examined climatic factors and the lignin content of litter as controlling decomposition on a world-wide basis. The importance of chemical composition in determining the rate of decomposition of leaflitter has been clearly demonstrated (Bocock 1964; [illegible] & King 196?; King & Heath 1967; Satchell & Lowe 1967; Anderson 1973; Edwards 1977; Heal <u>et</u> <u>al</u>. 1978; Cooper 1982; Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1984).

Decomposers

The soil fauna of temperate forests as well as tropical forests has been shown to be the main agents of litter decomposition ([illegible]; Madge 1965; 1969). Gupta & Singh 1977). The ability of termites to digest large quantities of woodlitter is universal in tropical ecosystems (Lee & Wood 1971). However, in South American rain forests, it has been shown that fungi are the main decomposers of leaflitter (Cruz Acosta 1964; Went & Slark 1968; [illegible] 1971; Fittkau & Klinge 1973).

Soil respiration

The amount of carbon dioxide evolving per unit soil surface and time has been termed as "Soil respiration" (Walter & Haber 1957). Soil respiration is generally governed by three biological processes (a) microbial respiration (b) root respiration and (c) faunal respiration and one non-biological process i.e. chemical oxidation

(Bunt & Rovira 1954). Soil respiration is thus a biological phenomenon of decomposition which has long been considered as an index of soil metabolism (Wollny 1831; Boussingault & Levy 1853; Mina 1962; Reiners 1968). Rates of soil respiration have been in fact used to calculate the amount of soil organic matter decomposition and have been compared with litterfall (Yoda & Kira 1969; Wanner 1970; Coutinho & Lambert 1971; Medina & Zelwer 1972; Ogowa 1974).

Temperature and moisture of the soil are two important factors determining the rate of respiration (Witkamp 1969; Medina & Zelwer 1972; Medina et al. 1980; Cowling & MacLean Jr. 1981; Singh & Ramakrishnan 1983; Das & Ramakrishnan 1984). Medina et al. (1980) have shown that differences in respiration rates between the soils of the podsol and the laterite forests in Amazon rain forests in Rio Negro basin is related to the development of root biomass. Rates of soil respiration have often been related to the input of litterfall (Wanner 1970; Medina & Zelwer 1972; Ogawa 1974).

Although the study of litterfall and decomposition is of vital importance in the functioning of an ecosystem, not much work has been done on this aspect under Indian conditions. In India litterfall studies in deciduous and in some evergreen forests have been done by some workers (Champion 1936; Puri 1953; Seth et al. 1963;

Singh 1968; Faruqi 1972; Billore & Amrithphali 1975; Das & Ramakrishnan 1984). Most of the Indian workers mentioned above above worked with reference to forest plantations while very few studies are available on natural forests of India (Boojh & Ramakrishnan 1981; Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983). Limited decomposition studies are also available from India (Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983; Das & Ramakrishnan 1984).

FINE ROOT SYSTEM

Fine root biomass

The root system of forest trees can be classified into a course (structural) and fine (smaller diameter) roots. The structural parts of the root system have been shown to contribute about 30% of the biomass of the tree components in the forest ecosystem (Ovington 1962). Considerable quantities of biomass are also accumulated in perennials with persistent woody root and rhizome systems. The quantity and activity of the smaller diameter root systems are of primary importance with respect to water and nutrient supply (Lyr & Hoffman 1967).

The fine root contribution to the total biomass is generally low. Józefaciuzowa (1975) estimated the percentage by weight of the fine root (<1 mm diameter) of the tree component of the two different scots pine stands as only 9 and 11% respectively. However, diameter analysis show that the major part of the length of the tree root systems consists of fine roots. Lyr & Hoffman (1967) have shown in four tree species that fine roots (< 1 mm diameter) accounted to about 86-99% of the total root length.

Information on the root biomass of the forest trees are extremely limited. This is mainly because of the technical difficulties in accessing of roots (Woodwell & Whittaker 1968a,b; Kira & Ogawa 1968). There is a comprehensive account of root system for the economically important forest trees of Europe (Kostler et al.1968), but no comparable work has been done on tropical forest trees (Jenik 1971; Kerfoot 1962).

A number of studies on root biomass are available from the tropical forests in Africa. Root biomass estimates are reported for an old secondary forest in Nigeria (Greenland & Kowal 1960), forest fallows in the Congo (Bartholomew et al.(1953), oil palms in Nigerian plantations (Rees & Tinker 1963), ivory coast (Huttel 1969;1973) and miombo forest in Zaire (Malaisse et al.1972). A few studies have also been reported from southeast Asia (Kira et al. 1964,1967; Ogawa et al.1965; Kira & Shidei 1967). The root mass estimation from Central Amazonia, Brazil are reported by Klinge (1973;1977) Klinge et al.(1973) Fittakau (1973) and Klinge & Fittakau(1973). Root biomass estimates in San Carlos De Rio Negro was done by Went & Stark (1968), Stark (1971), Stark & Spratt (1977). Bandhu (1970) studied the root biomass of some tree species in a dry deciduous forest and Ramakrishnan & Singh (1983) estimated the root biomass of a sub-tropical humid forest in India.

