

**STUDIES ON STRUCTURAL AND
FUNCTIONAL ASPECTS OF TWO
SUB - TROPICAL HUMID FOREST TYPES
OF MEGHALAYA**

BY

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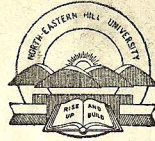


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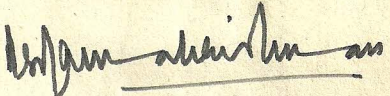
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I certify that the thesis entitled "STUDIES ON STRUCTURAL AND FUNCTIONAL ASPECTS OF TWO SUB-TROPICAL HUMID FOREST TYPES OF MEGHALAYA" submitted by Jasbir Singh for the Degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong, embodies the record of original investigation carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. Degree. This work has not been submitted for any Degree of any other University.

Date: September 22, 1980.

Place: Shillong.


Supervisor.

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PREFACE

The present study has two sections. One pertains to the 50 year old secondary forest at Lailad which forms one in the series developing subsequent to slash and burn agriculture (jhum) at lower elevations of the Jhasi Hills of Meghalaya. As such an attempt has been made to relate the present studies on the Lailad forest with the ecology of shifting agriculture in this region under "General considerations related to shifting agriculture (jhum) around Lailad" given at the end of this section. The study has 6 chapters dealing with study area, vegetation analysis, biomass production, litter dynamics, nutrient input into and output from the system and nutrient cycling.

Section II of the thesis is based on plantation studies on Shorea robusta Gaertn., growing at Umtesor which is in the same general geographical areas as that at Lailad. Shorea robusta which is a late successional tree and which is also an important component in a 50 year stand at Lailad has been studied in detail using 9 to 19 year old plantations. This section is divided

into 2 chapters one dealing with growth analysis and productivity of S. robusta and the other dealing with intra-system nutrient flow through soil, plant litter and biomass.

The thesis has a General Introduction dealing with a review of literature on forest ecosystem analysis. Each chapter has a brief 'Introduction' and 'Methods of Study.' Results and Discussion on the findings is given for each chapter, followed by 'Summary.'

GENERAL INTRODUCTION

Vegetation Analysis :

Vegetation may be defined as an assemblage of plants growing together in a particular location and may be characterised either by its component species or by a combination of structural and functional characters that characterise the appearance or physiognomy of the vegetation. Structural or physiognomic methods do not demand species identification and are often considered more meaningful for detailed ecological studies. The changing nature of vegetation is its dynamic nature, that is changes in the distribution and structure of components occur in due course of time. The long term changes of the vegetation 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 vegetation or community are a complex subject and have been reviewed by Margalef (1968) and Odum (1963).

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 examining plant community in greater detail as a dynamic unit.

In nature plants rarely grow isolated from one another. Individuals of a species are usually grouped into a population and populations of different species may be intermingled. Some of the plants grow more successfully than the others as indicated by their behaviour, size and number. 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 interrelations it forms with other species.

A common approach for vegetation analysis is the gathering of species abundance data from numerous study areas. A large number of such phytosociological studies have yielded considerable information on community-environment 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 of Ashton (1964a,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 of floristic data. Their results suggested that composition and classification methods are useful for analysing the vegetation and that certain species-rich communities also yield diagnostic and comprehensive ecological informations. Webb (1969), William and Webb (1969), Webb et al (1970), Budowski (1970) and Orloci and Mukkattu (1973) used physiognomical, structural and floristic features for vegetational analysis and classification. Many other workers considered the physical and chemical properties of the soil for composition and species distribution. A number of other workers based phenological studies for community analysis and classification. (Rees, 1964; Gibbs and Leston, 1970; Doubenmire, 1972; Frankie et al, 1974).

Biomass production :

Improved demands for forest products, the search for renewable source of raw materials and increased interest in the structure and function of forest ecosystems, in recent years, has stimulated research in biomass and production of different forest types throughout the world. The accumulation of large quantities of dry matter is a fundamental and distinguishing characteristic of forest ecosystems.

