ECOSYSTEM STRUCTURE AND FUNCTION OF SERAL COMMUNITIES OF DEGRADED ENVIRONMENT AT CHERRAPUNJI AND ADJOINING AREAS

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I certify that the thesis entitled "ECOSYSTEM STRUCTURE AND FUNCTION OF SERAL COMMUNITIES OF DEGRADED ENVIRONMENT AT CHERRAPUNJI AND ADJOINING AREAS" submitted by Shri Subhash Chandra Ram, 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 Ph.D. degree. This work has not been submitted for any degree on any other University.

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C O N T E N T S

PREFACE

The landscape of Cherrapunji, one of the wettest spots of the world, is largely barren. Much of the area is occupied by stunted grassy cover on a thin nutrient deficient soil with parental rock jutting out. A combination of factors such as, shifting agriculture practised in the past, exceptionally high rainfall resulting in a highly leached soil derived from limestone/sandstone formation have contributed to an arrested succession of grassland by degradation of an climax evergreen rain-forest. Frequent fires are common in these grasslands, with consequent impact on species composition, soil fertility and hydrological cycle.

The present study considers two major aspects of these degraded grasslands at Cherrapunji in north-eastern India: (i) structure of these grasslands, (ii) functional attributes of these grasslands with climax evergreen rain-forest (sacred grove) as a reference point.

The thesis starts with a 'General Introduction', surveying the literature pertaining to that of investigation, followed by a description of the study area and climate. Each of the subsequent five chapters deal with different aspects such as biomass, productivity, litter production and decomposition, soil fertility changes, nutrient cycling and ecophysiological attributes of some of the important species. These chapters are organized in a condensed form meant for simultaneous publication in scientific journals. Besides the results presented, each chapter has its own brief introduction, methods of study, discussion and summary. Therefore, some amount of repetition (though minimal) was unavoidable. The literature cited in the text, however, has all been put together at the end of the thesis.

The results presented here apart from its academic value in terms of vegetation development under stress conditions, has also applied implications from the point of view of land management under such stress conditions as prevailing here.

GENERAL INTRODUCTION

Features of the system

Cherrapunji located 51 Km south of Shillong is one of the wettest spots of the world receiving an average annual rainfall of 1037 cm which may go upto 2455 cm in an exceptional year as in 1974.

Climax vegetation of the area is a mixed evergreen rainforest, which now exists only as relict vegetation in the sacred groves, protected by the local community for religious reasons (Boojh & Ramakrishnan, 1983). Much of the area, however, is under grasslands representing various stages in degradation of the sites (Ramakrishnan et al., 1981).

Formation of the system

A combination of factors may be responsible for the formation of these degraded grasslands. These factors are:

(a) Anthropogenic factors:

Shifting cultivation, locally called as Jhum involves clear-cutting of forests, burning the slash and cropping for a year or two before the land is abandoned for natural regeneration of plant cover and nutrient recovery before the cropping operation is repeated on the same site. As long as Jhum cycle was a reasonable

20-30 years or more, Jhum was in harmony with nature. With increase in population pressure and decrease in land available due to desertification jhum cycle has come down to a very short 3-5 year. When the cycle is short, hazards of erosion are high and the land is colonized by weedy species and results in grassland formation under arrested succession. Under extreme climate at Cherrapunji the forest ecosystem is more fragile and the forest once cut down often does not recover to its original state due to infertile soil under high rain fall (Ramakrishnan et al., 1981; Ramakrishnan, 1985b; Ramakrishnan & Saxena, 1984).

(b) Climatological factors:

Clear-cutting of forest, followed by burning of the slash on steep slopes affects the amount of water passing through the sub-soil, dissolved substances and particulate matter being extensively lost from the upper layers. At Cherrapunji, where rainfall is extremely high, water nutrient and sediment losses are relatively much get exaggerated higher than in at other parts of the north-east, resulting in a barren landscape (Toky & Ramakrishnan, 1981).

(c) Geological factors:

In Cherrapinji, desertification has been more rapid and sudden. The climatic and human factors were accentuated by the peculiar geology with nutrient deficient soil over limestone and sandstone formations, with a network of underground tunnels with stalactites and stalagmites (Ramakrishnan, 1985a,b).

ECOSYSTEM FUNCTION

1. Biomass and productivity:

Informations regarding the primary productivity and biomass under subtropical and tropical conditions are limited. Work done on tropical grassland (including productivity) was reviewed by Basilevich and Rodin (1966) which can be summarized as follows:

(i) Total quantity of organic matter: Ghana equitorial savanna, 6660 g m^{-2}; African equitorial savanna (aerial biomass), 3000 g m^{-2}; Thailand mixed savanna (above and below-ground), 8000 g m^{-2}; India dry savanna, 3000 g m^{-2}.