Fine root and nutrient cycling

The distribution and nutrient contents of fine root biomass are of considerable importance to nutrient cycling in forested ecysystems, especially in the humid tropics where they may determine the relative fragility of the ecosystems. In tropical forests one should wonder to see the luxuriant growth of forests which may sometimes lead to the false assumption that the soil supporting such forests must contain a large supply of nutrients (Longman & Jenik 1974). However, it has been shown by many workers (Went & Start 1968; Stark 1971,1972; Klinge 1973; Klinge 1976; Singh & Ramakrishnan 1983; Ramakrishnan 1985 a,b). that the soils in the tropical forests with high rainfall, are highly leached, acidic and low in available nutrients. In particular the rooting habit of the forest trees is adopted to provide relative independence from the mineral soil for nutrition (Herrera et al. 1981). In these infertile, thin and highly leached soils, it has generally observed by many workers, the development of a dense surface feeding root mat which is in intimate contact with the decomposing litter. Went & Stark (1963) put forward the direct nutrient cycling theory which postulates the movement of nutrients from dead organic matter on the forest floor to living roots via mycorrhizal fungi. Quantitative data to support this view, are however limited. (Stark 1971; Klinge 1973;1976; Stark & Spratt 1977; Stark & Jordan 1977; Ramakrishnan & Singh 1983; Ramakrishnan 1985 a,b).

Fine root Production

Studies on growth of roots are very few and scattered. Lyr & Hoffman (1967), Kostler et al.(1968), Sutton (1969,1980), Head (1973), Hermann (1977), Russel (1977), Caldwell (1979), Perry (1982) and Santantonio & Hermann (1985) have reviewed a large spectrum of literature relating to growth of tree roots. Inspite of this, our knowledge of root production is still limited. Many of the studies on root growth are limited to seedlings or young trees planted in isolation. The relatively fewer studies of the forest ecosystems are mainly because of technical difficulties in accessing roots. Seedlings or young trees grown in isolation differ fundamentally from large trees in a forest; we currently lack an adequate basis to extrapolate from one to the other. Many of these studies are largely confined to temperate zones and very few studies on root growth are available in the tropical forests (Coster 1933; Nye & Greenland 1960; Kerfoot 1963).

Attempts to estimate root production and turnover in the forest ecosystems have started only recently. These efforts to quantify forest productivity of root are generally part of large-scale ecosystem studies, such as those of the International Biological Programme (Harris et al. 1980). Results of these studies reveal that fine root dynamics are an important carbon pathway in temperate forest ecosystems (Agren et al.1980} Harris et al.1980; Persson 1983; Fogel 1983).

Periodicity of fine root production

Periodicity of root growth create difficulties for compasing results of other studies directly. This is due to the different methods used, to differences between species composition and to varying environmental conditions (Lyr & Hoffman 1967). Fine root growth of temperate forests undergo large seasonal variation in growth activity or standing crop (Santantonio & Hermann 1985). Different authors observed peak root growth in different seasons and one or two or more peaks were commonly observed (Ford & Deans 1977; Harris et al. 1977; Persson 1978). However, in many studies, sampling was not conducted throughout the year; thus, all periods of fine root growth may not have been sampled.

Many workers have concluded that root growth occurs independently of shoot growth (cf. review of Sutton 1969) and that the periodicity of root activity is largely influenced by environmental conditions. Growth is greatly favoured by moisture and temperature conditions (Orlov 1960). Low moisture and low soil temperature in winter are widely considered to have an adverse effect on root growth (Lyr & Hoffman 1967; Hermann 1977; Russel 1977). Large number of fine roots may be killed periodically by drought or frost, but abundant regeneration occurs continuously (Persson 1978) Deans (1979) has shown seasonal influence of soil temperature and moisture on the root growth: as soil temperature increased root growth also increased, but this relation is overriden and halted by low moisture later in the season. Teskey & Hinckley (1981) found that the root elongation increased as environmental conditions became more favourable but that the number of growing roots and the projected rate of biomass accumulation increased at cool soil temperatures and low soil water potentials. In addition to the effect of soil temperature and moisture, some other factors such as growth regulatory substances carbohydrates availability, nutrient status, respiration rates, relations with symbionts, and competitive relationships (Lyr & Hoffman 1967; Sutton 1969, 1980; Riedacker 1976; Russel 1977; Caldwell 1979; Persson 1983) also determine productivity.

