistic manner, affects decomposition of senesced litters in both the long and short-term studies.

Table.6.1. Analysis of similarities (ANOSIM) of insect faunal assemblages in litter bags during 3 different phases of decomposition

Sample statistic (Global R): 0.296
Significance level of sample statistic: 1.5%

Phases of decomposition	R statistic	Significance level
First, Second	0.40	*P*>0.015
First, Third	0.26	*P*>0.015
Second, Third	0.25	*P*>0.015

Table.6.2. Multiple regression analysis of abundance of detritivores as a function of litter biochemical variables (C: N and total phenols)

Regression equation is

Detritivore = - 85.3 + 5.51 C: N - 3.79 phenols

Predictor	Coefficient	SE Coef	T	*P*
Constant	-85.27	30.31	-2.81	0.037
Phenols	-3.79	1.60	3.44	0.01
C: N	5.51	1.60	-0.32	0.72

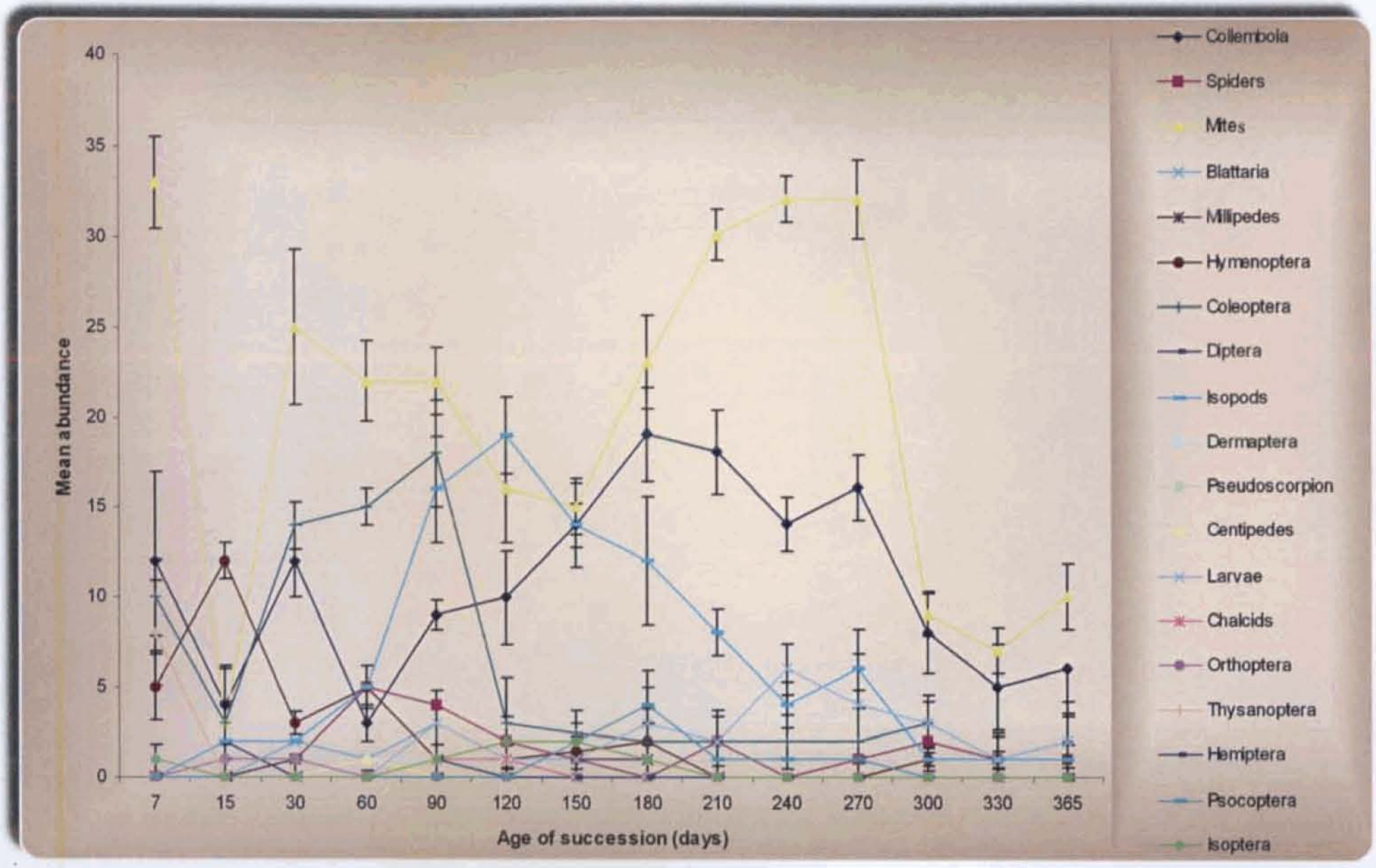


Figure.6.1 Succession pattern of arthropod fauna during different stages of litter decomposition in the evergreen forest at Periya

96B

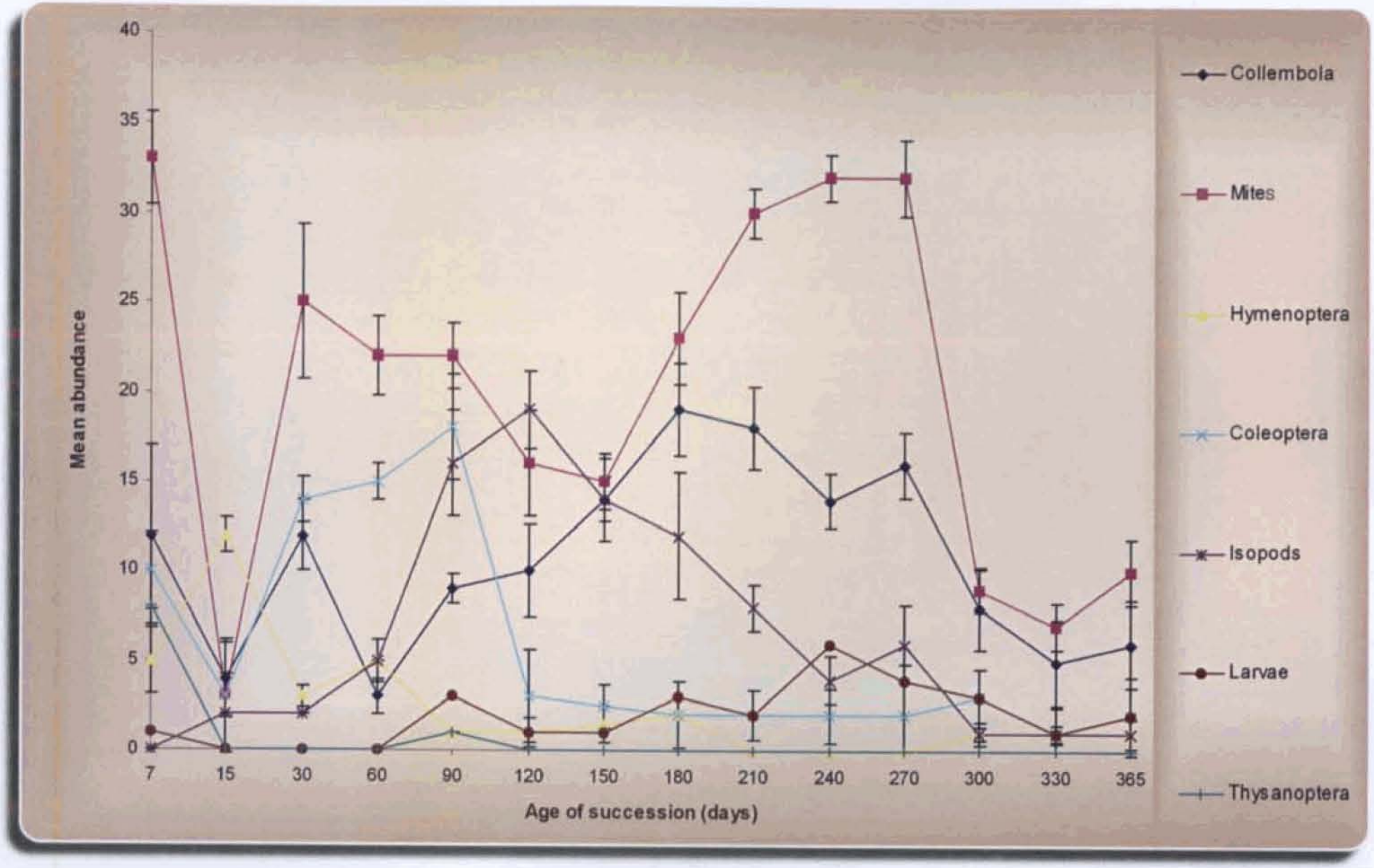


Figure.6. 2 Succession pattern of major arthropod fauna in litter bags at evergreen forest habitat

