

**STUDIES ON INTERRELATIONSHIP BETWEEN TREE
DIVERSITY AND N AND P DYNAMICS IN A HUMID
SUBTROPICAL FOREST ECOSYSTEM OF MEGHALAYA**



By
JENPUIRU KAMEI

**THESIS
SUBMITTED IN FULFILMENT
OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN BOTANY**

**NORTH-EASTERN HILL UNIVERSITY
SHILLONG
2007**

NORTH EASTERN HILL UNIVERSITY

DEPARTMENT OF BOTANY

August, 2007

I, Miss Jenpui Kamei, hereby declare that the subject matter of this thesis is the record of work done by me, that the contents of this thesis entitled "*Studies on interrelationship between tree diversity and N and P dynamics in a humid subtropical forest ecosystem of Meghalaya*" did not form basis of the award of any previous degree to me or to the best of my knowledge to anybody else, and that the thesis has not been submitted by me for any research degree in any University/ Institute.

This is being submitted to the North Eastern Hill University for the degree of Doctor of Philosophy in Botany.



Jenpui Kamei
(Jenpui Kamei)

[Signature]

(Head, Department of Botany
North-Eastern Hill University)

Department of Botany
School of Life Sciences
N.E.H.U., Shillong-22

[Signature]

(Supervisor)

ACKNOWLEDGEMENT

I express my heartfelt and sincere gratitude to my Supervisor Professor H.N. Pandey for his guidance, keen interest, generosity and encouragement throughout the study. I am thankful to my teacher Professor S.K. Barik for his valuable suggestion, encouragement and help in many ways till the end of the study. I am grateful to them for making my research experience interesting and challenging.

I am thankful to Professor N.K. Chrungoo, Head of the Department of Botany and Professor A.K. Misra, the previous Head of the Department of Botany for extending the laboratory and library facilities.

I am thankful to my labmates Dr. V. Ralte, Dr. S.D. Prabhu, Dr. Dibyendu Adhikari, Dr. A. Rahman, Kanhaiya, Shairi, Biswarupa, John, Mark, Arun, Eva, Ratul, Wishfully, Lucy and Debashree who rendered invaluable help and co-operation in the field as well as in the lab. I could not have done it without their help and moral support.

I extend my special thanks to Dr. Krishna Upadhaya who was always willing to help no matter what and brightened my days.

I am also grateful to Mr. Orstar Swer, headman of Swer village for kind permission, cooperation and support during the study period.

I am also thankful to all the teaching and non teaching staff of the Department of Botany for rendering as much possible help as they could.

Thanks to Vidya, Geetanjali, Raseshwori, Grace, Athailu, Kaguisillu, Stadwelson, Meena, Nabanita and Shiny who have always been ready to listen and kept me sane.

I extend my deep sense of gratitude to my parents, brothers, and sister-in-laws for their moral support and encouragement throughout the study. Words fail to express my thanks to my father for his direction, input and help in keeping my perspective.

Financial support received from UGC-DSA Programme and UGC-RGNF in Botany is gratefully acknowledged.

Above all, I thank Almighty Apou Tingkao Ragwang for showering His divine love and grace and for giving me the will power and strength in overcoming all hurdles during the completion of the work.

Shillong

Dated 24th Aug 2007

Jenpuru Kamei
(Jenpuru Kamei)

CONTENTS

	Page No.
CHAPTER I INTRODUCTION	1 - 7
CHAPTER II REVIEW OF LITERATURE	8 - 23
CHAPTER III STUDY SITE AND EXPERIMENTAL DESIGN	24 - 36
CHAPTER IV FOREST MICROCLIMATE AND SOIL PHYSICO-CHEMICAL PROPERTIES	37 - 56
CHAPTER V LITTER DYNAMICS	57 - 78
CHAPTER VI FINE ROOT DYNAMICS	79 - 90
CHAPTER VII NITROGEN AND PHOSPHOROUS INPUT, ACCUMULATION AND RELEASE THROUGH LITTER AND FINE ROOTS	91 - 108
CHAPTER VIII SOIL MICROBIAL BIOMASS C, N AND P AND NUTRIENT MINERALIZATION	109 - 130
CHAPTER IX GENERAL DISCUSSION	131 - 144
SUMMARY	145 - 152
REFERENCES	153 - 166