(ii) Structure of biomass: In savanna the proportion of green part is about 10%, and if trees are limited, the proportion of roots also increases upto 40%, the remainder is woody.

(iii) Annual increment: Annual fresh weight production of savannas is about 3000 g m^{-2} in a monsoon climate, an estimate for equitorial savannas is

1250 g m^{-2} (green parts, 750; woody, 200; and roots 300) and India dry savannas have annual increments of about 7500 g m^{-2} with green parts about 40%, perennial aerial parts 5% and roots 55%.

(iv) Litter: Ghana savannas have total litter of roughly 1150 g m^{-2} (green parts, 830; wood, 120; and roots 200), and dry savannas in India have about 7500 g m^{-2} (Van Dyne *et al.*, 1978).

Other studies done by Singh (1972) Singh and Yadava (1974) Shanker *et al.*,(1973), San Jose and Medina (1976) and Gupta and Singh (1982) in monsoonic grasslands found average values of about 3000 g m^{-2} of primary productivity. However, Shanker *et al.*(1973) in Jhansi, India and San Jose and Medina (1976) in Calabozo, Venezuela noted lower values (1019 g m^{-2} and 492 g m^{-2} respectively) for aboveground primary productivity.

Leith (1974) estimates that there are approximately 15 billion Km^2 of tropical grasslands all over the world and about 9 million Km^2 of temperate grasslands. His figures for average net primary productivity was calculated to be a mean 700 g m^{-2} yr^{-1} for tropical grasslands and 500 g m^{-2} yr^{-1} for temperate grasslands.

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Root turnover implies therate of replacement of roots. Through an ingenious method of calculation, Dahlman and Kucera (1965) estimated that about 25% of roots in a tall grass prairie are replaced each year. Using the same method Sims and Singh (1978) have calculated the root turnover values for four north American grasslands to range from 11 to 74% annually. Singh and Yadava (1974) reported that at Kurukshetra, India, the maximum amount of root biomass was replaced during winter (67%). In general 45 to 97% of roots are replaced each year in these grasslands. Strong seasonality in climate, more than one growth flush each year and the high temperature are suggested to be responsible for these high rates.

2. Nutrient cycling

Biomass production and nutrient uptake occur against the background of ecological and geochemical conditions on which they are dependent and with which they are interrelated (Bazilevich &Titlyanova, 1980) Plant growth and development, nutrient uptake, the grazing of plants by animals, the dying off of plants, transformation of plant remains and a number of other phenomena related to biological cycles constitute the biotic process. Another set of processes such as movement of chemicals in solution, their translocation by wind and their gravitational movement, etc. constitute the abiotic processes. Nutrient cycling may be summarized under different sub-headings:

Nutrient compartmentation:

With the development of vegetation some parts of nutrient pool is stored in the vegetation compartment and some part is returned to the soil surface by rain, from leaves and twigs, by litter, and in the form of dead root and root exudates. However, perennial grasses store nutrients in belowground parts like rhizome after re-translocation from aboveground parts to belowground (Williams 1955; Wetselaar & Farquhar, 1980; Noble & Marshall, 1983).

After the peak growth in grassland a massive transfer of living biomass to standing dead occur. Sims and Singh (1978b), for north American grasslands, calculated the rate of transfer from live to standing dead. The mean daily rates of transfer of material into the standing dead compartment averaged as 0.95 and 0.86 g m^{-2} d^{-1} for ungrazed and grazed grassland, respectively.

Once plant material reaches the standing dead compartment, it can remain in this compartment for varying length of time; eventually, however, all material in this compartment must be transferred to the litter. Kelly et al., (1969) estimated that the mean value for the rate of transfer to the litter compartment in an Andropogon community as 0.98 g m^{-2} d^{-1}. For a tropical mixed grassland in India, Singh and Yadava (1974) estimated that about 84% of the standing dead material is transferred to the litter compartment each year, approximately 73% of annual aboveground primary productivity.

Litter production, litter decomposition and soil respiration:

Plant detritus is a major component of the ecosystem and plays an important role in determining structure and function of ecosystem (Odum & de la cruz, 1963; Macfadyen 1963; Odum, 1983). Plant detritus act as an energy source for heterotrophic organisms and nutrient reservoir for internal cycling and regulates the hydrological cycle of the system. Plant roots also add considerable amount of soluble organic matter into the soil. This organic matter is metabolized by a host of organisms releasing the nutrients into the soil for reuse by the plants.