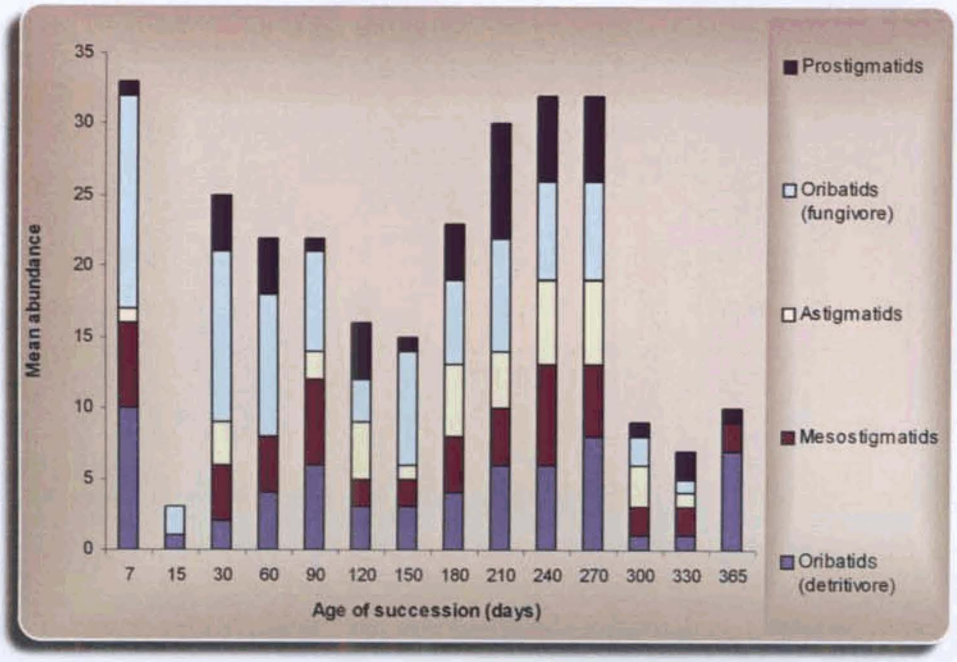


Figure.6.3 Abundance of mites during different stages of succession

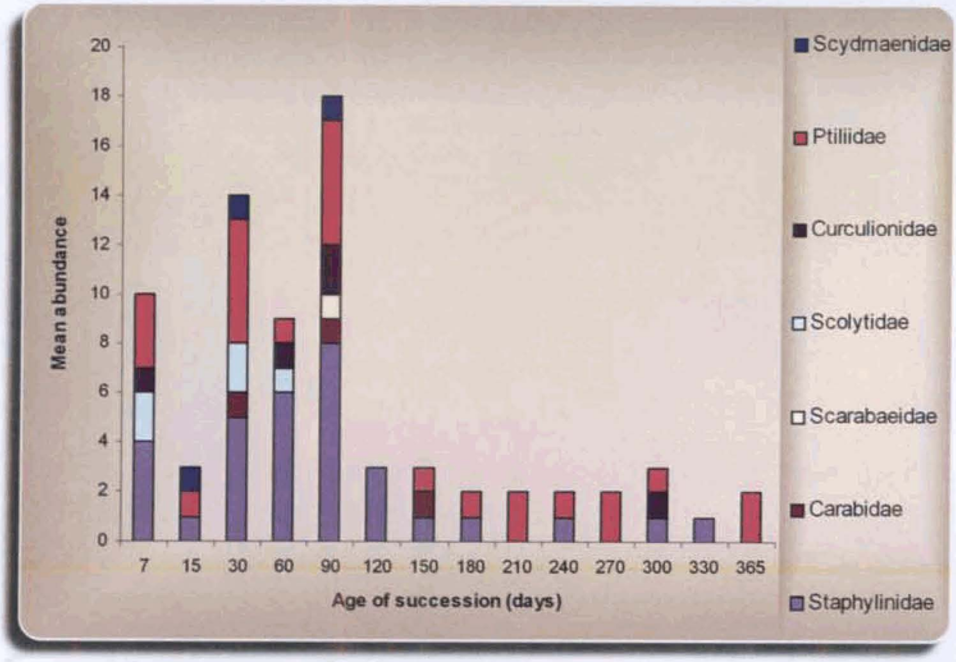


Figure.6.4 Abundance of Coleoptera during different stages of succession

96 D

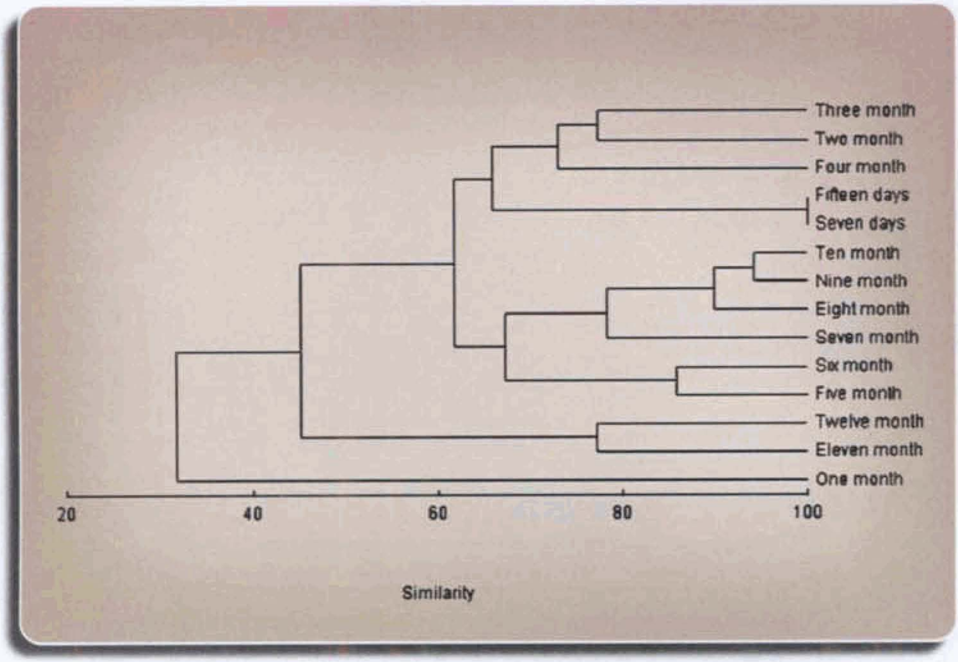


Figure.6.5 Dendrogram based on hierarchical agglomerative clustering (group-linking) of litter insect faunal assemblage during different months of succession of litter bags

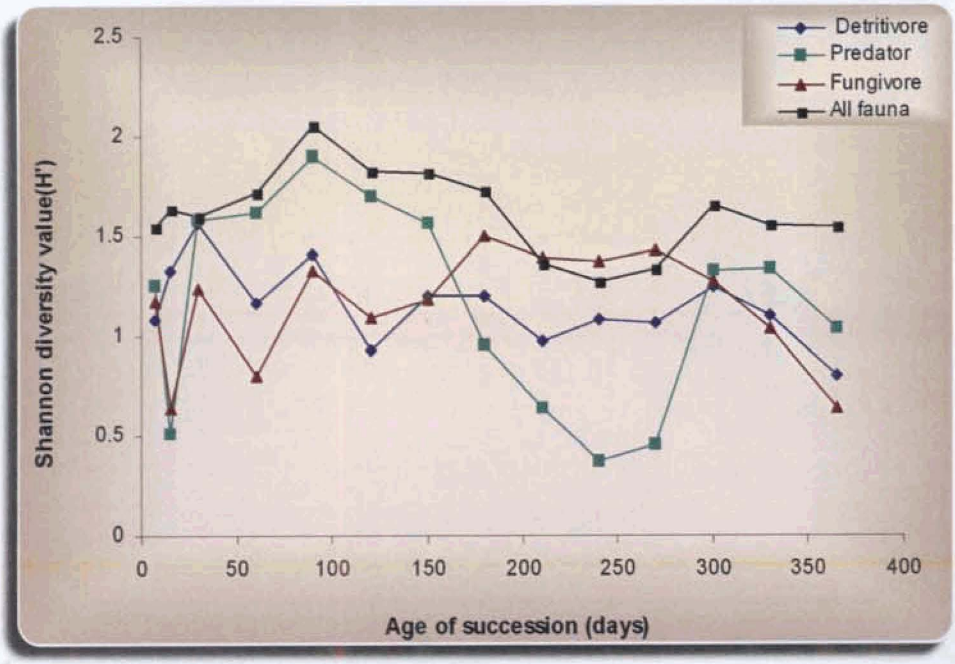


Figure.6.6 Diversity of guilds during different stages of succession

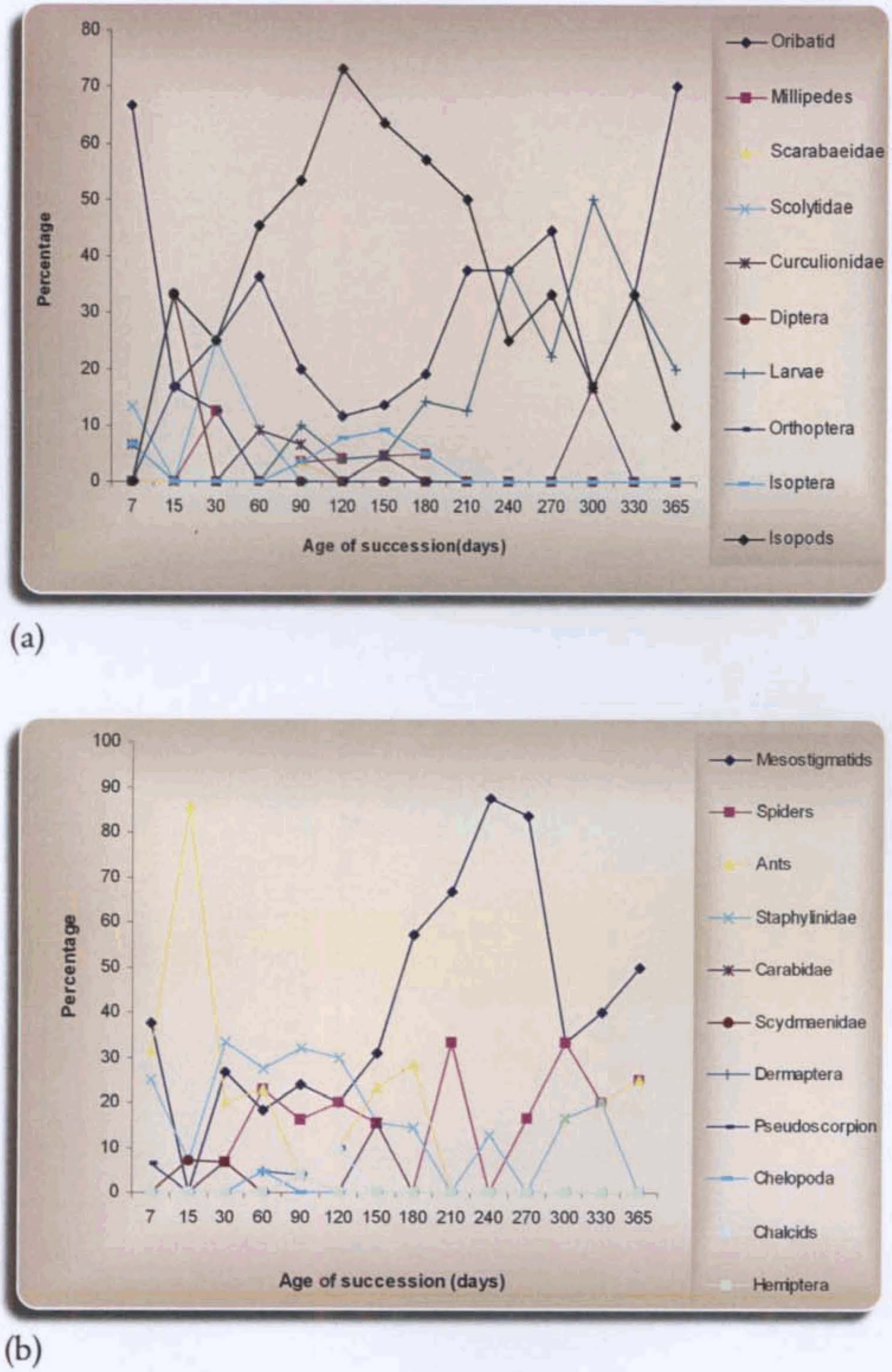
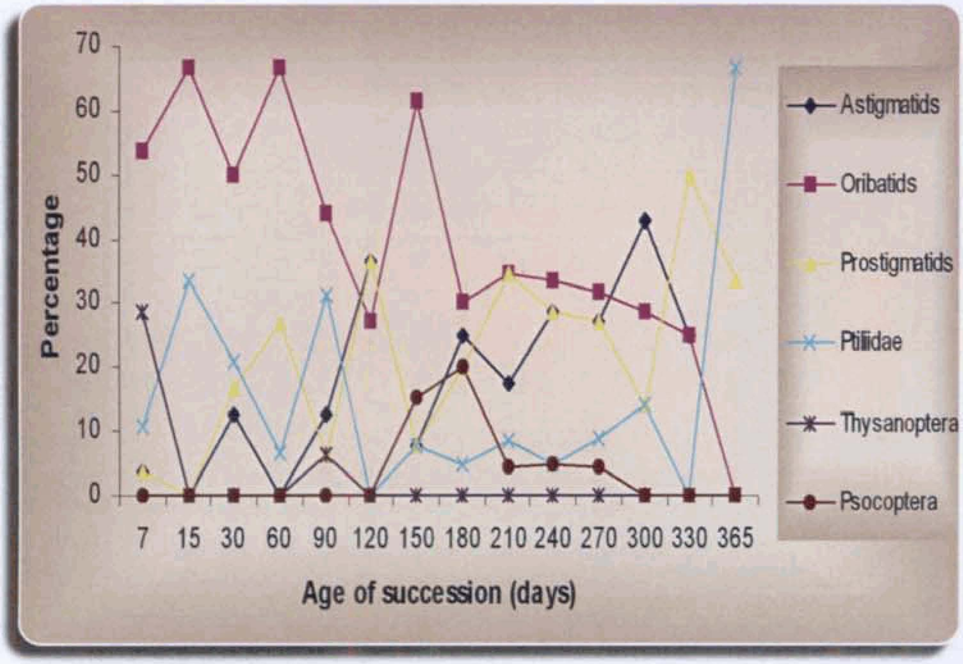
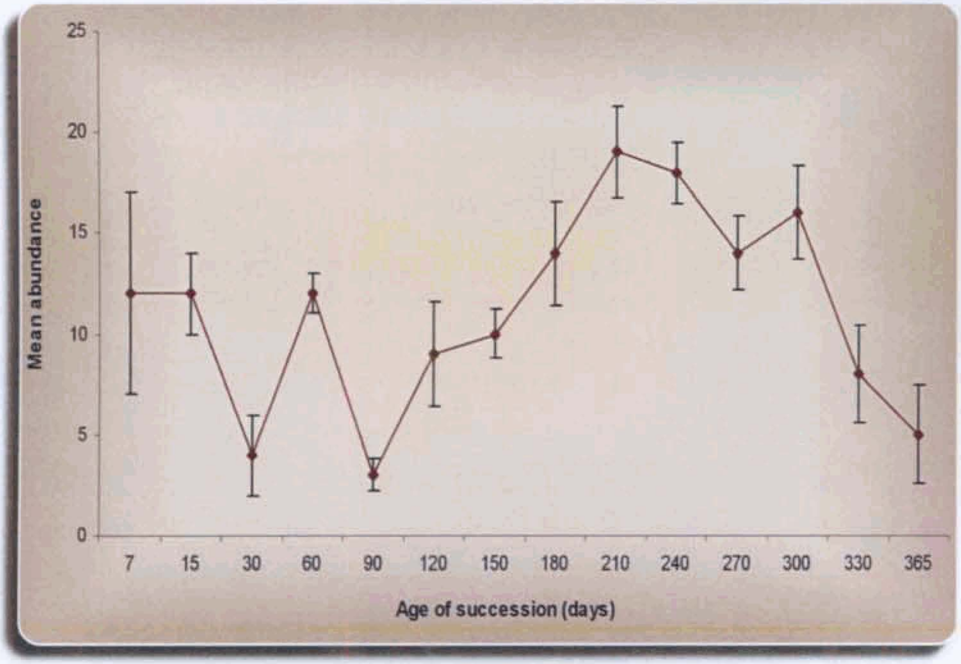