Kolesnikow (1968, 1971) suggested, from root studies an apple trees, that fine root death and renewal in trees is a natural cyclic process and bears a resemblance to leaf shedding in evergreen plants. He concluded that the absorptive roots constantly invade new, fresh soil layers throughout the growth period and that their life span and activity is short and extend over a period of few days only. Cyclic death and renewal of fine roots in a succession of favourable micro-sites may be an adaptive strategy for maintaining the largest number of active fine roots at a minimum metabolic cost and the seasonal changes of fine roots represents the outcome of an interplay of complex processes within an economy of limited resources (Santantonio & Hermann 1985).

NUTRIENT FLOW

Nutrient flow and energy balance are two basic features in understanding the complex organisation of an ecosystem. The study is of particular relevance in understanding the structure and function of the natural ecosystems and providing basic information to design appropriate alternatives for development. The detailed informations on nutrient cycling is of particular importance because it defines the relationship between soil and plants. Studies of the dynamics of mineral cycling have been reviewed by many workers (Laudelot & Meyer 1954; Greenland & Kowal 1960; Nye 1961; Dommergues 1963; Rodin & Bazilevich 1967; Ovington 1968; Odum & Pigeon 1970; Stark 1970; Galley et al 1975; Edwards & Grubb 1977; Herrera et al. 1981; Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983). While the information is limited, certain patterns are nevertheless suggested by these studies : (i) the uptake and return of nutrients may be greater per year in tropical forests than in other type of vegetation (ii) a larger proportion of the entire chemical inventory of the system is held in the vegetation (iii) in tropical forests the percentage of the vegetation in green parts, the proportion lost per year as litter, and the rate of decomposition of the litter are greater than in temperate forests and (iv) the rate of uptake is strongly influenced by the rate of evapotranspiration.

A vital characteristic of any ecosystem is the continuous flow of nutrient and energy through it. Within the intra-system cycle of an ecosystem, several workers have carefully evaluated the size and rates of exchange between various nutrient pools (Duvigneaud & Denaeyer-De Swet 1964; Ovington 1965; Cole et al. 1968; Borman & Likens 1970; Jorgensen et al. 1975). However, measurements of systems present major difficulties and only a few quantitative studies have so far been done.

The rate and magnitude of movement along individual pathways differ for different chemical elements and the general pattern of flow within the system depends upon many factors, particularly the nutrient status of the soil and the type and age of the woodland. Pioneering work by Ovington (1965), Rodin & Bazilevich (1967) and Duvigneaud and Denaeyer-De Swet (1970) along with the comprehensive reviews and synthesis of data by Bray & Gorham (1964), Bakuzis (1964), Overton et al.(1973), Larcher (1975), Jorgensen et al.(1975) and Lieth & Whittaker (1975), havebrought considerable attention to the process of nutrient cycling and production in forest ecysystems.

Nutrient input

Nutrient cycling involves input into the ecosystem from the atmosphere, and from the weathering of rocks and minerals in the soil, output through run-off and percolation water and internal circulation within the ecysystem. The internal circulation involves the transfer of nutrients from the vegetation to the ground through leaching by throughfall and stemflow, which does not involve the intervention of decomposers, and by litterfall, in which decomposers play a very important role. Nutrients are transferred to the vegetation through absorption. This overall cycling of nutrients is a continuous process and probably involves actual nutrients being recycled throughout the year (Remezov 1959).

The total ecosystem approach for quantifying nutrient budget and cycling in the northern hardwood forest has been successfully done by Bormann & Likens (1967). Several studies have demonstrated that rainfall may remove substantial amounts of nutrients from the foliage in horticulture plants (LeClere & Breazeale 1908; Mes 1954;

Tukey & Amling 1958; Tukey <u>et al</u>.1958). Others have shown that rain water which passes through the tree crown contain significantly higher quantities of many nutrient elements than rainfall collected in adjacent openings (Tamm 1951; Madgwick & Ovington 1959; Will 1959; [illegible] Rahman 1964; Cole <u>et al</u>. 1968; Likens <u>et al</u>. 1971; Eaton <u>et al</u>. 1973; Monokaran 1979; Singh & Ramakrishnan 1983).

Measurements of nutrients in throughfall and stemflow water have mainly been done in temperate woodlands (Madgwick & Ovington 1959; [illegible] Likens <u>et al</u>. 1971; Eaton et al. 1973). Such investigations in the tropics have been more recent (Nye 1961; Sollins & Drewy 1970; Kenworthy 1971; Turvey 1974, Johnson <u>et al</u>. 1975; Jordon 1978; Monokaran 1979; Prebble & Stirk 1980; Singh & Ramakrishnan 1983). In most of the studies, however, throughfall contributions to nutrient cycling have received more attention than contribution by stemflow. Almost half of the total amount of potassium arrives in the soil with canopy throughfall and stemflow annually (Carlisle <u>et al</u>.1967) Nebe 1973). The importance of water dripping from the tree crowns and the role of minor tree litter fractions (bud scales, male flowers, capsules, bark etc.) in the nutrient cycling of a sessile oak (<u>Quercus petreae</u>)woodland on low fertility siliceous site in a high rainfall area has been studied by Carlisle (1965) and Carlisle <u>et al</u>. 1966 a,b)