Total biomass itself is not a measure of productivity so far as forests are concerned. The biomass of forests is rather a function of age because stem biomass, which is accumulated year after year occupies extremely high percentage of the total biomass. In north temperate regions, productivity studies have been done for a number of species growing in even aged plantations or uneven aged natural or semi-natural woodlands (Westlake, 1963; Ovington, 1965; Whittaker, 1966; Whittaker and Woodwell, 1968). The geographical patterns of biomass distribution per unit area for the major types of terrestrial vegetation have been summarized by Rodin and Bazilevich (1967). Besides the information collected by these two authors additional data on biomass of different regions of the world was obtained during the International Biological Programme (Molchanov,

1964; Bazilevich, 1967; Kira and Shidei, 1967; Golley et al, 1969; Jenik, 1971; Whittaker, 1971).

In the past few years, biomass estimates of individual species have been published by a number of workers. Such studies included the information on the productive structure of the stand only. Although the weights of sample trees are frequently estimated by subsampling, very little information in the accuracy and precision of existing methods are available (Ellenberg, 1971; Hughes, 1971; Kestemont, 1972, 1973; Neuwirth, 1972; Yamakura et al, 1972; Egunjobi, 1975). Overton et al (1973) have discussed the physical problem of estimating weights of very large trees. Art and Marks (1971) presented a working table of major species, the age and the location of the stand, the oven-dry weight of biomass and net annual productivity for about 280 forest stands. Madgwick (1976) briefly reviewed the literature concerning the methodology of estimating sample trees and stand weights with emphasis on statistical methods.

Since 1955, many studies on primary productivity of forest ecosystems, have been published by Japanese workers in temperate and tropical forests. These studies were mostly based on harvest methods (Kira and Schidei, 1967

and Newbould, 1967). The data obtained from more than three hundred stands were reviewed by Kira and Schidei (1967); Tadaki and Hatiya (1968) and Satoo (1968, 1970, 1971) while Ogawa et al (1965) have made some critical account of plant biomass for two luxuriant forests of tropical Africa.

Burger (1951) estimated leaf and branch weights in a large number of Swiss woodlands which vary in age from 13 to 92 years. Moller (1947) evaluated the dry weights for leaves of oak, ash, birch, spruce, scots pine and larch. Satoo et al (1955, 1956, 1959), Satoo and Senda (1958) in Japan and Whittaker (1965) in USA estimated the leaf and branch biomass and reported that leaf biomass cannot increase infinitely with forest growth and that there must be a limit specific to species or groups of ecologically similar species.

The estimation of biomass of individual tree or a stand by harvest method is the basic procedure for production relations. But this is very laborious and is neither practical nor permitted under many circumstances. Therefore, allometric relations based on some easily measurable variables such as diameter at breast height, plant height, diameter at the crown base and various

measures of crowns have been used with success in developing prediction equations for individual tree components and stand of trees (Ovington and Madgwick, 1959; Attiwill, 1962; Baskerville, 1965; Ovington et al, 1967; Peterson et al, 1970; Zavitkovski and Stevensen, 1971). However, for estimation of crown, branch and foliage dry weight correlations with the diameter at the crown base or branch diameter usually give the best results (Attiwill, 1962; Peterson et al, 1970).

The woodland community with its various strata forms a complex association in which the reactions of different members are closely interrelated. Trees are the dominants of the community and by virtue of their size, stratification and longevity, they are able to determine to some extent the site conditions under which the associated plants live (Ovington, 1959). The contribution of ground vegetation is of great importance for a number of ecosystem processes (Ovington, 1962). In contrast to the tree cover, ground vegetation production has a high proportion of leafy material and a low proportion of biomass (Hughes, 1971). The production relationship between species in the ground vegetation which determine

the process of natural regeneration of the woodland has been evaluated by Toumey and Kienholz (1931). That the tree cover which intercepts radiation, precipitation and other environmental factors influence the growth and relative performance of species on different woodlands have been shown by Blackmann and Rutter (1947), Begley (1955) and Ford and Newbould (1970).