After a fire, biomass of grasslands communities generally increases resulting in the subsequent increase in annual litter production. Kucera and Ehrenreich (1962) in Andropogon scoparius and A. gerardi grasslands, Hadley and Kieckefer (1963) in _Andropogon gerardi_ and _Sorghastrum nutans_ type and Pandey (1974) in Indian grasslands found more aboveground productivity, biomass and litter production after a burn than that under without burn. San Jose and Medina (1976) in Venezuelan Savanna, found lesser litter production after the burn. Smith (1960) and Mott (1982) also obtained similar results.

Kelly _et al_. (1969) determined the transfer from green shoot compartment to standing dead compartment by summing the positive increases in standing dead biomass throughout the year, and by summing the losses from the living compartment. They found that values obtained through the above two methods were considerably different. Thus in an _Andropogon_ community summing the losses of living material yielded a higher value (417 g m^{-2}), while the sum of positive increase of standing dead yielded lesser (288 g m^{-2}) and it appears that not all the living biomass is converted to standing dead litter but some part is retranslocated to roots too.

Singh and Yadava (1974) and Sims and Singh (1978b) have calculated shoot mortality by adding the aboveground net production value for the sampling period to the initial live biomass and substracting from this, the value of live biomass at the end of the season. Sims and Singh (1978b) observed the daily rate of transfer of living biomass to standing dead to be higher in ungrazed than in grazed grassland (0.95 and 0.86 g m^{-2} d^{-1} respectively).

In tropical grasslands in India Singh (1968), Singh and Yadava (1974), Gupta and Singh (1982) have reported that a massive transfer from the live to standing dead compartment occurred during the post monsoon period, after the maturity of herbage produced in the rainy season.

Once the material has reached the standing dead compartment it can remain in this compartment for varying length of time; eventually, however, all material in the standing dead compartment must be transferred to litter. For the tropical mixed grasslands in India, Singh & Yadava (1974) have estimated that about 84% of the standing dead material is transferred to the litter compartments each year.

Decomposition of litter is a complex and a prolonged process. The decomposition rate constants vary with the nature of substrate and the characteristics of the environment (Satchell, 1974). Based on the work of temperate region Burges (1967) summarized the process of decomposition in five steps: (i) development of phylloplane microflora, (ii) colonization by Saprophytes, (iii) comminution and ingestion by invertebrates, resulting in incorporation of organic matter into soil and a great increase of surface area but little chemical change, (iv) Microbial colonization and utilization of faeces and comminuted litter resulting in chemical degradation of tissue and production of complex phenolic compound (humic acid) and (v) the formation of stable organo-mineral complex.

Shanks and Olson (1961) used litter bag technique to study leaf litter decomposition. Crossley and Hoglund (1962) tested different mesh sizes for litter of pine, oak and dogwood leaves and found 1 mm mesh size to be most suitable in their studies. In recent years the litter nag technique is well adapted by others too (Grigal & McColl, 1975; Gupta & Singh, 1981a; Melillo et al., 1982; Weider et al., 1983; Van der Valk & Attiwill, 1984; Toky & Ramakrishnan, 1984; Das & Ramakrishnan, 1985; Yavit & Fahey, 1986). Gupta and Singh (1981a) in Indian grassland have showed that position of bags affect the rate of decomposition. They also observed that litter species characterised by highest concentration of nitrogen, ash, acid detergent, cellwall component and lowest concentration of carbon, cellulose and lignin decomposed rapidly also supported by other flora, (ii) colonization by Saprophytes, (iii) comminution and ingestion by invertibrates, resulting in incorporation of organic matter into soil and a great increase of surface area but little chemical change, (iv) Microbial colonization and utilization of falces and comminuted litter resulting in chemical degradation of tissue and production of complex phenolic compound (humic acid) and (v) the formation of stable organo-mineral complex.