Figure.6.7 Abundance of different trophic groups during different stages of succession (a) detritivores and (b) predators



(c)



(d)

Figure.6.7 Abundance of different trophic groups during different stages of succession (c) fungivores and (d) microbidetritivorous Collembola

7. Conclusions

1. Data on the seasonal and layer wise distribution and diversity of litter insects in the wet evergreen forest of Wayanad were studied.
2. Ample evidence for the seasonal and layer wise variation in the quality of litter biochemical parameters also provided.
3. Species richness and checklist of the dung beetle fauna (Coleoptera: Scarabaeidae: Scarabaeinae) linked with the evergreen habitat is studied and a pictorial key of the collected dung beetle fauna provided.
4. Decomposition rates of the study habitat and its relationship with biochemical parameters of litter along with the insect assemblages associated were studied.

First time comprehensive insect faunal inventory in the wet evergreen rainforest of South Western Ghats showed the dominance of Coleopterans, Hymenopterans and Collembolans. Peaks of insect diversity were noticed during wet seasons, revealing a significant positive relation between insect diversity and rainfall. Significant seasonal variation in insect fauna was noticeable with Ptiliids (Coleoptera) dominating during pre-summer period and Psocopterans in the summer season. Fungivorous thrips and Psocopterans dominated the fresh layer; Coleopteran Ptiliids and Staphylinids dominated the fermentation and humus layers. Predatory Staphylinids and ants belonging to *Tapinoma* sp., *Strumigenys* sp., fungivorous Ptiliids, Thysanopterans and microbidetritivorous Collembolans were the dominant trophic categories during different seasons of the study period. The presence of two wet rainforests preferring ant genera *Acropyga* sp. and *Paratrechina* sp. exclusively in the evergreen forest is indicative of the influence of litter habitat conditions in determining the habitat preference of ants. First record of Carabids *Perigona nigriceps* and *Clivina* spp. from the wet evergreen forest of Wayanad were made in this study.

Checklist on dung beetle fauna of evergreen forests shows the existence of 29 species, all belonging to subfamily Coprinae comprising 4 tribes, Coprini, Onthophagini, Onitini and Oniticellini. Dominant tribe was Onthophagini with 16 species followed by Coprini comprising 6 species, tribe Onitini and Oniticellini with 3 species each. Of the 29 species reported, 4 are first record from South India; 6 species are endemic to South India of which 3 are endemic to Western Ghats including the 2, which are specific to Nilgiri Biosphere Reserve.

Significant seasonal variation in the chemical quality of freshly fallen litter and the F and H litter layers were recorded. As per both the litter quality indices (C: N and L: N), litter of high resource quality is shed during the monsoon seasons (northeast and southwest) and low quality during summer season. Peaks of insect diversity also coincide with wet seasons associated with high quality litter during these seasons. Fluctuations in Carbon, nitrogen, minerals and primary metabolites along layers showed depletion from L – H layers.

Litter decomposition rates of 2.94k/yr showed 99% decomposition after 574days, par with studies from other tropical forests. All nutrient concentrations decreased with decomposition. Release of N without net N accumulation, suggests that N was not a limiting factor for microorganisms because the initial N concentration in these litters was relatively high compared to other studies. Low incidence of Collembola during the early phases of succession, dominance of mites throughout the litterbags, preponderance of Isopods in the middle phase, abundance of detritivores and predators during 1st phase and fungivore dominance during middle phase are the features of litterbag succession studies. Though, there was little evidence of a trophic category being confined to a particular successional stage, detritivores were the prime trophic group in the litterbag as they more readily utilized herbaceous material with higher N content and lower content of structural polysaccharides.

LIST OF PLATES

LIST OF FIGURES

LIST OF TABLES

8. References

Aber, J.D. & Melillo, J.M. (1982) Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Canadian Journal of Botany*. 60, 2263-2269.

Adams, G. A. & Wall, D.H. (2000) Biodiversity above and below the surface of soils and sediments: linkages and implications for global change. *BioScience*. 50,1043-1048.

Aerts, R. (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*. 84, 597-608.

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

Aerts, R. & Chapin, F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*. 30,1–66.

Alvarez-Sanchez J. & R. Becerra Enríquez. (1996) Leaf decomposition in a Mexican Rain Forest. *Biotropica*. 28, 657-667.

Ananthakrishnan, T.N. (1996) *Forest Litter Insect Communities: Biology and Chemical Ecology*. New Delhi, Oxford & IBH.

Ananthakrishnan, T.N., Gopichandran, R. & Subramanian, V.R. (1993) Impact of chemical changes during decomposition of teak litter on the dynamics of natural insect communities at varying altitudes. *International Journal of Ecology and Environmental Sciences*. 18, 63-74.

Anderson, J.M. (1973) Carbon dioxide evolution from two temperate, deciduous woodland soils. *Journal of Applied Ecology*. 10(2), 361-378.

Anderson, J.M. (1975) Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *Journal of Animal Ecology*. 44, 475-195.

Anderson, J.M. (1978) Inter- and intra-habitat relationships between woodland *Cryptostigmata* species diversity and the diversity of soil and litter microhabitats. *Oecologia*. 32, 341-348.

Anderson, J.M. (1988) Spatiotemporal effects of invertebrates on soil processes. *Biology and Fertility of Soils*. 6, 216–27.

Anderson, J.M. (1991) The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications*. 1, 326-347.

Anderson, J.M. (1994) Functional attributes of biodiversity in land use systems. *In:* D.J. Greenland and I. Szabolcs (Eds.), *Soil resilience and sustainable land use*, CAB International, Wallingford, U.K. pp. 267-290.

Anderson, J.M. (1995) Soil organisms as engineers: Microsite modulation of macroscale processes. *In*: C.G. Jones and J.H. Lawton (Eds.), *Linking species and ecosystems*. Chapman and Hall, New York, USA. pp. 94-106.

Anderson, J.M. & Ingram, J.S.I. (1993) *Tropical soil biology and fertility: a handbook of methods*, second edition. C.A.B. International, Wallingford, UK, pp.221.

Anderson, J. M. & Swift, M. J. (1983) Decomposition in tropical forests. *In*: S. L. Sutton, T. C. Whitmore & A. C. Chadwick (Eds.), *Tropical rain* *forest: ecology and management.* Special Publication Series of the British Ecological Society, n. 2. Blackwell, Oxford, pp. 287-309. 498p.

Anderson, J.M., Proctor, J. & Vallek, H.W. (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf litter. *Journal of Ecology.* 71, 503-528.

Andresen, E. (2002) Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology.* 27,257-270.

Andresen, E. & Feer, F. (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. *In* P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. *Seed fate: predation, dispersal and seedling establishment.* CAB International, Oxon, UK.331-349 pp.

Arrow, G.J. (1931) *The fauna of British India, including Ceylon and Burma. Coleoptera, Lamellicornia, Part 3, Coprinae.* Taylor and Francis, London.

Arun, P.R. (2003) Butterflies of Siruvani Forests of Western Ghats, with notes on their seasonality. *Zoo's Print Journal.* 18(2), 1003–1006.

Arun, P.R. & Vijayan, V.S. (2004) Patterns in abundance and seasonality of insects in the Siruvani Forest of Western Ghats, Nilgiri Biosphere Reserve, Southern India. *The Scientific World Journal.* 4, 381–392.

Austin, A.T. & Vitousek, P.M. (2000) Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawaii. *Journal of Ecology*. 88,129–138.

Balthasar, V. (1963a) *Monographic der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region (Coleoptera: Lamellicornia)*, 1: pp.391, PI. XXIV. Verlag der Tschechoslowakischen Akademie der Wissenschaften. Prag.

Balthasar, V. (1963b) *Monographic der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region (Coleoptera: Lamellicornia)*, 2: pp. 627, PI. XVI. Verlag der Tschechoslowakischen Akademie der Wissenschaften. Prag.

Baraud, J. (1992) Coléoptères Scarabaeoidea d'Europe. *Faune de France* 78. 855pp., 11 plates. Lyon, Société Linnéene de Lyon.

Barrows, H.L. & Simpson, E.C. (1962) An EDTA method for direct routine determination of calcium and magnesium in soils and plant tissue. *Soil Science Society of America Journal.* 26, 443-445.

Bartholomew, W.V., Meyer, J. & Laudelout, H. (1953) Mineral nutrient immobilisation under forest and grass fallow in the yangambi region, with some preliminary results on decomposition of plant material on the forest floor. *Publ. Inst. Natn. Etude Agron. Congo Belge, Ser. Scient.* 57,27 pp.

Basset, Y. & Kitching. R. L. (1991) Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecological Entomology*.16, 391–402.

Basset, Y. (1991) The seasonality of arboreal arthropods foraging within an Australian rain forest tree. *Ecological Entomology* .16, 265-278.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: individuals, populations, and communities*, Third Edition. Blackwell Science Ltd., Cambridge, Massachusetts, USA.

Berg, B. (1986) Nutrient release from litter and humus in coniferous forest soils- a mini review. *Scandinavian Journal of Forest Research*. 1, 359-369.

Berg, B. (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*. 133, 13–22.

Berg, B. & Cortina, J. (1995) Nutrient dynamics in some decomposing leaf and needle litter types in a *Pinus sylvestris* forest. *Scandinavian Journal of Forest Research*. 10(1), 1-11.

Berg, B. & McClaugherty, C. (1987) Nitrogen release from litter in relation to the disappearance of lignin. *Biogeochemistry*. 4,219-224.