Litter dynamics :

The amount and composition of the annual litter fall has long been considered to be of major importance for exchange of organic and inorganic materials between living organisms and soil. The role of litter in the forest ecosystem has been recognised for a long period of time and consequently many investigations have been made in its relation to productivity, nutrient cycling, energy flow and decomposition of forest organic matter. Bray and Gorham (1964) in their review of literature on litter production by the major world's forests state that in "the study of the quantitative aspects of litter fall remains an important part of forest ecology, dealing with a major pathway for both energy and nutrient transfer". The litter is the fuel for nutrient cycling in the upper

soil horizons and is of importance in the nutrition of woodlands particularly on soils of low nutrient status, where the trees rely to a great extent upon the recycling of litter nutrients. In order to understand the biological process of the upper soil horizons, the quantity and composition of the litter and its pattern of fall throughout the year must be known.

The dynamics of litter accumulation process are of particular interest in the humid tropical forests where rates of litter production and decomposition are high. Litter in these forests accumulate on the soil until litter fall equals litter decomposition, after which a mean steady state ratio will be maintained.

Considerable amount of data exists for litter production and nutrient release in forest ecosystems, but still the literature on litter dynamics in tropical forests is much less and this is evident from the comprehensive review of work of Bray and Gorham (1964) which contain approximately 275 references of which a very minor fraction pertain to tropical forests. Seasonal litter fall in deciduous forests has been studied by Carlisle et al, (1966a), Sykes and Bunce (1970), Hughes (1971),^{and} Gosz et al (1972) but comparisons among species

and years have been limited largely to total annual litter fall.

The litter consists of dead or decaying leaves, twigs, branches, flowers, fruits, bark and other debris. Out of these, leaf happens to be the major source of litter which may fall seasonally as is the case of deciduous trees or it may continuously accumulate throughout the year as we find in evergreen forests. The litter is attacked by a variety of micro-organisms and is decomposed to such a degree that eventually it becomes an inseparable ingredient of the soil system.

Information on litter production in aspen stand is available for the U.S.S.R. (Rodin and Bazilevich, 1967) and also for Alaska (Van Cleve and Noonan, 1971). In northern Wisconsin, U.S.A., Crow (1974) studied litter fall in predominantly aspen and aspen-paper birch stands. In tropical forests of Africa nutrient content of litter has been studied by Laudelaout and Meyer (1954), Ney (1961), Hopkins (1966), Bernehard (1970) and Egunjobi (1974). Similar studies on litter fall and 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 and Zavlkovoski and Newton, 1971). In New Zealand's evergreen beech forests litter fall has been measured by Miller and Hurst (1957) and Miller (1963).

Many studies on the seasonal dynamics of litter fall in forest ecosystems are available though only a few detailed studies on the dynamics of wood litter have been published. The wood litter fall in forest ecosystem is generally characterised by a great annual variation but lack of a clear seasonal pattern. This is mainly due to the non-periodic occurrence of high wind force during which dead wood material is dislodged. However, other factors may act in a complex way creating a seasonal pattern in the dynamics of wood litter fall.

Bray and Gorham (1964) suggested that woody litter amounts to about 30% of the total annual litter fall. This means that a considerable proportion of litter fall in forest ecosystems accumulates as dead wood in the wood fraction of soil litter, constituting a significant nutrient and energy reservoir (Healey and Swift, 1971). The production of dead leaves and dead wood, which trophically form the basis for many consumer chains play an important role in ecosystem functioning (Duvigneaud, 1971; Kestemont, 1971).