Nutrient output

Losses of nutrients from the ecosystem are largely dependent on the nutrient status of the soil. Ecosystem with nutrient saturated soils would lose relatively more of their nutrients than those with nutrient depleted soils (Jordan et al. 1972). In northern hardwood forests (Likens et al. 1977) in which a large propertion of the nutrients is in the soil in exchangeable form would lose a relatively larger amount of it than tropical rain forests, as in these forests most of the nutrients are tied up in the biomass (Rodin & Brazilevich 1967; Odum 1971; Jordan et al. 1972; Edwards & Grubb 1982; Toky & Ramakrishnan 1983; Singh & Ramakrishnan 1983) and mineral soil has very low nutrient content (Went & Stark 1968; Stark 1971; Klinge 1972; Stark & Spratt 1977; Herrera et al. 1978; Singh & Ramakrishnan 1983). Toky & Ramakrishnan (1982) demonstrated that the shortening of jhum (shifting agriculture) cycle to 4-5 years in north-east India does not permit the recovery of soil fertility and has adversely affected the vegetational cover and biogeochemical and hydrological cycles. The amount of nutrient losses are also largely dependent on the degree of the release of nutrients from the decomposing litter (Singh & Ramakrishnan 1982).

Return of nutrients through litter

The most striking features of a woodland community from the nutrient circulation point of view is the annual return of nutrients to the soil through litterfall. Smirnova & Gorodentseva (1958) reported that in birch woodlands, annual defoliation returns 80-90% of the nutrients to the soil. Litter are the largest component for the nutrient cycling in the forest ecosystem. However, in open woodlands the well developed shrubs and herbs layer may contribute more litter than that from trees (Scott 1955).

The litter falling to the ground in woodlands is very heteregeneous being composed of organic materials differing greatly in structure and chemical composition and the mechanism and efficincy of litter breakdown varies greatly even in the same wood (Alway & Zon 1930; Wittich 1939; Mork 1944; Tarrant et al. 1951; Owen 1954; Gosz et al. 1972). The importance of organic matter in mature forest ecosystem was emphasised by some workers (Rodin & Bazilevich 1967; Likens et al. 1970; Pierce et al. 1972; Whittaker et al. 1974; Gosz et al. 1976). Nutrient cycling through decomposition of leaf and wood litter in tropical and temperate forests has been studied by many workers (Nye 1961; Witkamp & Olson 1963; Olson 1963; Bray & Gorham 1964; Ovington 1965; Bernhard 1970; Anderson 1973; Gosz et al. 1973; Chapman 1976; Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983). In a region of high rainfall and temperature with infertile soil, the root distribution is adapted to provide relative independence from the mineral soil for nutrition. A dense root-mat is formed in intimate contact with litter. At this point of contact mycorrhizal associations seem to play an active role in direct transfer of nutrients from decomposing litter to the roots (Went & Stark 1968; Klinge 1972; Stark & Spratt 1977; Herrera *et al*. 1978).

THE PRESENT STUDY

Cherrapunji being one of the wettest place in the world, receiving an annual average rainfall of 10372mm which in an exceptional year (1974) may go up to 24895mm, is characterised by infertile, thin, acidic and highly leached soils (Ramakrishnan 1978; 1985a,b). With a large fraction of the nutrients being held in the living biomass (Rodin & Brazilevich 1967; Edwards & Grubb 1982; Toky & Ramakrishnan 1983), the ecosystem is very fragile. The delicate ecosystem balance is upset after clear-cutting and the forest fails to recover (Ramakrishnan 1985a).

The sacred groves at Cherrapunji and its adjoining areas that is preserved for traditional religious beliefs is a sad reminder of what Cherrapunji looked like in the past. True, the forests are stunted as they are supported by an infertile soil. All the same, they form a dense canopy protecting the soil from ravages of the extreme climate.

Had it not been for the traditional belief of the Khasi tribes, that sacred grove is the abode of gods/deities and that removal of any plant/plant part including dead wood or twig is a taboo, even the sacred groves at Cherrapunji and its adjoining areas would have disappeared long ago. In fact, with the advent of christianity, most of the sacred groves, which were an integral part of every village, have disappeared and with that a unique way of preserving this national heritage of rain forest ecosystem (Ramakrishnan 1985a).

The Cherrapunji ecysystem that now stands desertified due to deforestation inflicted sometimes in the distant past is difficult to recover to its original state as represented by the relict sacred grove. The fact that jhum is banned by the village council and is practiced in peripheral areas is suggestive of the part played by it in creating the present landscape. The shapp boundary between the sacred grove and the landscape represented by degraded grasslands (Ram, 1986) indicates that the system will not recover through natural processes of revegetation. Artificially the cost could be enormous (Ramakrishnan 1985a).