Berg, B. & Staaf, H. (1981) Leaching, accumulation and release of N_2 in decomposing forest litter. *Ecological Bulletin*. 33, 163-178.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., Deanta, R.C., Couteaux, M., Escudero, A., Gallardo, A., Kratz, W., Madeira. M., Malkonen, E., Mcclaugherty, C., Meentemeyer, V., Munoz, F., Piussi, P., Remacle. J. & Desanto. A.V. (1993) Litter mass-loss rates in pine forests of Europe and Eastern United-States - Some relationships with climate and litter quality. *Biogeochemistry*. 20,127-159.

Berg, B., McClaugherty, C., Virzo De Santo, A., Johansson, M.B. & Ekbohm, G. (1995) De-composition of forest litter and soil organic matter —a mechanism for soil organic matter buildup? *Scandinavian Journal of Forest Research*. 10, 108–119.

Biswas, S. & Chatterjee, S.K. (1986) Scarabaeidae (Coleoptera) of Silent Valley, Kerala, India, with description of three new species. Silent Valley special issue. *Records of the Zoological Survey of India*. 82 (1-4), 79-96.

Biswas, S. & Mulay, S.V. (2001) Fauna of Nilgiri Biosphere Reserve. Fauna of Conservation Area Series II. *Zoological Survey of India*.129-142.

Blackburn, T. M. & Gaston, K. J. (1996) Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society of London* B. 351, 897–912.

Bocock, K L. (1964) Changes in the amount of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. *Journal of Ecology*. 52, 273–284.

Bocock, K. L. & Gilbert, O. J. (1957) The disappearance leaf litter under different woodland conditions. *Plant and Soil*. 9, 179-185.

Bockheim, J.G, Jepson, E.A. & Helsey, D.M. (1991) Nutrient dynamics in decomposing leaf litter of four tree species in northern Wisconsin. *Canadian Journal of Forest Research.* 21,267–286.

Boinski, S. & Fowler, N.L. (1989) Seasonal patterns in a tropical lowland forest. *Biotropica.*21, 223–233.

Borror, D.J., De Long, D.M. & Triplehon, C.A. (1996) *An introduction to the study of insects.* Saunders Publication.

Bosatta, E. & Staaf, H. (1982) The control of nitrogen turnover in forest litter. *Oikos.* 29, 143-151.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, J.D., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Arachchi, M.K., Peter, K.L.N., Schneider, J.C., Oommen, V.O. & Milinkovitch, C.M. (2004) Local endemism within the Western Ghats. Srilanka biodiversity hotspot. *Science.* 306, 479-481.

Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs.* 27,325-349.

Brown, M.J.F. (1997) Effects of harvester ants on plant species distribution and abundance in serpentine grassland. *Oecologia.* 112,237–243.

Bruehl, C.A., Gusalam, G. & Linsenmair, K.E. (1998) Stratification of ants in rain forests of Borneo. *Journal of Tropical Ecology.* 14, 285-297.

Bryan, R. P. (1976) The effect of the dung beetle, *Onthophagus gazella*, on the ecology of the infective larvae of gastrointestinal nematodes of cattle. *Australian Journal of Agricultural Research.* 27,567–574.

Bryant, J.P., Chapin, F.S. III. & Klein, D.R. (1983) Carbon/nutrient balance of boreal plants in relation to herbivory. *Oikos*. 40,357-386.

Bubb, K.A., Xu, Z.H., Simpson, J.A. & Saffigna, P.G. (1998) In situ measurements of soil mineral-nitrogen fluxes in hoop pine plantation. p. 253–272 *In* G. Cadisch and K.E. Giller, (ed.) Driven by nature: Plant litter quality and decomposition. CAB International of subtropical Australia. *New Zealand Journal of Forestry Science*.28, 152–164.

Buskirk, R .E. & Buskirk, W.H. (1976) Changes in arthropod abundance in a highland Costa Rican forest. *American Midland Naturalist* .95(2), 288-298.

Cambefort, Y. & Hanski, I. (1991) Population biology, p.36-50. *In* I. Hanski & Y. Cambefort (Eds.), *Dung beetle ecology*. New Jersey, Princeton University Press, 481p.

Cameron, G. N. & Lapoint, T.W. (1978) Effects of tannins on decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. *Oecologia*. 32 (3), 349-366.

Caritat, A., Bertoni, G., Molinas, M., Oliva, A. & Dominguez Planella, A. (1996) Litter fall and mineral return in two cork-oak forest in northeast Spain. *Annals of Forest science*. 53, 1049- 1058.

Chapin, F. S., Matson, P.A. & Mooney, H.A. (2002) *Principles of Terrestrial Ecosystems*. Springer-Verlag, New York.9.

Chahartaghi, M., Langel, R., Scheu, S. & Ruess, L. (2005) Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biology and Biochemistry*. 37, 1718-1725.

Chatterjee, S. & Sastry, A.R.K. (2001) Biodiversity 'Hotspots' conservation programme of WWF-India, 479-483.

Cheng, W. (1999) Rhizosphere feedbacks in elevated CO_2. *Tree Physiology*.19, 313–320.

Chuyong, G.B., Newbery, D.M. & Songwe, N.C. (2000) Litter nutrients and retranslocation in a central African rain forest dominated by ectomycorrhizal trees. *New Phytologist*. 148, 493–510.

Clark, D. A., Piper, S. C., Keeling, C. D. & Clark, D. B. (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America*.100, 5852–5857.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*. 18, 117–143

Clarke, K.R. & Gorley, R.N. (2001) Primer v5. User manual/tutorial, PRIMER-E, Plymouth UK, 91pp.

Clarke, K.R. & Warwick, R.M. (1994) Similarity-based testing for community pattern: the 2-way layout with no replication. *Marine Biology*. 118, 167-176.

Clifford, H. T. & Stephenson, W. (1975) *An introduction to numerical classification*. Academic Press, New York. 229 pp.

Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*. 53, 209-233.

Collins, N.M. (1980) The distribution of soil macro fauna on the West range of Gaming (Mount) Mulu Sarawak. *Oecologia*. 44, 263-275.

Coleman, D.C., Reid, C.P.P. & Cole, C.V. (1983) Biological strategies of nutrient cycling in soil systems. *Advances in Ecological Research*. 13, 1-55.

Colwell, R.K. & Gotelli, N.J. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*. 4,379-391.

Connel, J.H. (1978) Diversity in Tropical Rain Forests and Coral Reefs. *Science*. 199, 1302-1310.

Cornelissen, J. & Thompson, K. (1997) Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytologist*. 135,109–14.

Cottrell, A. (2006) Gretl version 1.1 Gunu general public license department of Economics Wake Forest University. http://www.ecn.wfu.edu./gretl. Accessed on Jan 2006.

Co^uteaux, M. M., Bottner, P. & Berg, B. (1995) Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution*. 10,63–66.

Cragg, R.H. & Bardgett. R.D. (2001) How changes in animal diversity within a soil trophic group influence ecosystem processes. *Soil Biology and Biochemistry*. 33, 2073-2081.

Cromack, K. Jr. & Monk, C. D. (1975) Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and white pine watershed. *In*: Howell, F. G., Gentry, J. B. and. Smith, M. H. (Eds) *Mineral Cycling in Southeastern Ecosystems,* pp.609-624. US Energy Research and Development Admin. Symposium Series, CONF- 740613, Washington, DC.

Cuevas, E. & Lugo, A.E. (1998) Dynamics of organic matter and nutrient return from litter fall in stands of ten tropical tree plantation species. *Forest Ecology and Management*. 112, 263–279.

Cuevas, E. & Medina, E. (1986) Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in the litter fall and efficiency of nutrient utilization. *Oecologia*. 68, 466–472.

Davis, A.J. (1993) *The ecology and behaviour of rainforest dung beetles in northern Borneo*. Ph.D Thesis, University of Leeds, UK.

Davis, A.J. (1998) Dung Beetle abundance and diversity in the Maliau Basin, Sabah, Malaysian Borneo. *Malayan Nature Journal*. 52, 3 &4, 181-191.

Davis, A.J. (2000) Does reduced-impact logging help reserve biodiversity in tropical rainforest? A case study from Borneo using dung beetles (Coleoptera: Scarabaeoidea) as indicators. *Environmental Entomology*.29, 467-475.

Davis, A.J. & Sutton S.L. (1998) The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. *Diversity and Distributions*. 4, 167–173

Davis, A.J., Holloway, J.G., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H. & Sutton, S.L. (2001) Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology*. 38, 593-616.

Davis, A.J., Huijbregts, H. & Krikken, J. (2000) The role of local and regional processes in shaping dung beetle communities in tropical plantations in Borneo. *Global Ecology and Biogeography*. 9, 281-292.

DeAngelis, D. L. (1992) *Dynamics of nutrient cycling and food webs*. Chapman and Hall, New York, New York, USA.

Decaens, T.P., Lavelle, J. J., Jimenesjaen, G., Escobar & Rippstein, G. (1994) Impact of land management on soil macro fauna in oriental Llanos of Colombia. *European Journal of Soil Biology*. 30, 157-168

del Arco, J.M., Escudero, A. & Garrido, V.M. (1991) Effects of site characteristics on nitrogen retranslocation from senescing leaves. *Ecology*. 72(2), 701–708.

Didham, R. K., Hammond, P.M., Lawton, J.H., Eggleton, P. & Stork, N.E. (1998) Beetle species responses to tropical forest fragmentation. *Ecological Monograph* .68 (3), 295-323.

Dilly, O. & Irmler, U. (1998) Succession in the food web during decomposition of leaf litter in black alder (*Alnus glutinosa* (Gaertn L.)) forest. *Pedobiologia* .42, 109–123.

Doube, B. M. (1983) The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bulletin of Entomological Research.* 73,357–371.

Duräes, R., Waldney, P., Martins, W.P. & Vaz-De-Mello, F.Z. (2005) Ecology, Behaviour and Bionomics of Dung Beetle (Coleoptera: Scarabaeidae) Assemblages across a Natural Forest-Cerrado Ecotone in Minas Gerais, Brazil. *Neotropical Entomology.* 34 (5), 721-731.

Dziadowiec, H. (1987) The decomposition of plant litter fall in an oak linden-hornbeam forest and oak-pine mixed forest of the Bialowieza National Park. *Acta Societatis Botanicorum Poloniae.* 56,169-185.

Edwards, N. B., Reichle, D.E. & Crossley, D.A. (1970) The role of soil invertebrates in turnover of organic matter and nutrients. Pages 147–172 *In* D. E. Reichle, editor. *Analysis of temperate forest ecosystems.* Springer-Verlag, Berlin, Germany.

Edwards, C.A., & Bohlen, P.J. (1995) The effects of contaminants on the structure and function of soil communities. *Acta Zoologica Fennica.* 196, 284-289.

Edwards, C. A. & Heath, J.W. (1963) The Role of Soil animals in breakdown of leaf materials. *In*: *Soil Organisms* 76-78, (J. Doeksen and J. van der Drift Eds.), North-Holland Publishing Company, Amsterdam.

Elkins, N. Z. & Whitford, W. G. (1982) The role of micro arthropods and nematodes on decomposition in a semi-arid ecosystem. *Oecologia.* 55, 303-310.

Ellenberg, H., Mayer, R. & Schauermann, J. (1986) Ökosystem-forschung; Ergebnisse des Sollingprojektes 1966– 1986. Eugen Ulmer Verlag, 597 pp.

Epstein, E. (1972) *Mineral Nutrition of Plants: Principles and Perspectives.* John Wiley & Sons, Inc., New York.

Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin.* 36,74-75.

Erwin, T.L. (1995) Measuring arthropod biodiversity in the tropical forest canopy. *In*: Lowman MD, Nadkarni NM, Eds. *Forest Canopies.* San Diego: Academic Press, 109-126.