In temperate deciduous forests 19-39% of total annual litter fall is formed by the wood fraction (Christensen, 1975, 1978) resulting in a significant amount of dead wood in the forest floor. Although dead wood is poor in nutrients, a remarkable amount of minerals and especially energy may be released through the dead wood fraction which play an important role in mature forest ecosystem (Healey and Swift, 1971). Generally a relationship between peak wood fall and maximum wind speed always exists. In a temperate forest, Gosz et al (1972) found a bimodal pattern of wood fall and they pointed out that branch fall is apparently a good indicator of storm intensity. In a moist semi-deciduous forest in tropical West Africa, the peak wood fall corresponds to the dry season when the trees are expected to be under greatest water stress, and a complex combination of intrinsic and extrinsic factors influences the timing and triggering off of litter fall (Jones, 1955). Addicott (1970) noted that almost all discrete parts of several high plant species are abscised. However, abscission of organs other than leaves and to a lesser extent flowers and fruits has received only sporadic attention. 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) as compared with chemical and microbiological sides of the process (Kaarik, 1974).

Most of the studies on litter decomposition pertain to leaf litter only. However, wood litter also form a large proportion of the substrata decomposed on forest floor. The non-^{leaf}litter accounts for about $\frac{1}{3}$ of the total litter fall in most forests, sometimes as much as $\frac{1}{2}$ in climax forests (Kira and Schidei, 1967). Woody organs decomposed more slowly than leaves, while their original shape and volume are maintained for quite a long time under the protection of bark which is very resistant to decay. Yoneda (1975 I,II) made an attempt to estimate 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.

Litter decomposition is a desimilation process mediated by a succession of organisms and associated enzyme systems (Alexander, 1961). The oxidation and hydrolytic process converts the raw litter to carbon-dioxide and stabilised organic matter or humus. The mineralisation of organic to CO_2 which represents a major carbon loss or

output route whereas humus formation may be regarded as a key carbon reservoir or conservation pathway. In most of the terrestrial systems, the decomposition of litter forms the major source of energy and nutrients for the soil and litter organisms of the deciduous woodlands. A great proportion of carbon fixed by the autotrophs return to the soil in the form of litter. The most important groups of organisms which play a role in decomposition are bacteria, actinomycetes, fungi, protozoa, nematodes, worms etc. 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 and Gilbert, 1957; Edwards and Heath, 1963; Howard, 1965; Van-Cleave, 1971; Anderson, 1973b, Gosz et al., 1973; Howard and Howard, 1974; Jensen, 1974; Suffling and Smith, 1974; Wood, 1974). The process and organisms concerned in decomposition had mainly been studied by Bell (1974), Dickinson (1974), Edwards (1975), Frankland (1974), Harding and Stuttard (1974), Jensen (1974), Mason (1974), Millar (1974), Pugh (1974), William and Gray (1974), and Wood (1974).

The soil respiration is another biological phenomenon of decomposition which has long been considered as an

index of soil metabolism (Wollny, 1831; Boussingault and Levy, 1853, Mina, 1962 and Reiners, 1968). Measurements of soil respiration are widely accepted as being the most important approach for studying the biological activities and the carbon and energy flows with respect to detritus ecology. The soil respiration is generally governed by the three biological process (a) microbial respiration (b) root respiration and (c) faunal respiration and one non-biological process i.e. chemical oxidation (Bunt and Rovira, 1954).

Although the study of litter production is of great significance in forest ecology, not much work has been done on this aspect under Indian conditions. In India estimation of annual litter production in deciduous and in some evergreen forests have been made by Champion (1936), Puri (1953), Seth et al (1963), Singh (1968), Faruqi (1972) Billore and Amrithphali (1975) have also determined the nutrient content of litter fall. Most of the Indian workers mentioned above have worked with reference to forest plantations while practically no work is available on natural humid mixed forest types of India.