List of Figures

		Page No.
Figure 3.1	Map showing geographical location of the study site	25
Figure 3.2	Mean monthly rainfall (mm) and temperature (°C) at Cherrapunjee during the study period (September 2004 to September 2005)	27
Figure 3.3	Distribution and canopy cover of tree species in <i>Myrica esculenta</i> plots	33
Figure 3.4	Distribution and canopy cover of tree species in <i>Rhododendron arboreum</i> plots	34
Figure 3.5	Distribution and canopy cover of tree species in <i>Neolitsea cassia</i> plots	35
Figure 3.6	Distribution and canopy cover of tree species in Mixed plots	36
Figure 4.1	Monthly variations in light intensity in open and in different experimental plots	41
Figure 4.2	Relative average percent reductions in light intensity in different experimental plots in relation to open areas outside the forest	42
Figure 4.3	Monthly variations in air temperature in different experimental plots and outside the forest in open	43
Figure 4.4	Relative average percent reductions in air temperature in different experimental plots in relation to open area outside the forest	43
Figure 4.5	Monthly variations in relative humidity in different experimental plots and in open area outside the forest	44
Figure 4.6	Monthly variations in soil temperature in the experimental plots	47
Figure 4.7	Monthly variations in soil moisture content in the experimental plots	48
Figure 4.8	Monthly variations in soil pH in different experimental plots	49
Figure 5.1	Monthly litterfall patterns of leaf litter of dominant tree species and total litter of the experimental plots	63
Figure 5.2	Decay pattern of leaf litter of dominant tree species and mixed leaf litter (including leaf litter of dominant species) in the experimental plots	70
Figure 6.1	Monthly variations in fine root dry mass in different experimental plots	83
Figure 6.2	Monthly fine root productions in different experimental plots	84
Figure 6.3	Decay patterns of fine roots in different experimental plots	87
Figure 7.1	N release pattern from confined leaf litter in different experimental plots	98
Figure 7.2	P release pattern from confined leaf litter in different experimental plots	99
Figure 7.3	N release patterns from decaying fine roots in different experimental plots	102
Figure 7.4	P release pattern from decaying fine roots in different experimental plots	103
Figure 8.1	Variation in ammonium nitrogen (NH ₄ -N) in surface soil layer (0–10 cm) in different experimental plots	117
Figure 8.2	Variation in nitrate nitrogen (NO ₃ -N) in surface soil layer (0–10 cm) in different experimental plots	117
Figure 8.3	Net nitrification rate in surface soil layer (0–10 cm) of experimental plots	118
Figure 8.4	Net N mineralization rate in surface soil layer (0–10 cm) of experimental plots	118
Figure 8.5	Variation in inorganic phosphorus (PO ₄ -P) in surface soil layer (0–10 cm) in experimental plots	119
Figure 8.6	Net P mineralization rate in surface soil layer (0–10 cm) of experimental plots	119