Ezhoe, H. (1995) Evolutionarily stable seasonal timing for insects with competition for renewable resources. *Evolutionary Ecology.* 9, 328–339.

Facelli, J. M. & Pickett, S.T.A. (1991) Plant litter: its dynamics and effects on plant community structure. *Botanical Review.* 57, 1-32.

Favila, M.E. & Halffter, G. (1997) The use of indicator groups for measuring biodiversity as related to community structure and function. *Acta Zoologica Mexicana.* 72, 1-25.

Field, J. G., Clarke, K.R. & Warwick, R.M. (1982) A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series.* 8,37-52.

Filser. J. & Fromm. H. (1995) The vertical distribution of Collembola in an agricultural landscape. *Polskie Pismo Entomologiczne*. 64. 99-112.

Fittkau. E.J. & Klinge, H. (1973) On biomass and trophic structure of a central Amazonian rainforest ecosystem. *Biotropica*. 5, 2-14.

Flanagan, P.W. & Van Cleve, K. (1983) Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. *Canadian Journal of Forest Research*. 13, 795-817

Floren. A. & Linsenmair K.E. (1994) Zur Diversität und Wiederbesiedlungsdynamik von Arthropoden auf drei Baumarten in einem Regenwald in Sabah, Malaysia. *Andrias Sonderband*.13, 23-28.

Fodgen, M.P.L. (1972) The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis*. 114,307-343.

Fog, K. (1988) The effect of added nitrogen on the rate of decomposition of organic matter. *Biological Reviews*. 63, 433–462.

Fonte. S.J. & Schowalter, T.D. (2004) Decomposition of green fall vs. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica*. 36 (4), 474-482.

Forests and Wildlife Department Working Plan. North Wayanad Division, Forests and Wildlife Department, Government of Kerala, India, 2001.

Frith. C.B. & Frith, D.W. (1985) Seasonality of insect abundance in Australian upland tropical rainforest. *Australian Journal of Ecology*. 10, 237–248.

Galante. E., García-Román, M., Barrera, I. & Galindo. P. (1991) Comparison of spatial Gases. *Global Change Biology*. 4,745-758.

Gallardo. A. &. Merino. J. (1992) Nitrogen immobilization in leaf litter at two Mediterranean ecosystems in SW Spain. *Biogeochemistry*. 12. 213–228.

Gaston. K. J. & Hudson. E. (1994) Regional patterns of diversity and estimates of global insect species richness. *Biodiversity Conservation*. 3. 493–500.

Giller. P. S. (1996) The diversity of soil communities, the 'poor man's tropical rainforest.' *Biodiversity and Conservation*. 5, 135–168.

Golley, F. (1983) Decomposition *In*: Ecosystems of the World 14A, *Tropical Rain Forest Ecosystems, Structure and Function*, edited by F.B. Golley, Elsevier Scientific Publishing Company, Amsterdam

Gonza'lez, G. & Seastedt, T. R. (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology*. 82, 955–964.

Graham, E. A., Mulkey, S.S., Kitajima, K., Phillips, N.G. & Wright, S.J. (2003) Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences, USA*. 100, 572-576.

Greenslade, P.J.M. & Greenslade, P. (1973) Epigaeic Collembola and their activity in a semi-arid locality in southern Australia during summer. *Pedobiologia*. 13, 227–235.

Greenslade, P.J.M. & Greenslade, P. (1984) Invertebrates and environmental assessment. *Environment and Planning*. 3, 13-15.

Grime, J.P., Cornelissen, J.H.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos*. 77,489–494.

Hågvar. S. (1998) The relevance of the Rio-Convention on biodiversity to conserving the biodiversity of soils. *Applied Soil Ecology*. 9. 1-7.

Hågvar. S. & Kjøndal, B. R. (1981) Succession, diversity and feeding habits of micro arthropods in decomposing birch leaves. *Pedobiologia*. 22, 385-408.

Halffter, G. & Favila, M. (1993) The Scarabaeinae (Insecta: Coleoptera) and animal group for analyzing, inventorying and monitoring biodiversity in tropical rain forest and modified landscapes. *Biology International*. 27, 15-21.

Halffter, G. & Mathews, E.G. (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana*.v.12/14, 1-312.

Halffter, G., Favila, M.E. & Halffter, V. (1992) A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomologica Mexicana*. 84, 131-156.

Hammer, Ø, Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*. 4: 9pp. http://palaeoelectronica.org/2001_1/past/issue1_01.htm

Hanlon, R. D. G. & Anderson, J.M. (1979) The effects of Collembola grazing on microbial activity in decomposing leaf litter. *Oecologia*. 38, 93-99.

Hansen, R.A. (2000) Effects of habitat complexity and composition on a diverse litter micro arthropod assemblage. *Ecology*. 81, 1120-1132.

Hansen, R.A. & Coleman, D.C. (1998) Litter complexity and composition are determinants of the diversity and species composition of Oribatid mites (Acari: Oribatida) in litter bags. *Applied Soil Ecology*. 9, 17-23.

Hanski, I. & Cambefort, Y. (1991) *Dung beetle ecology*. Princeton University Press, 481p.

Hassall, M., Visser, S. & Parkinson, D. (1986) Vertical migration of Onychiurus subtenuis (Collembola) in relation to rainfall and microbial activity. *Pedobiologia*. 29, 175–182.

Hasegawa, M. & Takeda, H. (1995) Changes in feeding attributes of four collembolan populations during the decomposition process of pine needles. *Pedobiologia*. 39, 155-169.

Hättenschwiler, S. (2005) Effects of tree species diversity on litter quality and decomposition. *In*: Scherer-Lorenzen M, Körner Ch, Schulze E-D (Eds) Forest diversity and function: temperate and boreal systems. *Ecological Studies*. Vol 176. Springer, Berlin Heidelberg New York, pp. 149-164.

Hättenschwiler, S. & Vitousek, P.M. (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology and Evolution*. 15, 238-243.

Hättenschweiler, S., Hagermann, A.E. & Vitousek, P.M. (2003) Polyphenols in litter from tropical montane forests across a wide range in soil fertility. *Biogeochemistry*. 64, 129–148.

Hättenschwiler. S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Reviews of Ecology, Evolution and Systematics*. 36, 191-218.

Heal, O. W., Anderson, J.M. & Swift, M.J. (1997) Plant litter quality and decomposition: An historical overview. *In* G. Cadisch and K. E. Giller (Eds.). *Driven by nature: Plant litter quality and decomposition*, pp. 3–30.CAB International, Wallingford, England.

Heath, G.W., Arnold, M.K. & Edwards, C.A. (1966) Studies in leaf litter breakdown. I. Breakdown rates of leaves of different species. *Pedobiologia*. 6, 1-12.

Heneghan, L., Coleman, D.C., Zou, X., Crossley, Jr.D.A. & Haines.B.L. (1998) Soil micro arthropod community structure and litter decomposition dynamics: a study of tropical and temperate sites. *Applied Soil Ecology*. 9, 33-38.

Heneghan, L., Coleman, D.C., Zou,X., Crossley, JR.D.A. & Haines, B.L. (1999) Soil microarthropod contributions to decomposition dynamics: Tropical –Temperate comparisons of a single substrate. *Ecology*. 80 (6), 1873-1882.

Hijii, N. (1987) Seasonal changes in abundance and spatial distribution of the soil arthropods in a Japanese Cedar (*Cryptomeria japonica* D. Don) plantation, with special reference to Collembola and Acarina. *Ecological Research*. 2, 159–173.

Hirabuki. Y. (1991) Heterogeneous dispersal of tree litter fall corresponding with patchy canopy structure in a temperate mixed forest. *Vegetatio*. 94, 69-79.

Hoekstra, J.M., Bell, R.T., Launer, A.E. & Murphy, D.D. (1995) Soil arthropod abundance in coast redwood forest: effect of selective timber harvest. *Environmental Entomology*. 24, 246–252.

Holdridge. L. R. (1967*) Life Zone ecology*. Tropical Science Center. San Jose. Costa Rica.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., Van Der Putten, W.H., De Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M. & Wolters, V. (2000) Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms and Feedbacks. *Bioscience*. 50 (12), 1049-1061.

Hopkins, B. (1978) Decomposition and biogeochemical cycles. *In Tropical Forest Ecosystems,* a *state-of-knowledge report*. UNESCO/UNEP/FAO, Natural resources research XIV, Paris. 270-285 pp.

Horgan, F.G. (2002) Shady field boundaries and colonization of dung by coprophagous beetles in Central American pastures. *Agriculture, Ecosystems and Environment*.92, 25-39.

Hughes, R. G. (1986) Theories and models of species abundance. *American Naturalist*. 128,897-899.

Huhta. V.. Persson. T. & Setälä, H. (1998) Functional implications of soil fauna diversity in boreal forests. *Applied Soil Ecology*. 10.277–288.

Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology. 52, 577-586.

Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C.. Rose, S.L., Reid, C.P.P. & Morley, C.R. (1987) The detrital food web in a short grass prairie. *Biology and Fertility of Soils*. 3, 57-68.

Huston, M.A. (1994) *Biological diversity – the coexistence of species on changing landscape*. Cambridge University Press, Cambridge, UK.

Hyvönen, R. & Persson, T. (1996) Effects of fungivores and predatory arthropods on nematodes and tardigrades in microcosms with coniferous forest soil. *Biology and Fertility of Soils*. 21, 121-127.

Iiyama, K. & Wallis, A.F.A. (1990) Determination of lignin in herbaceous plants by an improved acetyl bromide procedure. *Journal of the Science of Food and Agriculture*.51, 145–61.

Irmler, U. (2000) Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. *Pedobiologia*. 44, 105-118.

Jackson M. L. (1958) Soil chemical Analysis. Constable, London. 498 pp.

Jackson, R.B., Schenk, H.J., Jobbágy, E.G., Canadell, J., Colello, G.D., Dickinson, R.E., Field, C.B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Kleidon, A., Neilson, R.P., Parton, W.J., Sala, O.E. & Sykes, M.T. (2000) Belowground consequences of vegetation change and their treatment in models. *Ecological Applications.* 10,470-483.

Jamaludheen, V. & Kumar, B. M. (1999) Litter of nine multipurpose trees in Kerala, India-variations in the amount, quality, decay rates and release of nutrients. *Forest Ecology and Management.* 115, 1-11.

Jansen, D. H. (1983) Seasonal change in abundance of large nocturnal dung beetles (Sacarabaeidae) in Costa Rican deciduous forest and adjacent horse pasture. *Oikos.* 41, 274–283.

Janzen, D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day and insularity. *Ecology.* 54(3), 687-708.

Janzen, D.H. (1987) Insect diversity of a Costa Rican dry forest: why keep it and how? *Biological Journal of Linnaean Society.* 30,343–356.

Jenny, H., Gessel, S.P. & Bingham, F.T. (1949) Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Science.* 68, 419-432.

Jha, C.S., Dutt, C.B.S. & Bawa, K.S. (2000) Deforestation and land use changes in Western Ghats, India. *Current Science.*79 (2), 231-238.

Jobbágy E. G. & Jackson, R.B. (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications.* 10, 423-436.

Johnson, R.A. & Wichern, D.W. (1992) *Applied multivariate statistical analysis.* Third Edition. Prentice Hall, Englewood Cliffs, NJ.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*. 69, 373-386.

Kai. H.K.& Corlett, T.R. (2002) Seasonality of forest invertebrates in Hong Kong, South China. *Journal of Tropical Ecology*. 18, 637-644.

Kaneko, N. & Salamanca, E.F. (1999) Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecological Research*. 14, 131-138.