Rainfall interception, throughfall, stemflow and nutrient losses through run off and percolation :

The amount of incoming precipitation transmitted to

or into the soil is of great importance to understand the water regime of plant communities. The diverse physiognomical structure of various plant associations plays an important role in precipitation interception and the amount of precipitation which is arriving on the soil surface. The precipitation generally falling on vegetation is usually leached in different ways. Some of the water reaches the ground through the canopy, some through the tree trunk and some part is intercepted by the vegetal cover which never reaches the ground. The amount of water which drips down through the forest canopy is referred to as throughfall; stemflow refers to the precipitation which reaches the ground by running down the boles of trees. The amount of water which is retained by the vegetal cover subsequently evaporates back to the atmosphere and is called the intercepted water. The interception of precipitation by vegetal cover is an important aspect of hydrological cycle influencing the water budget and nutrient movement, and plays an important role in the net rainfall reaching the ground surface. The quantities and modes of flow of precipitation to the forest floor have been studied for a long time. Interception studies have been reviewed by Kittredge (1948) and Zinke (1967). A number of studies

have been done on this aspect by different workers (Hamilton and Rowe, 1949; Hoover, 1953; Ovington, 1954; Voigt, 1960; Rutter, 1963; Helvey, 1967; Smith, 1974).

Interception by the canopy usually affect the chemistry of the throughfall in a number of ways (Eaton et al, 1973). (1) Some of the chemicals which the precipitation contain are retained in the canopy and will not appear in the throughfall at that time (2) some of the nutrients may be leached into the water at the time of interception by the leaves and deposited as salts on the leaf surface as the water evaporates (3) although the concentration of nutrients in throughfall increases than in the original precipitation, it is apparent that nutrients can be absorbed into the leaves from the water (Boynton, 1954; Carlisle et al, 1965 and Wittwer and Teubner, 1969) or be taken up by the microflora on the surface of the leaves and branches (Carlisle et al, 1967). Moreover, the extent of precipitation interception by the forest canopy is affected by tree species, size and form of the tree as well as storm size and intensity (Ovington, 1954b; Gieger, 1965; Carlisle et al, 1965).

In forest ecosystems, a significant portion of the

nutrient is recycled into the soil by means of leaf litter and its decomposition and also through precipitation. Duvigneaud et al (1971) reported that in temperate forests $\frac{3}{4}$ of the total amount of circulating minerals are returned to the soil with leaf litter, throughfall and stem flow. Almost half of the total amount of potassium arrives into the soil with canopy throughfall and stem flow annually (Carlisle et al, 1967; Nebe, 1973). A large portion of magnesium finds its way back to the soil in the same way, and in case of calcium and sodium the return through litter and decomposition is probably of greater significance. The importance of water dripping from the tree crowns and the role of minor tree litter fraction (bud scales, male flowers, cupules, bark, etc.) in the nutrient cycling of a sessile oak (Quercus petraea) woodland on a low fertility siliceous site in a high rainfall area has been demonstrated by Carlisle (1965) and Carlisle et al (1966a, b).

A significant amount of nutrients is also transferred from the various plant parts to the soil as precipitation which passes through the forest canopy, the elements being added directly to the available nutrient pool without the intervention of any process of decomposition on the forest floor. The total ecosystem approach for quantifying nutrient

budget and cycling phenomena of the northern hardwood forest has been successfully done by Bormann and Likens (1967). Several studies (LeClerc and Breazeale, 1908; Nes, 1954; Tukey and Amling, 1958; Tukey et al, 1958) have demonstrated that rainfall may remove substantial quantities of nutrients from the foliage of horticultural plants. Others have shown that rainwater which passes through the tree crown contain significantly higher quantities of many nutrient elements than rainfall collected in adjacent openings (Tamm, 1951; Madgwick and Ovington, 1959; Will, 1959; Voigt, 1960; Rahman, 1964; Cole et al 1968; Tarrant et al 1968). It is only recently that the study of input and deposition of nutrients from the atmosphere by way of precipitation into the ecosystem has attracted attention. Nye (1961); Carlisle et al (1967) and Reiners (1972) have measured the quantity of nutrient in precipitation received by different ecosystems and emphasized the role of vegetation in enriching the mineral content of rainwater. The quantity of minerals present in rainwater can be of special significance in the nutrient cycle of ecosystems especially in nutrient poor areas (Allen et al, 1968).