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The rate of decomposition varies with plant material and its environment. A low rate of decomposition has been reported for Californian pine forest ranging from 1 to 3% per annum (Jenny *et al.*, 1949). The values for temperate grassland communities range from 0.14 to 0.082% per day (Koelling & Kucera, 1965; Redmann, 1975). Gupta and Singh (1977) in an Indian tropical grassland observed a higher decomposition rate 0.3% per day. Mobility of elements during decomposition vary. Phosphorus (Ramezov *et al.*, 1961; Van der Valk & Attiwill, 1984) and potassium (Ramezov, 1961; Attiwill, 1968; Gosz *et al.*, 1973; Grigal & McColl, 1977; Van der Valk & Attiwill, 1984; Yavit & Fahey, 1986) are very mobile elements after decomposition. Llyod (1971), McLean & Wein (1978), Mishra and Ramakrishnan (1983a) Das and Ramakrishnan (1985) have shown higher mobility of potassium than other elements. Attiwill (1968), Gosz *et al* (1973), Grigal and McColl (1977), however, observed lesser mobility for phosphorus. Nitrogen generally shows a net gain in concentration as well as quantity during litter decomposition (Tchagina *et al.*, 1968; Gosz *et al.*, 1973; Das & Ramakrishnan, 1985; Yavit & Fahey, 1986), which may be due to fixation, absorption of atmospheric ammonia, throughfall input and immobilizationof nitrogen by microbes (Melillo *et al.*, 1982).

Soil respiration represent the sum of all soil metabolic functions in which carbon dioxide is produced (Lundegardh, 1927). Under field conditions, carbon dioxide was measured by Lundegardh (1924) and Feher (1933) with an isolation chamber. The widely accepted method for soil and root respiration measurement is the alkali absorption method (Kuchera & Kirkham, 1971; Coleman, 1973; Saito, 1975; Wildung _et al_., 1975; Gupta & Singh, 1981b; Singh & Ramakrishnan, 1982; Das & Ramakrishnan, 1985).

Though soil respiration is affected by several parameters like temperature (Edwards & Sollins, 1973; Mediana & Zelwer, 1972), moisture (Kuchera & Kirkhame, 1971), soil aeration, soil depth and mineral status of soil, temperature and moisture play an important role in evolution of carbon dioxide from soil.

In temperate grasslands, maximum soil respiration may be in the range of 2300 to 2700 mg CO_2 m^{-2} hr^{-1} (Yastrebov, 1958; Makarov, 1958; de Jong & Schapper, 1972) but most of the studies indicate a value well below 500 mg CO_2 m^{-2} hr^{-1} (Singh & Gupta, 1977). In a tropical savanna, Medina and Zelwar (1972) observed 257 to 532 mg CO_2 m^{-2} hr^{-1}, whilst Gupta and Singh (1981) in an Indian grassland estimated 55 to 378 mg CO_2 m^{-2} hr^{-1}.

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Water and nutrient losses:

After a fire in a grassland ecosystem, the remaining component loose their ability to hold the nutrients. It is to be expected that after the fire the run-off will increase. Frequent burning also adversely affect the hydrological regime with increased run-off and infiltration losses from the system, because of lack of plant cover (Wright et al., 1976; 1982). Heavy water losses during the early phase of monsoon in the absence of plant cover was observed by Toky & Ramakrishnan (1981), Mishra & Ramakrishnan 1983a) during studies of slash and burn agricultural systems in north-eastern India.

The loss of water and nutrients suffered following clearing and burning, are reduced after the development of vegetation cover. The accumulation of nutrients in the vegetation compartment of the ecosystem reduces their loss through water seepage and run-off (Odum, 1969).

Ecosystems with nutrient-saturated, high exchange capacity soil would loose relatively more of their nutrients than those with nutrient unsaturated and/or low exchange capacity soils (Jordan et al., 1972) as in the case of laterite soils that are sandy (Toky & Ramakrishnan, 1981). For example the northern hardwood forest ecosystem

(Likens et al., 1977) in which a large percentage of total ecosystem nutrients is in the soil in exchangeable form, would loose a relatively large proportion of nutrients. In contrast, tropical rainforests would lose a relatively small proportion of their total nutrients, as in these forests most of the nutrients are tied up in the biomass (Jordan et al., 1972; Odum, 1983); and mineral soil has very low nutrient content (Went & Stark, 1968).

Nutrient uptake:

Uptake of nutrients for annual primary production is directly dependent upon both aboveground plant production and root production (Bazilevich &Titlyanova, 1980). Considerable differences exist between various types of grassland ecosystems. Uptake of nitrogen for formation of aboveground primary production increases in parallel with production in all types of grassland ecosystem.

Uptake of nutrients is related to the seral status of the community. During the development of vegetation after a fire, when there is a rapid accumulation of biomass, nutrient uptake is high. Toky and Ramakrishnan (1983a,b), Mishra and Ramakrishnan (1983c,d) also observed higher uptake of nutrients in developing communities upto a period of 15-20 years after slash and burn agriculture in northeastern India. Risser and Parton (1982) in tall grass prairie found a reduction of nutrient uptake both in root and shoot component after repeated fire.