Kaneko, N., McLean, M.A. & Parkinson, D. (1995) Grazing preference of *Onychiurus subtenuis* (Collembola) and *Oppiella nova* (Oribatei) for fungal species inoculated on pine needles. *Pedobiologia*. 39, 538 – 546.

Kantarcõ, M.D. (1978) Aladağ kütlesinin (Bolu) kuzey alanlarindaki Uludağ gőknar ormanlarinda yükselti-iklim kusaklarina gore bazi ölü örtü ve toprak özelliklerinin analitik olarak araşturilmasi. *Istanbul Űniv. Orman Fakültesi Dergisi. Seri-A,* 28, 60-116.

Karaöz, M.Ö. (1991) Atatürk Arboretumu'ndaki Bazı İğne Yapraklı Plantasyonlarda Ölü Örtünün Kimyasal Özellikleri Üzerine Araştırmalar. *Istanbul Űniv. Orman Fakültesi Dergisi, Seri A, C.41, Sayı 2, Sayfa* 68-86.

Karaöz, M.Ö. (1993) Bazı Yerli ve Yabancı Ağaç Türlerine Ait Plantasyonlarda Ölü Örtü Miktarı İle Bunlardaki Besin Maddesi Rezervleri Üzerine Araştırmalar. *Istanbul Űniv. Orman Fakültesi Dergisi,* Seri A, C.43, Sayı 1,Sayfa 93-115.

Kato. M.. Inoue. T.. Hamid. A.A., Nagamitsu. T.. Ben. M.M.. Nona. A.R., Itino. T., Yamane, S., Yumoto. T. & Merdek. M.B. (1995) Seasonality and vertical structure of light attracted insect communities in a dipterocarp forest in Sarawak. *Researches on Population Ecology*. 37, 59–79.

Kayang. H., Sharma, G.D. & Mishra, R.R. (1994) Effect of an isopod grazing *Burmoniscus sp.*) upon microbes and nutrient release from the decomposing leaf litter of *Alnus nepalensis* D. Don. *European Journal of Soil Biology*.30, 11-15.

Kayang, H., Sharma, G. D. & Mishra, R. R. (1996) The influence of isopod grazing on microbial dynamics in decomposing leaf litter of Alnus nepalensis D. Don. *European Journal of Soil Biology*. 32 (1), 35-39.

Keenan, R.J., Prescott, C.E., Kimmins, J.P., Pastor, J. & Dewey, B. (1996) Litter decomposition in western red cedar and western hemlock forest on northern Vancouver Island, British Columbia. *Canadian Journal of Botany*. 74, 1626-1634.

Khanna, P.K. & Ulrich, B. (1991) Ecochemistry of Temperate Deciduous Forests. In: E. Röhrig and B.Ulrich (Eds.) Ecosystems of the World 7, 'Temperate Deciduous Forests', Elsevier, 121 - 163.

Khiewtam, R. & Ramakrishnan, P.S. (1993) Litter and fine root dynamics of relict sacred grove forest of Cherrapunji in North-Eastern India. *Forest Ecology and Management*, 60,327-44.

Klein. B.C. (1989) Effect of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology*. 70. 1715-1725.

Klinge. H. (1977) Preliminary data on nutrient releases from decomposing leaf litter in a Neotropical rain forest. *Amazoniana*. 6,193-202.

Kremen. C., Colwell. R.K., Erwin. T.L., Murphy. D.D., Noss. R.F. & Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*. 7, 796-808.

Kumar, M.B. & Deepu, J.K. (1992) Litter production and decomposition dynamics in moist deciduous forests of the Western Ghats in Peninsular India. *Forest Ecology and Management*. 50,181-201.

Laakso, J. & Setälä, H. (1999). Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos*. 87,57-64.

Lagerloef, J. & Andren, O. (1985) Succession and activity of microarthoropods and enchytraeids during barley straw decomposition. *Pedobiologia*. 28, 343-357.

Lasebikan, B.A. (1988) Studies in soil fauna in Africa: current status and prospects. *Journal of African Zoology*. 102,301–311.

Laskowski, R., Niklinska, M. & Maryanski. M. (1995) The Dynamics of Chemical Elements in Forest Litter. *Ecology*. 76, 1393-1406.

Laudelout. H. & Meyer, J. (1954) Les cycles d'éléments minéreaux et de matière organique en forêt equatoriale congolaise. *Actes et comptes rendus du V Congress intern. Sci. Sol. Léopolduille,* 2. 267-272.

Laurance. W. F. (1998) Forest fragmentation: another perspective. *Trends in Ecology and Evolution.* 11,75.

Laurance. W. F. (1999) Gaia's lungs: Are rainforests inhaling earth's excess carbon dioxide? *Natural History* (April). p. 96

Lavelle. P., Blanchart. E., Martin, A., Spain. A.V., Toutain F., Barois, I. & Scaefer, R., A. (1993) Hierarchical model for decomposition in terrestrial ecosystems: application to soils of humid tropics. *Biotropica.* 25, 135-150.

Lavelle P., Bignell D., Lepage M., Wolters V., Roger P., Ineson P.et al. (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal Soil Biology*. 33, 159–193.

Lavelle, P., Barros, E., Blanchart, E., Brown, G., Desjardins, T., Mariani, L. & Rossi. J. (2001) SOM management in the tropics: Why feeding the soil macro fauna? *In*: Martius C. et al. (Eds), *Management of Organic Matter in tropical Soils: Scope and Limitations*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 53–61.

Lawrence, G.B., David, M.B., Bailey, S.W. & Shortle, W.C. (1997) Assessment of soil calcium in red spruce forests in the northeastern United States. *Biogeochemistry*. 38,19–39.

Lawrence, K. L. & Wise, D.H. (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia*. 44, 33-39.

Lee, K. E. & Pankhurst, C. E. (1992) Soil organisms and sustainable productivity; *Australian Journal of Soil Research*. 30, 855–892.

Lensing, J.R., Todd, S. & Wise, D.H. (2005) The impact of altered precipitation on spatial stratification and activity-densities of springtails (Collembola) and spiders (Araneae). *Ecological Entomology*. 2, 194-200.

Levings, S.C. & Windsor, D.M. (1985) Litter arthropod populations in a tropical deciduous forest: relationships between years and arthropod groups. *Journal of Animal Ecology*. 54,61-69.

Linsenmair, K.E. (1990) Tropische Biodiversität: Befunde und offene Probleme. *Verhandlungen der Deutschen Zoologischen Gesellschaft (Stuttgart)*. 83, 245-261.

Linsenmair, K.E. (1997) Biodiversity and sustainable management of tropical litter types in a *Pinus sylvestris* Forest. *Scandinavian Journal of Forestry Research*. 10,1-11.

Lobo, J.M, Martin Piera, F. & Veiga, C.M. (1988) Las trampas pitfall con cebo, sus posibilidades en el estudio de Scarabaeoidea (Col.). I. Caracteristicas determinantes de su capacidad de captura. *Revue D Ecologie et De Biologie Du Sol*. 25, 77-100.

Lodge, D.J., McDowell, W.H. & McSwiney, C.P. (1991) The importance of nutrient pulses in tropical forests. *TREE*. 9(10), 384–387.

Loranger. G., Ponge, J.F., Imbert D. et al. (2002) Leaf decomposition of litter in two semi-evergreen tropical forests: influence quality. *Biology and Fertility of Soils*.35,247-252

Lumaret. J.P. & Kirk, A.A. (1991) South temperate dung beetles. pp 97-115 *In* I. Hanski, & Y. Cambefort (Eds.). *Dung Beetle Ecology*. Princeton University Press, Princeton, New Jersey.

Luxton, M. (1982) The biology of mites from beech woodland soil. *Pedobiologia*. 23, 1-8

Mac Arthur, R.H. (1969) Patterns of communities in the tropics. *In* R.H.Lowe-McConnel (Ed.). *Speciation in tropical environments*. Academic press. London.

Madge, D. S. (1965) Leaf fall and litter disappearance in a tropical forest. *Pedobiologia*. 5,273–288.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing. 256 p.

Maity, S.K. & Joy, V.C. (1999) Impact nutritional chemical compounds of leaf litter on detritivore soil arthropod fauna. *Journal of Ecobiology*. 11,193–202.

Marinoni. R.C. & Ganho, N.G. (2003) Fauna de Coleoptera no Parque Estadual de Vila Velha, Ponta Grossa, Paraná, Brasil. Abundância e riqueza das famílias capturadas através de armadilhas malaise. *Revista Brasileira de Zoologia*. 20 (4), 727-736.

Martín A., Rapp, M., Regina, S I. & Gallardo. J.F. (1994) Leaf litter decomposition dynamics in some Mediterranean deciduous oaks. *European Journal of Soil Biology*. 30. 119-124.

Martin, A., Gallardo, J.F. & Santa Regina. I. (1996) Aboveground litter production and bioelement potential return in an evergreen oak (*Quercus rotundifolia*) woodland near Salamanca (Spain). *Annals of Forest Sciences*. 53, 811-818.

Martin, A., Gallardo, J.F. & Santa Regina, I. (1997) Long-term decomposition process of leaf litter from *Quercus pyrenaica* forest across a rainfall gradient. *Annals of Forest Sciences*. 54, 191-202.

Mathew, G. (2004) *Biodiversity Documentation for Kerala.Part.7: Insects*. KFRI Handbook No. 17.

McAlecee, N., Lambshead, P. J. D., Paterson, G. L. J. & Gage, J. D. (1997) Biodiversity Professional (software). Beta-Version. The Natural History Museum and The Scottish Association for Marine Sciences.

McGrath, D.A., Comerford, N.B. & Duryea, M.L. (2000) Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agro forest. *Forest Ecology and Management*. 131(13), 167–181.

Meetenmeyer, V. (1978) Macroclimate and lignin control of decomposition rates. *Ecology*. 59, 465-472.

Melillo, J.M., Aber, J.D. & Uratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*. 63, 621-626

Meiwes. K. J. & Beese, F. (1988) Ergebnisse der Untersuchung des Stoffhaushaltes eines Buchenwaldökosystems auf Kalkgestein. Berichte des Forschungszentrums Waldökosysteme. Reihe B, Göttingen 9, 1-141.

Mittal, J.P. (1993) The changing pattern of livestock farming in arid environments. *In*: Cincotta, R.P. and Pangare G. (Eds) *Pastoralism and Pastoral Migration in Gujarat*. Institute of Rural Management, Anand, India.

Monties, B. (1989) *Lignins. In. Methods in Plant Biochemistry*. Volume 1. Plant Phenolics Edited by Harborne, J.B.4, 113-157.

Moore, J.C., Walter, D.E. & Hunt, H.W. (1988) Arthropod regulation of micro- and mesobiota in below –ground detrital food webs. *Annual review of Entomology*. 33, 419-439.

Murali, K. S. & Sukumar, R. (1993) Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. *Oecologia*. 94, 114–119.

Myers, N. (1988) Threatened biota's: 'hotspots' in tropical forests. *Environmentalist*. 8, 187-208

Myers, R.J.K., Palm, C.A. & Cuevas, E. (1995) The synchronization of nutrient mineralization and plant nutrient demand. *In:* The Biological Management of Tropical Soil Fertility (Eds Woomer PL, Swift MJ). pp. 81–116.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*. 403, 853-858.

Nair, S.C. (1991) The Southern Western Ghats: a biodiversity conservation plan. Indian National trust for art and cultural heritage. (ed. Jayal ND). *Studies in ecology and sustainable development.* Volume 4.