The leaching of elements from the forest canopy by

precipitation is mainly dependent on the fact that an element must be present, indicating either a biological requirement or a non-selective uptake of the element by the plants. Elements which are present in large amounts in the leaves are leached in larger absolute quantities, but in some cases leaching may be independent of the amounts present in the leaves.

The atmosphere is a source of chemical to terrestrial ecosystems, as well as a source of water vapour for precipitation. Chemicals may become bonded with water vapour and delivered in a dissolved form with precipitation. Some of the chemicals like chlorine and sodium are commonly dissolved in precipitation which falls along ocean coasts (Grumbell and Fisher, 1966) or chemicals may adhere to dust particles which become temporarily suspended in the atmosphere and returned to the surface as dry fall out between storms. The large surface area of the foliage which is exposed to wind and interception of rainwater by forest vegetation, plays an important role as a trapping device for dust particles, and rainfall which drips from the foliage (throughfall) may be substantially enriched in some chemical elements.

Precipitation water carries certain quantities of nutrients from air borne dust, gases, etc; the composition of which undergoes significant changes once they gain access to the ecosystem (Tamm, 1958; Stenlid, 1958; Tukey, 1970). This rainwater when falling on foliage surface, branches and stems of trees in forested ecosystems washes off the dust and thereby leaches a portion of the nutrient elements from them.

The chemistry of precipitation varies from area to area depending on the origin of air masses. Gore (1968) reported that 32.14 kg/ha of sodium is deposited annually by the precipitation from maritime air masses at Moor House, U.K. but Likens et al (1971) reported that the annual deposition of sodium is only 1.5 kg/ha at Hubbard Brook where air masses are primarily continental. The Ca/Mg ratio in precipitation has been used as an indicator of the source of air borne chemicals by some workers (Eriksson, 1952). Again, the intensity of rainfall affects the nutrient input through precipitation. Mecklenburg et al, (1966) and Attiwill (1966) showed that the amount of nutrients leached per unit quantity is greater during a low intensity of rain than it is during a heavy rain. Attiwill (1966) found that the decrease in nutrient content

of leaves is greatest during the first hours of wetting.

The stimulation of nutrient mobilisation in the forest soil after clear cutting has been known for a long time but no attempt has been made so far to measure the losses of nutrient from the system through run-off of water or that percolating through the soil. The clear cutting of forest cover tends to increase stream water flow (Lull, 1959; Hornbeck et al, 1970; Pierce et al, 1970; Pierce et al, 1972) and stream temperature (Tamm, 1958). The amount of nitrogen discharged from a forested ecosystem after clear cutting is equivalent to the amount of nitrogen that is annually returned to the system under undisturbed conditions and losses of cations were 2 to 3 times greater than from an undisturbed system (Bormann et al, 1968, 1969).

Nutrient Cycling :

Ecosystem represents complex organization of living organisms, interacting with each other and with their physical environment. In attempts to understand such complex systems, ecologists group their components into a number of more or less easily definable categories. One of the most important functions of the forest ecosystem is nutrient cycling and a knowledge of this is needed to obtain high productivity required to meet the increasing demands for forest products.

The detailed information on nutrient cycling is especially important because it defines the relationship between soil and plants. Numerous studies have been conducted in different geographical regions of the world assessing the means and distribution of nutrients in various forest ecosystems. Much of this work has been summarized by Rodin and Bazilevich (1967) and Ovington (1968). Cole et al (1968) Marks and Bormann et al (1972) emphasized the effect of fertilizer and clear cutting in nutrient cycling.

During the past decade, ecologists have become increasingly interested in the flow of nutrients through ecological systems and in the role that these particular ecosystems play in the larger biogeochemical cycles of the earth. 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 (Duvigneaud and Denaeyer-De Smet, 1964; Ovington, 1965; Cole et al, 1968; Bormann and Likens, 1970 and Jorgensen et al 1975) have carefully evaluated the size and rates of exchange between various nutrients pools. However, measurements of systems present major difficulties and only a few quantitative studies have so far been done (Likens et al, 1967), particularly in tropics.