List of Tables

		Page No.
Table 3.1	Composition, density (per 300m ²) and basal area (m ² per 300m ²) of tree species in the experimental plots	29
Table 3.2	Shrubs present in experimental plots	30
Table 3.3	Herbs present in experimental plots	31
Table 3.4	Mean density, basal area and canopy cover of tree species in the experimental plots (each value is a mean of 3 replicates)	31
Table 4.1	Two way ANOVA showing effects of months and experimental plots on light intensity (Lux), air temperature (°C) and relative humidity (%)	44
Table 4.2	Mean light intensity (Lux), air temperature (°C) and relative humidity (%) in different experimental plots (each value is a mean of 39 measurements taken between September 2004 and September 2005)	45
Table 4.3	Proportion of soil particles (%), textural class, bulk density (BD, g cm ⁻³), porosity (%) and water holding capacity (WHC, %) in different experimental plots	46
Table 4.4	Seasonal variation in soil organic carbon content (SOC, %) and soil organic matter content (SOM, %) in different experimental plots	50
Table 4.5	Seasonal variation in total Kjeldahl nitrogen (TKN, %) in soils of the experimental plots	51
Table 4.6	Seasonal variation in soil available phosphorus (µg g ⁻¹) in the experimental plots	51
Table 4.7	Two way ANOVA showing effects of months/seasons and experimental plots on temperature (°C), moisture content (SMC %), pH, organic carbon (SOC %), organic matter (SOM %), total Kjeldahl nitrogen (TKN %) and available phosphorus (Av.P µg g ⁻¹) in soils of the experimental plots	52
Table 4.8	Mean physico-chemical properties of soils of the experimental plots (each value is a mean of 45 replicates taken across five seasons)	52
Table 5.1	Monthly litterfall (kg ha ⁻¹) in <i>Myrica esculenta</i> plots	64
Table 5.2	Monthly litterfall (kg ha ⁻¹) in <i>Rhododendron arboreum</i> plots	64
Table 5.3	Monthly litterfall (kg ha ⁻¹) in <i>Neolitsea cassia</i> plots	65
Table 5.4	Monthly litterfall (kg ha ⁻¹) in Mixed plots	65
Table 5.5	Mean annual accumulation (kg ha ⁻¹), production (kg ha ⁻¹ yr ⁻¹), turnover rate (k, yr ⁻¹) and turnover time (yr) of litter on the forest floor in different experimental plots	66
Table 5.6	Initial chemical composition of leaf litter of dominant tree species and mixed leaf litter in the experimental plots. (± SE, n=3)	68
Table 5.7	Annual decay constant (k) of leaf litter of dominant tree species and mixed leaf litter in different experimental plots	71
Table 5.8	Mean weight loss (%) of leaf litter of dominant tree species and mixed leaf litter (including leaf litter of dominant tree species) in different experimental plots (each value is a mean of 39 measurements taken between September 2004 and September 2005)	71
Table 5.9	Analysis of variance of weight loss between litter types in different plots	71
Table 5.10	Relationship between weight loss of leaf litter of dominant tree species and soil properties and decay rate and chemical composition	71
Table 5.11	Relationship between weight loss of mixed leaf litter (including leaf litter of dominant tree species) and soil properties, decay rate, and chemical composition	72
Table 6.1	Mean annual dry mass (kg ha ⁻¹), production (kg ha ⁻¹ yr ⁻¹), turnover rate (k, yr ⁻¹) and turnover time (t, yr) of fine roots in different experimental plots	85
Table 6.2	Initial chemical composition of pre decomposing root in different experimental plots (± SE, n=3)	85
Table 6.3	Annual decay constant (k) of fine roots in different experimental plots	86
Table 6.4	Analysis of variance showing effect of months and experimental plots on weight loss	86
Table 6.5	Relationship between weight loss of root and soil properties and decay rate and chemical composition	87
Table 7.1	Chemical composition of litter in different experimental plots (±SE, n=3)	95