Nair, K.S. (1999) Some generalizations based on faunistic studies in Silent Valley. *In*: Manoharan, T.M., Biju, S.D., Nayar, T.S. and Easa, P.S. (Eds). *Silent valley: whispers of reason.* Kerala Forest Department. 277-283 pp.

Nambiar, E.K.S. & Fife, D.N. (1991) Nutrient retranslocation in temperate conifers. *Tree Physiology.* 65, 185–207.

Nealis, V.G. (1977) Habitat associations and community analysis of south Texas dung beetles (Coleoptera: Scarabaeinae). *Canadian Journal of Zoology.* 55, 138–147.

Newbery, D.M., Alexander, I.J. & Rother J.A. (1997) Phosphorus dynamics in lowland African rain forest: The influence of ectomycorrhizal trees. *Ecological Monographs.* 67(3), 367–409.

Nummelin, M. & Hanski, I. (1989) Dung beetles of the Kibale Forest, Uganda; comparison between virgin and managed forests. *Journal of Tropical Ecology.* 5, 349–352.

Ollinger, S., Smith, M., Martin, M., Hallett, R., Goodale, C. & Aber, J. (2002) Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology.* 83,339–355.

Olson, J.S. (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology.* 44, 322–332.

Orchard, V.A. & Cook, F.J. (1983) Relationship between soil respiration and soil moisture. *Soil Biology and Biochemistry*. 15,447-453.

Paine, R.T. (1996) A conversation on refining the concept of keystone species. *Conservation Biology*. 9, 962–964.

Palm, C.A. & Sanchez, P.A. (1990) Decomposition and nutrient release patterns of the leaves of three tropical legumes. *Biotropica*. 22, 330–338.

Parker, G.A. & Courtney, S.P. (1983) Seasonal incidence: adaptive variation in the seasonal timing of life history stages. *Journal of Theoretical Biology*. 105, 147–155.

Pascal, J.P. (1988) *Wet Evergreen Forests of the Western Ghats of India: Ecology, Structure, Floristic Composition and Succession.* French Institute, Pondicherry.

Pascal, J.P. (1991) Floristic composition and distribution of evergreen forests in the Western Ghats, India. *Palaeobotanist*. 39(1), 110-126.

Pastor, J., Aber, J.D., McClaugherty, C.A. & Melillo, J.M. (1984) Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*. 65, 256-268.

Peck, S.B. & Forsyth, A. (1982) Composition, structure and competitive behaviour in a guild of Eucadorian rainforest dung beetles (Coleoptera: Scarabaeidae). *Tropical Zoology*.60, 1624-1634.

Pereira, A.P., Graca, M. & Molles. M. (1998) Leaf litter decomposition in relation to litter physico-chemical properties, fungal biomass, arthropod colonization, and geographical origin of plant species. *Pedobiologia*. 42, 316-327.

Pfeiffer, W.J. (1996) Litter invertebrates. In: Regan, D.P., Waide. R.B. (Eds.), The food web of a tropical rain forest. The University of Chicago Press, Chicago and London, pp. 137- 183.

Perez- Harguindeguy, N., Diaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido, M. & Castellanos, A. (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil*. 218(1/2), 21-30.

Peterson, H. & Luxton, M. (1982) A comparative analyses of soil fauna population and their role in decomposition processes. *Oikos*. 39, 287–388.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* .13,131-144.

Pielou, E.C. (1975) *Ecological Diversity*. Wiley Interscience New York, USA.

Plowman, K.P. (1979) Litter and soil fauna of two Australian subtropical forests. *Ausralian Journal of Ecology*. 4, 87–104.

Pragasan, L.A. & Parthasarathy, N. (2005) Litter production in tropical dry evergreen forests of south India in relation to season, plant life-forms and physiognomic groups. *Current Science*. 88, 8.

Prescott, C.E. (1996) Influence of forest floor type on rates of litter decomposition in microcosms. *Soil Biology Biochemistry*. 28, 1319-1325.

Rai, S.N. & Proctor, J. (1986) Ecological studies on four rainforests in Karnataka, India, II. Litter fall; *Journal of Ecology*. 74, 455-463.

Rapp, M. & Leonardi, S. (1988) Evolution de la litiere au sol au cours d'une annee dans un taillis de chene vert (Quercus ilex). *Pedobiologia*. 32,177-185.

Rashid, G. H. & Schaefer, R. (1988) Seasonal variation in the nitrogen mineralization and mineral nitrogen accumulation in two temperate forest soils. *Pedobiologia*. 31,381-390.

Rawat, G.S., Desai, A., Somanathan, H. & Wikramanayake, E.D. (2001) South Western Ghats montane rain forests (IM0151) Available from http://worldwildlife.org/wildworld/profiles/terrestrial/im/im0151_full.html. (Date of Access: July 2006).

Reddy, M.V. & Venkataiah, B. (1989) Influence of microarthropod abundance and climatic factors on weight loss and mineral nutrient contents of *Eucalyptus* leaf litter during decomposition. *Biology and Fertility of Soils*. 8, 319–324

Regina, C.C., Luiza, O, Fla Vio J. Luiza, O., Romilda, Q., Pai Vaw, Terezinha F. Momteirow, Lucine, I.A.S., Sousza. & Bartkruijt. (2004) Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Global Change Biology*. 10, 592–600.

Ribeiro, E. F. & Schubart, H. O. R. (1989) Oribatídeos (Acari: Oribatida) colonizadores de folhas em decomposição sobre o solo em três sítios florestais da Amazônia Central. *Bol. Mus. Emílio Goeldi,* 5(2), 243-276.

Richardson, D.M., MacDonald, I.A.W., Hoffmann, J.H. & Henderson, L. (1997) Alien plant invasions. *In* R.M. Cowling, D.M. Richardson and S.M. Pierce, Editors. *Vegetation of Southern Africa.* Cambridge University Press, Cambridge, UK, 535-570 pp.

Ricklefs, R. E. (1975) Seasonal occurrence of night-flying insects on Barro Colorado Island Panama Canal Zone. *Journal of New York Entomological Society.* 83, 19- 32.

Robinson, C. T. & Gessner, M. O. (2003) Litter decomposition. - *In*: Ward, J. V. and Uehlinger, U. (Eds.), *Ecology of a glacial flood plain.* Kluwer, pp. 217-230.

Rodgers, W. A. & Panwar, H. S. (1988) Planning a wildlife-protected areas network in India. *Department of Environment, Forests and Wildlife/Wildlife Institute of India report.* Wildlife Institute of India, 1-2.

Rosenstock, S.S. (1998) Influence of Gambel Oak on breeding birds in ponderosa pine forests of northern Arizona. *Condor.*100,485-492.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time.* Cambridge University Press, New York, 436 pp.

Rustad, L.E., & Cronan, C.S. (1988) Element loss and retention during litter decay in a red spruce stand in Maine. *Canadian Journal of Forest Research.* 18, 947–953.

Sabu, K.T. (2005) *Litter insect dynamics with special reference to ecological succession and chemical ecology along varying altitudes in the Wynad and Coorg forests of Western Ghats*. Project report submitted to Ministry of Environment and Forests, Govt. of India.

Sachs, L. (1992) *Angewandte Statistik*. Springer, Heidelberg.

Sah, J.G. (1990) *Nutrient and biomass patterns of willow* (*Salix* spp.) *clones as affected by fertilization and spacing in a wood-grass energy plantation system in New York*. PhD thesis, SUNY-ESF, Syracuse, NY. 289 pp

Santiago, L. S., Kitajima, K., Wright, S. J. & Mulkey, S. S. (2004) Coordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest. *Oecologia*. 139,495–502.

Santos, P.F., Phillips, J. & Whitford, W.G. (1981) The Role of mites and nematodes in early stages of buried litter decomposition in a desert. *Ecology*. (Washington D C) 62 (3), 664-669.

Sariyildiz, T. & Anderson, J.M. (2005) Variation in the chemical composition of green leaves and leaf litters from three deciduous tree species growing on different soil types. *Forest Ecology and Management*. 210, 303–319

Scha¨dler, M. & Brandl, R. (2005) Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biology and Biochemistry*.37, 329–337.

Scheffler, P.Y. (2002) *Dung beetle (Coleoptera: Scarabaeidae) ecology in the intact and modified landscape of Eastern Amazonian.* Pennsylvania. USA: The Pennsylvania state University. Ph.D Thesis in Ecology.

Scheffler, P.Y. (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology.*21, 9-19.

Schimel, J.P. & Gulledge, J. (1998) Microbial Community Structure and Global Trace Gases. *Global Change Biology.* 4, 745-758.

Schlesinger, W.H. (1997) *Biogeochemistry: An Analysis of Global Change.* Academic Press, San Diego.

Schneider, K., Migge, S., Norton, R. A., Scheu, S., Langel, R., Reineking, A. & Maraun, M. (2004) Trophic niche differentiation in soil micro arthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/N^{14}$). *Soil Biology and Biochemistry.* 36,1769–1774.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science.* 2,369-404.

Schofield, J. A., Hagerman, A. E. & Harold, A. (1998) Loss of tannins and other phenolics from willow leaf litter. *Journal of Chemical Ecology.* 24, 1409-1421.

Schuur, E. A. G. (2001) The effect of water on decomposition dynamics in mesic to wet Hawaiian Montane forests. *Ecosystems.* 4, 259-273.

Schuur, E.A.G. & Matson. P.A. (2001) Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia.* 128, 431–442.

Seastedt, T.R. (1984) The role of micro arthropods in decomposition and mineralization processes. *Annual Review of Entomology* .29, 25–46.

Seneviratne, G. (2000) Litter quality and nitrogen release in tropical agriculture: a synthesis. *Biology and Fertility of Soils.* 31, 60-64.

Seta¨la¨, H. (2002) Sensitivity of ecosystem functioning to changes in trophic structure, functional group composition and species diversity in belowground food webs. *Ecological Research.* 17, 207–15.

Seta¨la¨, H., & Huhta, V. (1991) Soil fauna increase *Betula pendula* growth—laboratory experiments with coniferous forest floor. *Ecology.* 72,665–671.

Sgardelis, S.P., Sarkar, S., Asikidis, M.D., Cancela de Fonseca, J.P. & Stamou, G.P. (1993) Phenological patterns of soil micro arthropods from three climate regions. *European Journal of Soil Biology.* 29, 49–57.

Shannon, C.E. & Weaver, W. (1949) *The mathematical theory of communication.* Urbana. IL: University of Illinois Press.

Shattuck, S.O & Barnett, N.J. (2001) Australian ants online, CSIRO, Australia www.ento.csiro.au/science/ants/formicinae. Dated 10.07.2006

Simpson, E.H. (1949) Measurement of diversity. *Nature* 163-688

Singh, K. P. (1968) Litter production and nutrient turnover in deciduous forests of Varanasi. *Proceedings of the Symposium on Recent Advances in*

Tropical Ecology (Part II) (ed. by R. Misra & B. Gopal), pp. 655-665. International Society for Tropical Ecology.

Singh, K. P., Singh, P. K. & Tripathi S K. (1999) Litter fall, litter decomposition and nutrient release patterns in four native tree species raised on coal mine spoil at Singrauli, India. *Biology and Fertility of Soils*. 29, 371-378.

Smith, V.C. & Bradford, M.A. (2003) Do non-additive effects on decomposition in litter-mix experiments result from differences in resource quality between litters? *Oikos*. 102, 235-242.

Songwe, N.C., Okali, D.U.U. & Fasehun, F.E. (1995) Litter decomposition and nutrient release in a tropical rainforest, Southern Bakundu Forest Reserve, *Cameroon. Journal of Tropical Ecology*. 11, 333-350.