Therefore, the aim of the present study is to look at the ecosystem function of these relict forests represented by a sacred grove and a reserve forest protected by the Village Council. The study is aimed at an understanding of Vegetational structure, Phenological functions such as leaf flushing, leaffall, flowering and fruiting behaviour of the over-and understorey species. It also aims to understand the structure and function of these relict forests with respect to Litter Dynamics, internal cycling of nutrients through litter. Nutrient input through rainfall into the soil and the output of nutrients from the ecosystem through surface run-off and percolation water has also been assessed.

While discussing the results, the forest ecosystem function has been compared with the degraded grassland ecosystem attributes(Ram 1986). Religious beliefs of the people with respect to the sacred groves at Cherrapunji and its adjoining areas is the only way by which some of these relict forests could be preserved.

ECOSYSTEM FUNCTION OF PROTECTED FORESTS OF CHERRAPUNJI AND ADJOINING AREAS

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D E D I C A T E D

TO

MY BELOVED MOTHER LATE

MRS. BAMA KHIEWTAM

UMNIUH - TMAR.

CONTENTS

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PREFACE

The study at Cherrapunji on the sacred grove and reserve forest was undertaken as part of a programme on the ecological processes related to desertification of this high rainfall area. Apart from being a wettest spot of the workd, the geology and past anthropogenic influences were considered as contributing to forest degradation into desertified grassland types. Small patches of these relict forests are the vestiges of what was extensive once earlier.

Starting with a chapter on general introduction which is a review of literature related to this work, the study area and climate has been described subsequently. The five chapters following this embodies original research on Vegetation and Phenology, Litter Dynamics, Fine Root Biomass, Nutrient Flow through Water and Litter and Socio-Cultural Aspects related to the Concept of the Sacred Grove.

Each of these five Chapters are prepared as papers meant for publication, each with its own Introduction, Methods of study, Results and Discussion. Hence some overlap in writing could not be avoided. A summary outlining the salient points is given at the end of each chapter. The literature cited in the text is set at the end of the thesis.

Whenever possible and required the data on the sacred grove has been compared with that of degraded grasslands based upon another study (Ram 1986). This study on the rainforest ecosystem, developed under stress due to climate, geology and extremely susceptible to human interference is significant for understanding of this highly fragile ecosystem and its functional attributes.

GENERAL INTRODUCTION

VEGETATION AND PHENOLOGY

Vegetation

Vegetation is generally defined as an assemblage of plants growing together in a particular region which is characterised either by its component species or by a combination of structural and functional characters. The changes in vegetational structure result in succession and several communities may succeed one another to establish a climax community which is controlled by the climate of the region (Clements 1916) or the stable community may be the result of cyclic changes (Tansley 1935). However, the dynamics of vegetational structure are a complex phenomena (Odum 1963; Margalef 1968).

Vegetation has been described or classified in accordance with the major philosophies, the discontinuous and continuous concepts. The discontinuous concept, the more traditional approach, provides a description that enable one to discuss a gross vegetational unit. Gleason's (1926) individualistic concept provides a framework for understanding plant community in greater detail as a dynamic unit.

In nature plants seldom grow isolated from one another. Individuals of a species are generally grouped into a population and populations of different species may be intermingled. Some of the species or even individuals of a species may grow more successfully than others as seen from their behaviour and size. The characteristics of the species which differ according to the genetic pattern and physiology determine not only the kind of habitats it can occupy, but also the kind of interactions with other species.

A common approach for vegetation analysis is through species abundance data from many study areas. A large number of such phytosociological studies have yielded considerable information on community-environmental relationships and the nature of the community itself in temperate regions. However, many analyses of tropical forests are based on structural, physiognomical and floristic compositions (Knight 1975). The early works in this respect are mostly descriptive with a focus on the kind and number of species in the forest. As species identification become more feasible and as better quantitative methods developed, studies occurred more frequently on the identification and causes of floristic patterns in relation to succession and site. With regard to site relationships, the studies by Ashton (1964 a,b), Greig-Smith et al. (1967), Bruning (1968), Tracey (1969), Webb (1969), Webb et al. (1967 a,b; 1970; 1972), Hatheway (1971), and Austin et al. (1972) are notable for their use of complex quantitative methods in the analysis vegetational data. Their results suggested that composition and classification methods are useful for analysing the vegetation and that species - rich communities also yield diagnostic and comprehensive ecological informations. Webb (1969), William & Webb (1969), Webb _et al_.(1970), Budowski (1970) and Orloci & Mukkattu (1973) used physsiognomical, structural and floristic features for vegetational analysis and classification.