Table 7.2	Chemical composition of pre-decomposing fine roots in different experimental plots (\pm SE, $n=5$)	96
Table 7.3	Mean annual accumulation (kg ha^{-1}), input ($\text{kg ha}^{-1}\text{yr}^{-1}$), turnover rate (k, yr^{-1}) and turnover time (t, yr) of N and P through litter on the forest floor in different experimental plots	96
Table 7.4	Mean annual accumulation (kg ha^{-1}) and input ($\text{kg ha}^{-1}\text{yr}^{-1}$) of N and P through fine roots and their turnover in different experimental plots	96
Table 7.5	Annual mineralization constant (k_N and k_P) of leaf litter of dominant tree species and mixed leaf litter in different experimental plots	100
Table 7.6	Annual mineralization constant (k_N and k_P) of fine roots in different experimental plots	102
Table 7.7	N and P released (%) of initial content from decaying leaf litter and fine roots in different experimental plots during 400 days	104
Table 7.8	Relationship between weight remaining and nutrient mineralization and N and P concentration in decomposing litter (leaf litter of dominant tree species, mixed leaf litter and root) across the experimental plots	104
Table 8.1	Seasonal variation in soil microbial biomass carbon ($\mu\text{g g}^{-1}$) in different experimental plots (\pm SE)	114
Table 8.2	Seasonal variation in soil microbial biomass nitrogen ($\mu\text{g g}^{-1}$) in different experimental plots (\pm SE)	114
Table 8.3	Seasonal variation in soil microbial biomass phosphorus ($\mu\text{g g}^{-1}$) in different experimental plots (\pm SE)	115
Table 8.4	Two-way ANOVA showing effects of seasons and experimental plots on soil microbial biomass carbon (MBC $\mu\text{g g}^{-1}$), microbial biomass nitrogen (MBN $\mu\text{g g}^{-1}$) and microbial biomass phosphorus (MBP $\mu\text{g g}^{-1}$)	115
Table 8.5	Mean soil microbial biomass –carbon (MBC $\mu\text{g g}^{-1}$), –nitrogen (MBN $\mu\text{g g}^{-1}$) and –phosphorus (MBP $\mu\text{g g}^{-1}$) and their contribution (%) to soil organic carbon (SOC) and total nitrogen (TKN) in different experimental plots (each value is a mean of 45 replicates across 5 seasons)	116
Table 8.6	Two way ANOVA showing the effects of months and different experimental plots on ammonium nitrogen ($\text{NH}_4\text{-N}, \mu\text{g g}^{-1}$), nitrate nitrogen ($\text{NO}_3\text{-N}, \mu\text{g g}^{-1}$), phosphate phosphorus ($\text{PO}_4\text{-P}, \mu\text{g g}^{-1}$) and N and P mineralization rate ($\mu\text{g g}^{-1}\text{month}^{-1}$)	120
Table 8.7	Mean concentration of ammonium nitrogen ($\text{NH}_4\text{-N}, \mu\text{g g}^{-1}$), nitrate nitrogen ($\text{NO}_3\text{-N}, \mu\text{g g}^{-1}$), phosphate phosphorus ($\text{PO}_4\text{-P}, \mu\text{g g}^{-1}$) and N and P mineralization rate ($\mu\text{g g}^{-1}\text{month}^{-1}$) in different experimental plots [values are the means of 13 months across the year ($n=117$)]	120
Table 8.8	Relationship between MBC, MBN and MBP ($\mu\text{g g}^{-1}$) and soil physico-chemical properties and litter quality in the experimental plots	124
Table 8.9	Relationships between nitrification, N and P mineralization ($\mu\text{g g}^{-1}\text{month}^{-1}$) and soil physico-chemical properties, litter quality and microbial biomass in the experimental plots ($n=36$)	126
Table 8.10	Results of multiple regression analysis for effect of soil physico-chemical properties, soil microbial biomass and litter quality on nitrification, N and P mineralization	127
Table 10.1	Summary of the results obtained in the experimental plots of the humid subtropical forest ecosystem of Meghalaya. Each value is a mean of monthly/seasonal data collected across the year	146

List of Plates

Plate 1 An overview of Swer forest

Page No.

26

The most striking feature of the earth's biota is its extraordinary diversity, estimated to include about 10 million different species. Of the estimated 2,97,000 – 5,10,000 plant species of the world's biota (Schippmann *et al.* 2002), only 1,70,000 have been described to date (Groombridge and Jenkins 2000), and their distribution is highly uneven. About seven per cent of the world's total land area is home to half of the world's species, with the tropics alone accounting for 5 million.

India contributes significantly to this latitudinal biodiversity trend. A rich and varied heritage of biodiversity, encompassing a wide spectrum of habitats from tropical rainforests to alpine vegetation and from savanna to coastal wetlands is encountered in the country. There are nearly 47,000 species of plants, which includes 17,000 angiosperms (Trivedi 2002), accounting for 10.78% of the global total. Of the 17,000 species of flowering plants, 5,725 are endemic to the Indian subcontinent accounting for 33.5% of the total flora, of which, 2,532 are restricted to the Himalayas. The Red Data Books (Jain and Shastry 1984; Nayar and Shastry 1988–90) list 623 threatened species of which 550 are endemic including some valuable medicinal plants.

The vegetation of northeastern India has 1,63,799 km² area under forest accounting for 25% of the total forest cover of the country (FSI 1999), and harbours approximately 7,500 species of angiosperms. Meghalaya in northeast India with an actual forest cover of around 15,584 km² (FSI 2001) harbours about 3,128 species of flowering plants and contributes about 18% of the total flora of the country. It includes 1,237 endemic species (Khan *et al.* 1997) and 53 threatened plant species (Nayar and Sastry 1988). In Meghalaya, very few studies are available on endemic and threatened plant

species. Most of these species are restricted to Biosphere Reserves, National Parks, Wild Life Sanctuary, community and reserved forest, and sacred groves.