Quantitative approach of nutrient budgets for a terrestrial ecosystem may be determined by measuring the meteorological, geological and biological inputs and outputs (Bormann and Likens, 1967). The terrestrial ecosystem participates in the various larger biogeochemical cycles of the earth by input and output through the system. Geological input and output through balance of mineral elements in an ecosystem may be positive or negative, that is elements can be accumulating in the systems or the system can be in the process of depletion. Accumulation of elements in the biotic portion of the ecosystem often occurs as a result of successional process (Odum, 1969) as the amount of biomass in an system increases. The elements through geological inputs are generally carried into the system by moving water or colluvial action, or both, and outputs generally refer to the elements which are leaving the system in the form of dissolved or particulate matter in moving water, through the diffusion or transport of gases or particulate matter by wind (meteorological output) or as a result of the activity of animals including man (biological output). Meteorological input enters the ecosystem through the atmosphere in the form of gaseous materials and of dissolved or particulate matter in precipi-

tation, dust and other wind borne materials.

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 and Bazilevich (1967) and Duvigneaud and Deneyer-De Smet (1970) along with comprehensive reviews and synthesis of data by Bray and Gorham (1964), Bakuzis (1964), Overton et al (1973), Larcher (1975), Jorgensen et al (1975) and Lieth and Whittaker (1975) have brought considerable attention to the process of nutrient cycling and production in forest ecosystems.

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 the litter from the vegetation cover. Smirnova and Gorodentseva (1958) reported that in birch woodlands of about 70 years age, annual defoliation returns 80 to 90 percent of the nutrients to the soil. Litter which include the leaves, bark, branches, dead stems, inflorescences and seeds are usually the largest components for the nutrient cycling in the forest ecosystem. However, in open woodlands the well developed

shrubs and herb layers may contribute more litter than that from trees (Scott, 1955). The litter falling to the ground in woodlands is very heterogenous being composed of organic material differing greatly in structure and chemical composition and the mechanism and efficiency of litter breakdown varies greatly even in the same wood. (Alway and Zon, 1930, Wittich, 1939; Mork, 1944; Tarrent et al, 1951; Owen 1954; Gosz et al, 1972). The importance of soil organic matter in mature forest ecosystem was emphasized by Rodin and 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 (Laudelout and Meyer, 1954; Nye, 1961; Witkamp and Olson, 1963; Olson, 1963; Bray and Gorham, 1964; Ovington, 1965; Bernhard, 1970; Anderson, 1973; Gosz et al, 1973; Lousier and Parkison, 1976).

In order to evaluate the quantitative and qualitative aspects of productivity or to explore the nutrient cycling in the ecosystem, the knowledge of water circulation pattern in time and space is very important. Water circulation itself is a very complex process and it mainly deals with

the pathway of water reaching the ecosystem in the form of precipitation to the soil, water in the soil, output of nutrient through water etc. And it is only in the last two decades that the study of the nutrients input and deposition from the atmosphere by way of precipitation is becoming of increasing interest. (Tamm, 1951, Viro, 1953, Madgwick and Ovington, 1959; Tukey and Tukey, 1959; Voigt, 1960; Nye, 1961; Carlisle et al, 1965, Likens, et al, 1967; Bormann and Likens 1967; Tarrant et al, 1968; Cole et al, 1968; Allen et al, 1968; Ulrich et al 1971; Reiners 1972; Szabo and Csontos, 1975).

Available nutrient not only enter the ecosystem from outside but are added by the action of physical chemical and biological weathering of rock and soil minerals. Physical and chemical weathering of the mineral soil and sub-soil increases the availability of nutrients in forest ecosystems but little is known of the release of nutrients by this process under natural conditions. The release of nutrients by weathering will depend greatly upon the soil type and underlying rocks but is also influenced by climate and the nature of the woodland.