There is much argument over the possible reasons for the great species diversity in tropical forests (Corner 1954; Federov 1966; Margalef 1968; Richards 1969). Species diversity may be studied as the relationship of physical environmental factors to diversity or as the role of biotic factors (Ricklefs 1973). Presumably the physical environment, including present conditions and past history, determines the pattern of biotic interactions. A complete explanation of diversity would link biotic processes and environmental variables to explain how patterns of immigration, speciation, competitive exclusion and extinction produce patterns of diversity (Mac Arthur & Wilson 1967; Longman & Jenik 1974; Rosenzweig 1975). Diversity measured by any index has an intimate aim to sample size and to spatio-temporal structure of the assemblage studied. Mac Arthur (1965) and Whittaker (1972) distinguished between "within" and "between" habitat diversity while Margalef (1968, 1969) introduced the index of species spectrum in which diversity is a function of spatial scale. Some workers based phenological studies for community analysis and classification (Rees 1964; Gibbs & Leston 1970; Doubenmire 1972; Frankie et al. 1974).

Phenology

Phenology is generally the study of the different phases of the life cycle of organisms that occur around the year (Leith 1970). It provides the basic knowledge for understanding the functional rhythm of the plant species in the ecosystem. The phenology of any particular species is generally classified into various phases, depending upon the various biological events in the life cycle. Each event is referred to as a phenophase and the whole sequence of various phenophases occurring around the year is referred to as phenodynamics. The elaboration of the phenodynamics for each species in a community is referred to as phenological spectrum.

The significance of phenological studies have long been recognised (Leith 1970; 1971; Leith & Radford 1974). It helps in understanding the productivity and ecosystem function (Leith 1970; 1971; Leith & Radford 1974). However, few phenological studies originate in the tropics (Rees 1964; Mc Clure 1966; Gibbs & Leston 1970; Nevling 1971). Many of these studies in the tropics were of an investigative type, lacking comparative and quantitative informations. However, recently systematic attempts in this direction have been made by some workers (Frankie et al. 1974; Putz 1979;

Borchert 1980; Opler *et al*. 1980; Primack 1980). Many of the phenological investigations in the tropical forests have been carried out in markedly seasonal climate (Njoku 1963; 1964; Fournier & Salar 1966; Boaler 1966; Jeffers & Boaler 1966; Janzen 1967; Croat 1969; 1975; Hopkins 1970; Smythe 1970; Nevling 1971; Daubenmire 1971; Foster 1973; Burger 1974; Frankie *et al*. 1974; Malaise 1974; Putz 1979; Boojh & Ramakrishnan 1981; Shukla & Ramakrishnan 1982). Strong annual phenological cycles are evident in these areas. Studies in more or less aseasonal climate are by Medway (1922); Holttum (1931; 1940), Corner (1952), Mc Clure (1966); Koriba (1958), Ng (1977), Baker & Baker (1936), Brookfield (1969), Koelmeyer (1959), Frankie *et al*. (1974) and Jackson (1978).

Because trees are subject to different environmental conditions, depending upon their position in the canopy, tree species were divided into over-and understorey by Frankie *et al*. (1974) for a detailed comparative study. Temperature, humidity, rainfall and wind speed vary seasonally in tropical forests (Richards 1952). All these factors alone or in combination play a vital role in triggering phenological changes in tropical systems (Longman &Jenik 1974). The climatic changes also bring about fluctuations in pollination, seed dispersal, predators and competitors (Lieberman 1982).

Flushing and leaffall

The adaptive significance of different types of leaf flushing behaviour have not yet received the kind of analysis that Janzen (1967) provided for flowering and fruiting behaviour. Jackson (1978) has discussed the adaptive advantages of different kinds of leaf flushing behaviour in forests. According to him, the most advantageous strategy of leaf flushing in a perennial plant in an aseasonal environment would be retention and photosynthetic use of an old leaf until a new leaf is grown. Such a strategy would result in maximum leaffall during the optimal growing season or to a continuous level of leaffall if new leaf growth were to be continuous. In fact, seasonal cold or drought stress is usually present and leaves must be shed to minimise the effects of this stress. Because cold stress in cold temperate forests has a relatively sudden and predictable onset, cold temperature forests normally have a pulse of leaffall at the end of the warm season (Bray & Gorham 1964). In most of tropical forest-types, investigators have observed maximum leaffall corresponding with the relatively xeric conditions or the driest part of the year (Holttum 1931; Baker & Baker 1936; Taylor 1960; Madge 1965; Hppkins 1966; Fittkau & Klinge 1973; Frankie et al.1974; Reich & Borchert 1982; Boojh & Ramakrishnan 1982; Shukla & Ramakrishnan 1982). In some tropical forests a wet season maximum leaffall has been reported (Cornforth 1970; Edwards 1977; Jackson 1978; Brassel *et al*. (1980). The only forests found to have non-seasonal leaffall are Malaysian dipterocarps (Mitchell, cited in Bray & Gorham 1964) which are characterised by relatively uniform climate.