Sacred groves are small patches of forest protected by local people out of reverence and respect, fear and sentiment. They are the home of the local flora and fauna. Tree felling and hunting of animals are strictly prohibited here. Leaves, fruits or roots may be removed only for medicinal purposes. Ecologically the sacred groves represent the climax vegetation of the area. In Meghalaya, it ranges from moist deciduous forests at lower elevation to subtropical semi-evergreen to evergreen forest in the precipitous zone at higher elevation between 1200–1900 m a.s.l.

Forests in India have been and are being exploited intensely for centuries (Veitch *et al.* 2003). Although the degree of anthropogenic pressure varies in different parts of the country, human disturbances have become a wide spread feature in most of the forested areas throughout the Himalayas (Singh *et al.* 1984). In the northeastern region, dependence on forest for fuelwood as a source of energy, coupled with shifting cultivation has been causing deforestation (Ramakrishnan 1987). Due to the ever-increasing population, fuelwood consumption is also increasing rapidly in the region (Arunachalam *et al.* 2004). In Meghalaya, the main causes of biodiversity loss are shifting cultivation, deforestation, mining, habitat destruction, over extraction, fragmentation and land use changes (SoE 2005). Lately, the pressure on forests in the state has increased many folds leading to encroachment in sacred groves by the indigenous tribes themselves for their various needs.

The biodiversity declines are already pronounced in many areas. Such local declines are often even more dramatic than global declines, and the beneficial effects of

many organisms on local processes are lost long before the species become globally extinct (Naeem *et al.* 1999).

Human modifications to the living community in an ecosystem as well as to the collective biodiversity have a strong potential to alter ecological properties, ecosystem goods and services which they provide to humanity. Therefore, ecologists have raised concern about how a change in species diversity alters functioning of the ecosystem such as productivity and processes leading to transfer of C and nutrients within the ecosystem and its stability.

An understanding of the relationship between biological diversity and functioning of ecosystems can help improve a wide range of policies involving agriculture, forestry, fisheries and land use, transcending traditional conservation-based policies (Mooney *et al.* 1995). Although every organism contributes to ecosystem processes, the nature and magnitude of individual contributions vary considerably. An understanding of the ecosystem level consequences of individual species is also essential to examine the interactions between biological diversity and ecosystem function. If we cannot establish that individual species are significant, we are unlikely to be able to detect the much more subtle and complex effects of species diversity. Individual species matter, or at least some of them do, and the loss or gain of those species alters the net effects of terrestrial ecosystem on the atmosphere, the hydrosphere or the long-term fertility of soils (Ehrlich and Mooney 1983).

When discussing the effects of biodiversity on ecosystem function it is important to be specific about which components of biodiversity are affecting which components of functioning. Variation in ecosystem properties can result from fluctuations in the environment from year to year, directional changes in conditions, abiotic disturbance or

biotic disturbance. There is no a priori reason to expect that different ecosystem properties have a single pattern of response to changes in different components of biodiversity, or that change in either direction is inherently “good” or “bad” (Hooper *et al.* 2005).

The natural forest is never homogenous in structure; it is always an irregular mosaic of developing and developed stages of community, often called as gap, building and mature phases. The young, mature and senescent individuals of most tree species are unevenly distributed and cause patchiness in the forest structure and composition (Richards 1996). The forest vegetation produces a complex 3-dimensional mosaic of microclimates varying vertically from canopy top to the forest floor and horizontally from point to point beneath the canopy. At a larger scale, microclimates vary between canopy gaps of different sizes, between building and mature phases, and between different forest types. Each of the contrasting microclimates has a role to play in accounting for biology of individual plants and animals in the forest.

The structure and function of forest ecosystem is determined by the plant component more than any other living component of the system. The importance of plant control at the ecosystem level lies in driving nutrient cycling back to the plants. This is possible due to the high proportion of total stock of nutrients that is held in shoot system and the “leak-proof” efficiency of the forest floor and soil compartments of the ecosystem (Richards 1996).

The flow of nutrients within the forest ecosystems occurs through: 1) root nutrient absorption via the processes of uptake and assimilation, 2) nutrient allocation to biomass construction and maintenance, 3) nutrient translocation from senescent tissue, 4) return of nutrients in above and below ground litter and 5) microbially mediated release of

inorganic nutrients into soils solution i.e. mineralization during organic matter decomposition (Barnes *et al.* 1998).