Songwe, N.C., Fasehun, F.E. & Okali, D.U.U. (1997) Leaf litter dynamics of two tree species and litter nutrient content in Southern Bakundu Forest Reserve, Cameroon. *Journal of Tropical Ecology*. 13 (1),1-13.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1979) The relationship of plant and insect diversities in succession. *Biological Journal of Linnean Society*. 12, 327-348.

St John, T.V. (1980) Influence of litter bags on growth of fungal vegetative structure. *Oecologia*. 46,130-132.

Stachurski, A. & Zimka, J. R. (1975) Methods of studying forest ecosystems: Leaf area, leaf production and withdrawal of nutrients from leaves of trees. *Ekologiya Polska*. 23, 637-316.

Stohlgren. T.J. (1988) Litter dynamics in two Sierran mixed conifer forest: I Litter fall and decomposition rates. *Canadian Journal of Forest Research.* 18, 1127-1135.

Stork. N.E. (1987) Guild structure of arthropods from Bornean rainforest trees. *Ecological Entomology.* 12, 69-80.

Stork, N. E. (1988) Insect diversity: facts, fiction and speculation. *Biological Journal of Linnean Society.* 35, 321–337.

Stork, N.E. (1993) How many species are there? *Biodiversity Conservation.* 2, 215–232.

Sundarapandian, S.M. & Swamy, P.S. (1999) Litter production and leaf- litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. *Forest Ecology and Management.* 123,231–244.

Sundarapandian, S.M., Chandrasekaran, S. & Swamy, P.S. (2005) Phenological behaviour of selected tree species in tropical forests at Kodayar in the Western Ghats, Tamil Nadu, India. *Current Science.* 88, 5.

Swamy, H.R. & Proctor, J. (1994) Litter fall and Nutrient Cycling in Four Rainforests in the Sringeri area of the Indian Western Ghats. *Global Ecology and Biogeography.* 4(5), 155–165.

Swift, M. J. & Anderson, J.M. (1989) Decomposition. *In*: Lieth, H., Werger, M.J.A. (Eds.), Tropical Rain Forest Ecosystems. *Biogeographical and Ecological Studies.* Elsevier, Amsterdam, pp. 547–569.

Swift, M.J. & Boddy, L. (1984) Animal- microbial interaction in wood decomposition. In J.M. Anderson, A.D.H. Rayner and D.W.H. Walton (Eds). *Invertebrate- microbial interactions.* Cambridge University Press. Cambridge. pp. 89-131.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) Decomposition in terrestrial ecosystems. Blackwell, Oxford, pp. 372.

Taylor, B.R., Parkinson, D. & Parsons, W.F.J. (1989) Nitrogen and lignin as predictors of litter decay rates: a microcosm test. *Ecology*. 70,97-104.

Tian, G. & Badejo, M.A. (2001) Soil fauna and soil fertility. *In*: Sustaining Soil Fertility in West Africa. *SSSA Special Publication*. 58, 45–67.

Tian, G., Kang, B. T. & Brussaard, L. (1992) Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions - decomposition and nutrient release. *Soil Biology and Biochemistry*. 24,1051-1060.

Tian, G., Brussard, L., King, B.T. & Swift, M.F. (1997) Soil fauna-mediated decomposition of plant residues under constrained environmental and residue quality condition. (Eds. Gadisch, G., Giller, K.E.) *Nature*. CAB international publishing, Walingford, 125-134.

Toda, M. & Kitching, R. L. (Eds). (1999) "IBOY-DIWPA: Biodiversity assessment program in the Western Pacific and Asian region." *Forest ecosystems: the assessment of plant and animal biodiversity in forest ecosystems*. 2, 1-71.

Torreta. N.K & Takeda, H. (1999) Carbon and nitrogen dynamics of decomposing litter in a tropical hill evergreen forest. *European Journal of Soil Biology.*35 (2), 57-63.

Turner. I.M. & Corlett, R.T. (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology and Evolution.* 11, 330-333.

Usher. M.B. (1970) Seasonal and vertical distribution of a population of soil arthropods: Collembola. *Pedobiologia.* 10, 224–236.

Valiela, L, Wilson, J., Buchsbaum, R., Rietsma, C., Bryant, D., Foreman, K. & Teal, J. (1984) Importance of chemical composition of salt marsh litter on decay rates and feeding by detritivores. Symposium on Detritus Dynamics in Aquatic Ecosystems. *Bulletin of Marine Science.* 35, 261-269.

Valiela, I., Teal J.M., Allen S.D., Van Etten R.. Goehringer D. & Volkmann S. (1985) Decomposition in salt marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic matter. *Journal of Experimental Marine Biology and Ecology.* 89, 29–54.

Vanlauwe, B., Diels, J., Sanginga, N. & Merckx. R. (1997) Residue quality and decomposition: an unsteady relationship? *In*: Cadisch G. and Giller K.E. (Eds.), *Driven by nature: plant litter quality and decomposition. CAB International.* pp 157-166.

Veiga C.M, Lobo, J.M. & Martin Piera F. (1989) Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades de Scarabaeoidea

(Col.). II. Analisis de efectividad. *Revue d'Ecologie et de Biologie du Sol.* 26: 91-109.

Veneklaas, E. J. (1991) Litter and nutrient fluxes in two montane tropical rain forests, Colombia. *Journal of Tropical Ecology.* 7,319-336

Vineesh, P.J., Vinod, K.V. & Sabu K. Thomas. (2003) Litter arthropod dynamics and C:N values of deciduous forest at Thirunelli. *Proceedings of the STEC sponsored national seminar on biodiversity conservation and participatory forest management.* 71-76pp.

Visalakshi, N. (1993) Litter fall, standing crop of litter and their nutrients in two tropical dry evergreen forests in India. *International Journal of Ecology and Environment Science.* 19, 163–180.

Vitousek, P. (1982) Nutrient Cycling and Nutrient Use Efficiency. *American Naturalist.* 119, 553-572.

Vitousek, P.M., Turner, D.R., Parton, W.J & Sanford, R.L. (1994) Litter decomposition on the Mauna Loa matrix: patterns, mechanisms and models. *Ecology.* 75, 418-429.

Vogt, K. A., Grier, C. C. & Vogt, D. J. (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Advances in Ecological Research.* 15, 303-377.

Vossbrinck, C.R., Coleman, D.C. & Woolley, T.A. (1979) Abiotic and biotic factors in litter decomposition in semiarid grassland. *Ecology.* 60, 265-271.

Wachendorf, C., Irmler, U. & Blume, H.P. (1997) Relationships between litter fauna and chemical changes of litter during decomposition under different moisture regimes. *In*: Cadisch G, Giller KE (Eds) *Driven by nature: plant litter quality and decomposition*. CAB International, Wallingford, Oxfordshire, pp 135–144.

Walkley, A. & Black, I. (1934) An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Science*. 37,29-38.

Wallace, A.R. (1869) *The Malay Archipelago*. (1962 Reprint. The Malay Archipelago. New York: Dover Publications.)

Wardle, D.A. & Lavelle, P. (1997) Linkages between soil biota, plant litter quality and decomposition. *In* Gadisch, G., Giller, K.E. (Eds.), *Driven by nature: plant litter quality and decomposition*. CAB International Publishing, Walingford, pp. 107–124.

Waring, R.H. & Schlesinger, W.H. (1985) Forest Ecosystems: Concepts and Management. Academic Press, New York, 340 pp.

WCMC (World Conservation Monitoring Centre) (1992) *Global Biodiversity*. Chapman and Hall, London

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*. 33,125-160.

Whitmore, T.C. (1990) *An introduction to Tropical Rainforests*. Claredon Press, Oxford, UK.

Whittaker, R.H. (1965) Dominance and diversity in land plant communities. *Science.* 147, 250-260.

Wieder, R. K. & Lang, G.E. (1982) A critique of the analytical methods used in examining decomposition data obtained from litterbags. *Ecology.* 63, 1636–1642.

Wieder, R.K & Wright, S.J. (1995) Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. *Ecology.*76 (6), 1971–1979.

Wilson, E.O., ed. (1988) *Biodiversity,* National Academy of Sciences. Washington. D. C. U.S.A.

Wilson, T.G. (1992) The effects of complex social life on evolution and biodiversity. *Oikos.*83,13–18.

Wise, D. H. & Schaefer, M. (1994) Decomposition of leaf litter in a mull beech forest: comparison between canopy and herbaceous species. *Pedobiologia.* 38,269-288.

Witkamp, M. & Crossley, D. A. Jr. (1966). The role of micro-arthropods and micro flora in breakdown of white oak litter. *Pedobiologia.* 6,293-303.

Witkamp, M. & Olson, J.S. (1963) Breakdown of confined and nonconfined oak litter. *Oikos.* 14, 138-147

Witkamp, M. & Van der Drift, J. (1961) Breakdown of forest litter in relation to environmental factors. *Plant and Soil.*15, 295-311.

Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance in tropical insects. *Journal of Animal Ecology.* 47,369-81.

Wolda, H. (1987) Altitude, habitat and tropical insect diversity. *Biological Journal of Linnean Society*. 30, 313–323.

Wolda, H. (1988) Insect Seasonality, Why? *Annual Review of Ecology and Systematics*, 19, 1-18

Wolters, V., Silver, W.L., Bignell, D.E., Coleman, D.C., Lavelle, P., Van Der Putten, W.H., De Ruiter, P.C., Rusek, J., Wall, D.H., Wardle, D.A., Brussaard, L., Dangerfield, J.M., Brown, V.K., Giller, K.E., Hooper, D.U., Sala, O., Tiedje, J. & Van Veen, J.A. (2000) Effects of Global Changes on Above- and Belowground Biodiversity in Terrestrial Ecosystems: Implications for Ecosystem Functioning. *Bioscience*. 50 (12), 1089- 1098.

Wood, T.E., Lawrence, D. & Clark, D.A. (2005) Variation in leaf litter nutrients of a Costa Rican rain forest is related to precipitation. *Biogeochemistry*. 73, 417–437.

Wright, S.J. (1992) Seasonal Drought, Soil Fertility and the Species Density of Tropical Forest Plant Communities. *Trends in Ecology and Evolution*, 7, 260-263.

Wright, I.J. & Cannon, K. (2001) Relationships between leaf lifespan and structural defences in a low nutrient, sclerophyll flora. *Functional Ecology*.15, 351–359.

Wright, I.J. & Westoby, M. (2002) Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist*.155, 403–416.

Wright, S.J. & Cornejo, F. (1990) Seasonal drought and leaf fall in a tropical forest. *Ecology*. 71 (3), 1165-1175.

Yavitt, J. B. & Fahey, T.J. (1986) Litter decay and leaching from the forest floor in *Pinus contorta* (lodgepolepine) ecosystems. *Journal of Ecology*. 74, 525-545.

Zak, D.R., Pregitzer, K.S., Curtis, P.S., Teeri. J.A., Fogel, R. & Randlett, D.L. (1993) Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles. *Plant Soil* .151, 105–117.

Zimmer, M. (2002) Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. *Biological Reviews*. 77, 455-493

Zimmer, M. & Topp, W. (1998) Nutritional biology of terrestrial isopods (Isopoda: Oniscidea): Copper revisited. *Israel Journal of Zoology*. 44, 453-462.

Zimmer, M. & Topp, W. (2000) Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea). *Journal of Animal Ecology*. 69,1071-1082.

Zimmer, M., Pennings, S.C., Buck, T.L. & Carefoot, T.H. (2002) Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. *Functional Ecology*. 16,596–607.

Zimmer, M., Pennings, S.C., Buck, T.L. & Carefoot, T.H. (2004) Salt marsh litter and detritovores: a closer look at redundancy. *Estuaries*. 27, 573–769.