Flowering and fruiting

Synchronisation of flowering with particular seasons have generally been observed in rain forest trees (Richards 1952; Holttum 1953; Rees 1964; Ashton 1969; Groat 1969; Medway 1972; Frankie *et al*. 1974). Investigations in tropical forests have shown that most wet forest flowering occurs chiefly during dry seasons (Duke & Black 1953; Holttum 1953; Snow 1962; Njoku 1963; Janzen 1967). This pattern has been attributed to a triggering mechanism for flowering in response to the sequences of dryness and wetness (Opler *et al*. 1976). Frankie *et al*. (1974) found twice as many seasonally flowering species in bloom in the dry season as in the wet season. A change in photoperiod has also been suggested to be an important stimulus in triggering flowering (Njoku 1958, 1963). Moisture content is one of the major determinants for the production of fruits (Lieberman 1982). High moisture requirement for proper development of fleshy-fruits was suggested by Zahner (1968). Animal dispersed fleshy-fruited species largely occur during wet season and wind-dispersed dry fruits tend to be more during the dry season (Frankie et al. 1974; Lieberman 1982; Shukla & Ramakrishnan 1982).

Very little quantitative information on vegetation and phenology from north-eastern India is available. Earlier studies on vegetation are mainly through the efforts of Ramakrishnan and his coworkers (Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983). Phenological information on north-eastern forests are also very limited (Boojh & Ramakrishnan 1982; Shukla & Ramakrishnan 1982).

LITTERFALL AND DECOMPOSITION

The role of litter and its composition in the forest ecosystem function has long been recognised. Bray & Gorham (1964) in their review of literature on litter production have stated that"the study of quantitative aspects of litterfall remains an important role of forest ecology, dealing with a major pathway for both energy and nutrient transfer". The litter is the source for nutrient cycling and is important in the nutrition of woodlands particularly on soils of low fertility, where the trees depend mainly on the recycling of litter nutrients. The dynamics of litter accumulation processes are of particular importance in the humid tropics where rates of litterfall and decomposition are very high.

Litterfall

Since the classic work of Ebermayer (1876) considerable amount of data on litterfall has accumulated and it has been discussed in detail by many workers (Lutz & Chandler 1946; Aadtonen 1948; Bray & Gorham 1964; Jordan 1971; Janzen 1974; Jordan & Murphy 1978). While most of the studies on litterfall have been done in temperate forests, tropical and sub-tropical forest ecosystems have also received some limited attention (Jenny *et al*. 1949; Laudelot & Meyer 1954; Malaisse *et al*. 1975; Klinge & Rodriques 1968; Singh & Ramakrishnan 1981; Shukla & Ramakrishnan 1983; Toky & Ramakrishnan 1983). However, only a few studies are available on tropical and sub-tropical montane forests (Jenny *et al*.1949; Edwards 1977; Saxena *et al*. 1978; Tanner 1980; Boojh & Ramakrishnan 1982).

Seasonality of litterfall

The pattern of litterfall varies greatly throughout the different climatic zones. In deciduous forests of the northern hemisphere, leaffall is concentrated in short autumnal season with a pronounced peak in October-November (Viro 1955; Witkamf & Van der drift 1961; Carlisle *et al*. 1966; Duvigneaud *et al*. 1969; Anderson 1973). In eucalypt forests in Australia maximum litterfall occurs in summer (Specht & Brouwer 1975; O'Connel & Menage 1982). In tropical moist tropical forests, Klinge (1978) found that there is no seasonality of litterfall in Mocambo and central Catu forests, but Manaus forest showed maximum leaffall in the middle of dry season in South America.

In humid equatorial forests litterfall is more or less continuous all around the year with a tendency for extensive falls during or shortly after relatively dry periods. Thus, Laudelot & Meyer (1954) found that litterfall at Yungambi in Congo was low during the rainy season and reached a peak at the end of the dry season. Nye (1961) found in the moist tropical forests in Ghana that the litterfall to be high during February-March. In Nigeria, Madge (1965) and Hopkins (1966) found that maximum leaffall occurred during dry seasons of November to March. In South-east China, Rodin & Brazilevich (1967) found that leaffall occurred all the year round, but with a peak from March to May, where March-April is the dry season followed by the wet season starting in May.

Temperature, water and nutrients are the main factors responsible for the seasonal litterfall (Jorgensen et al. 1975). The seasonal litterfall pattern largely depends upon the factors responsible for leaf senescence and abcission in the component species and have been discussed in detail by Whitmore (1975), Addicott (1978) and Jackson(1978) Rain has been considered to be a factor responsible for increase in litterfall, as the increase weight of wet senesced material in the canopy causes them to fall (Brassel et al. 1980).Wind velocity has also been implicated with litterfall rates (John 1973; Hopkins 1966;

Brazzel et al. 1980). Turnbull & Madden (1983) demonstrated relationships of leaffall with tree basal area and maximum temperature, which according to them are useful parameters for predictive models aimed at a clearer understanding of the process of litter accession, accumulation and decomposition. However, it is anticipated that litterfall are not correlated with one single factor (Hopkins 1966; Klinge 1979).