Nutrients entering forest ecosystem from mineral weathering, atmospheric deposition and biological fixation can enter soil solution where they are absorbed by plant roots. Within the plant, absorbed nutrients participate in a wide array of physiological processes, and in some cases, nutrients are mobilized (i.e., translocated) prior to the shedding of some plant tissues. Plant litter on the forest floor plays a critical role in determining soil properties and substrate supply for microorganisms. Most of the nutrients leaving the aboveground biomass as litter or as leachates reach the forest floor rapidly, where soil microorganisms decompose them. The decomposition of litter by microbes into inorganic ions and turnover of labile soil organic matter is affected by the litter quality and timing of litter input, besides microenvironmental conditions on the forest floor. During the process of decomposition, soil bacteria, actinomycetes and fungi assimilate the organic compounds contained in plant litter into their cells for biosynthesis i.e., growth and maintenance. In humid tropical forest dense networks of fine roots, which are concentrated on the forest floor and the underlying mineral soil layer, rapidly absorb ecosystem nutrients released during decomposition of litter. Thus, the rate at which nutrients flow within the forest ecosystems is controlled by the physiological activities of plants and soil microorganisms, and their requirement for growth.

Although microbial biomass represents a relatively small standing stock of nutrients compared to soil organic matter and above ground biomass of trees, but act as a labile source of nutrients for plants, a pathway for incorporation of organic matter into the soil, and a temporary sink for nutrients. The soil microbes associated with tree species differing in quality of leaf litter often have variable amounts of microbial biomass

(Bauhas *et al.* 1998), rates of decomposition of organic matter (Melillo *et al.* 1982), mineralization (Vitousek *et al.* 1982, Zak and Pregitzer 1990) and nitrification (Finzi *et al.* 1998a, Lovette and Reuth 1999). The phenological diversity of trees in the forest helps reduce nutrient loss from the system by allowing plant uptake to take place concurrently with microbial mineralization (Baillie 1996).

In forest ecosystems, major pathways of nutrient losses are through leaching and denitrification. Leaching of growth limiting nutrients like N and P in particular occurs when precipitation exceeds the amount of water lost through transpiration and evaporation from the soil surface. Nutrients eventually enter ground or surface waters where they then become a nutrient input for aquatic ecosystems. Denitrification, on the other hand, is the microbially mediated reduction of nitrate to nitrous oxide or nitrogen, which returns N to the atmosphere (Tiedje 1988). This results in the loss of limiting nutrients, potentially influencing the productivity of terrestrial ecosystems.

The focus of ecological research over the past decade has been on the study of relationship between biodiversity and ecosystem functioning (Schulze and Mooney 1993). However, ecologists have different views on the importance of species diversity in ecosystem functioning because empirical studies have not demonstrated any consistent relationship between the number of species in a system and the rates of ecological processes. Several studies have provided clear evidence that biological communities do indeed regulate ecological processes (Tilman *et al.* 1997, Tilman 1999, Hooper and Vitousek 1997, Zak *et al.* 2003a, Spehn *et al.* 2005, Jonsson 2006, Lanta and Leps 2006), but these studies have often reached different conclusions about the contribution that species diversity itself make to ecosystem functioning. Interpretation of the experiments on the relationship between species and ecosystem processes has been controversial

(Loreau *et al.* 2002). Most of these studies were undertaken under controlled conditions where species diversity in the experimental design was manipulated by altering either their composition or abundance or both.

The present study though is an attempt in the same direction, but differ significantly in its approach since it has been carried out in an undisturbed humid subtropical forest ecosystem characterized by high tree diversity showing highly uneven distribution pattern in the community. The relationship between tree diversity and N and P dynamics on the forest floor was investigated in the permanent plots dominated by different tree species by collecting data on production and decay of litter and fine roots, soil microbial biomass dynamics and nutrient mineralization. The following specific aspects were studied at monthly/ seasonal intervals, to achieve the objective:

1. Tree species composition and their phytosociological attributes,
2. Microclimatic condition and physico-chemical properties including N and P status of soil,
3. Accumulation, production and decomposition of tree litter,
4. Accumulation, production and decomposition of fine roots,
5. N and P input, accumulation and release through litter and fine roots and
6. N and P mineralization and soil microbial biomass C, N and P dynamics.