Litterfall pattern

Litterfall pattern is mainly influenced by the prevailing climatic conditions at different climatic zones. The predominant role of climate upon litter production has been revealed by Bray & Groham (1964). According to them, the mean litterfall ranges from 1 t. ha^{-1} for Artic -Alpine zone, 11t.ha^{-1} for equatorial regions and 3.5 - 5.5 1t.ha^{-1} for cool and warm temperate forests respectively. Recent estimates of litterfall from tropical forests range from 5.5 - 15.3 t.ha^{-} yr^{-1} (Madge 1965; Muller & Neilson 1965; Kira & Iwata 1967; Wiegert 1970; Hains & Foster 1977; Jackson 1978; Brassel et al. 1980; Tanner 1980; Singh & Ramakrishnan 1981; Boojh & Ramakrishnan 1982; O'Connel & Menage 1982; Turnbill & Madden 1983). Rate of litterfall is thus highest in the tropics and generally decreases with increase in latitudes. It has also been shown that the rate of litterfall decreases with decrease in light available during the growing season along a world-wide gradient of decreasing light availability (Jordan 1971). The litterfall pattern may also vary according to topography, vegetation type, species composition and many other biotic and abiotic factors which have been dealt at length by Bray & Gorham (1964).

Litter fractions

Leaflitter by and large constitute the major portion of the total litterfall all over the world, its contribution being 60-70% of the total litter (Bray & Gorham 1964). In tropical forests its contribution ranges from 4.4-6.9 $t.ha^{-1}$ (Klinge & Rodrigues 1968; Cornforth 1970; Wiegert 1970; Edwards 1977; Irmler & Klinge 1979; Tanner 1980; Boojh & Ramakrishnan 1982; Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983). Litter fractions other than leaf have been less investigated except the wood litter (Klinge & Rodriques 1968; Jordan & Murphy 1978; Klinge 1978; O'Connel & Menage 1982; Boojh & Ramakrishnan 1982; Singh & Ramakrishnan 1983; Toky & Ramakrishnan 1983). Quantitative aspects of the accumulation and turnover of wood litter on the forest floor have been very poorly understood so far, except in a very limited number of forest types (Satchell 1971). Flower and fruitfall have also received very little attention (Klinge 1978; Irmler & Klinge 1979; Boojh & Ramakrishnan 1982).

Nutrient content of the litter

The amount and quality nutrients in litter has long been considered to be of vital importance for exchange of organic and inorganic materials between living organisms and the soil. Litter is a fuel for nutrient cycling in the upper soil horizons and is of importance in the nutrition of plants. In order to study the biological process of the upper soil horizons, the amount and composition of the litter must be known. In the tropical forests of Africa, nutrient contents of litter has been studied (Laudelout & Meyer 1954; Nye 1961; Hopkins 1966; Bernehard 1970; Egunjobi 1974). Similar studies on the nutrient content of the forest litter are available for European forests (Tarrant et al. 1951; Metz 1952; Owen 1954; Scott 1955; Wright 1957; Kendrick 1959; Monk et al. 1970; Zavillkovaski & Newton 1971). Studies on nutrient content of litter in humid sub-tropical montane forests are available from north-eastern India (Toky & Ramakrishnan 1983; Singh & Ramakrishnan 1983; Mishra & Ramakrishnan 1983; Das & Ramakrishnan 1984).

Decomposition

Many of the studies on decomposition are confined to leaflitter only. However, woodlitter also form a significant proportion of the substrata decomposed on forest floor. The non-leaflitter accounts for about 1/3 of the total litterfall in most forests, sometimes as much as 1/2 in climax forests (Kira & Schidei 1967). Woody organs decompose relatively slowly than leaves and supply on the long run the forest with considerable amount of nutrients. An attempt was made to study the rate of decomposition of wood litter in a warm temperate evergreen oak forest of Japan, adopting loss of weight and carbon dioxide evolution as measures of decomposition rate (Yoneda 1975 a,b).

In most of the terrestrial systems, the decomposition of litter forms the major source of energy and nutrients for the soil and litter organisms. Much attention has recently been paid to techniques used for studying decomposition of litter and the rate of decomposition of different types of plant litter in different climatic zones (Bocock & Gilbert 1957; Edwards & Heath 1963; Howard 1965; Van-Cleave 1971; Anderson 1973; Gosz _et al_. 1973; Howard & Howard 1974; Hensen 1974; Suffling & Smith 1974; Wood 1974; Brinson 1977; Fogel & Cromack 1977; Mac Lean & Wein 1978; Edmonds 1979; Staaf 1980; Singh & Ramakrishnan 1983; Das & Ramakrishnan 1983; & Toky & Ramakrishnan 1984). Many of these studies have examined the organic and inorganic constituents in litter and micro-climatic variables at the study site. Some recent studies have looked upon the importance of the carbon-nitrogen ratio and lignin content in controlling decomposition (Phillips _et al_. 1930 Peevy & Norman 1948; Pinck _et al_. 1950; Allison 1973). Meentemeyer (1978)