Pattern of nutrient cycling:

Nutrient cycling probably varies with the nutrient supply to the system, with the time available for the system to develop on the site, and also the environmental conditions.

Lot of information related to nutrient cycling are available from temperate system. Bazilevich and Titlyanova (1980) concluded some basic facts about nutrient cycling in temperate environment which are as follows:

(i) The rate of elemental cycling in grassland is much higher than in forest or desert eco-systems.

(ii) The index of the degree of ecosystem openness is smaller in climax steppe and prairie ecosystem than it is in other grassland ecosystems (meadows and grassy swamps) or in forest or desert eco-systems.

(iii) The functioning regimes of steppes and prairies is particularly stationary, while climax forest and desert ecosystems are characterized by unbalanced input and output exchange processes (particularly with respect to minerals), Steppes steeps and prairies are the most stable ecosystems on this critarion.

(iv) Grassland ecosystems are high speed systems, specific rates of the processes of production, dying off of plants and intake of nutrient elements all being higher than those of other ecosystem types.

(v) The specific rates of abiotic processes are generally much smaller than the rates of biotic procesees for ecosystem of all types. The specific rates of abiotic processes are the smallest in climax grassland ecosystems (Steppes and prairie).

PLANT STRATEGY UNDER DEGRADED ENVIRONMENT

Although there are many conceivable adaptations to improve plant nutrient status or efficiency of nutrient use in growth and reproduction, no plant species exhibits all traits of adaptation and indeed certain characteristics seldom occur together (high root absorption capacity and slow relative growth rate) (Chapin, 1980). There are, however, certain combinations of interdependent physiological characteristics that recur repeatedly in phylogenetically unrelated species and appear important in successful exploitation of particular environments. These groups of physiological traits are the basis of plant adaptive strategies described by Grime (1979). Grime provides evidence for three primary plant strategies in (a) stress tolerant species characteristic of unfavourable (stressful) environment and in (b) competetive species and (c) rudral species that characterize favourable habitats in which disturbance is infrequent or frequent, respectively. Thus where light and water are not unduly limiting, extremely nutrient-deficient sites are dominated by slow growing stress tolerant species, nutrient rich sites by rapidly growing competetive and ruderal species and intermediate sites by a combination of the two and by plants with intermediate characteristics.

Growth pattern:

Chapin (1980) stated that plants with high relative growth rates have high nutrient requirements to support new tissue production and rapid root production and leaf turnover. At the opposite extreme, infertile soils are most successfully exploited by stress tolerant species that have inherently low capacities for photosynthesis and nutrient absorption. Clarkson (1967), Rorison (1968), Grime and Hunt (1975), Grime (1979) suggested that slow growing species that absorb nutrients in excess of immediate growth requirements (luxury consumption) during nutrient flushes may use these reserves to support growth after soil reserves are exhausted. Fast growing tree species such as Pinus kesiya in nutrient poor soils, however, are adapted to a strategy for rapid nutrient turnover rates so that a high flux of soil nutrient pool is maintained (Ramakrishnan & Das, 1983; Das & Ramakrishnan, 1985).

Nutrient Use:

A high nutrient use efficiency (dry matter production per gram nutrient) is an adaptation to nutrient stress (Loneragan & Asher, 1967; Jeffery, 1968; White 1972, 1973; Garten, 1978). However, such an evolution may be misleading some times when there is luxury uptake and large vacuolar storage of nutrients (Bielesky, 1973; Hayness & Goh, 1978). Respiration, photosynthetic or net assimilation rates per gram nutrient uptake may be a more strong expression of nutrient use efficiency. Saxena & Ramakrishnan (1981, 1983, 1984a) have done much work on nutrient uptake and use efficiencies of developing communities after slash and burn agriculture and found that plant species with C_3 pathway for photosynthesis had higher nutrient uptake but low nutrient use efficiency and species with C_4 pathway had lower nutrient uptake but higher nutrient use efficiency, than C_3 plants.

Resource allocation and reproductive strategies:

Cody (1966) put forth the concept based on the principle of allocation which says that organisms have certain limited energy available to spend for different purposes. Harper and Ogden (1970) applied it for the first time to Senecio vulgaris, and pointed out that the proportion of allocation of biomass may reflect the pattern of energy allocation provided there is a strong correlation between total biomass and total calories. This was later supported by others (Hickman & Pitelka, 1975). Harper and Ogden (1970) also suggested certain major patterns of energy allocation in annual, biennial and perennial plants based on quantitative analysis. In annual plant species much of the energy is devoted to reproductive structures whereas in perennials emphasis is given on storage of energy for future growth and development, at the expense of the reproductive budget (Hickman, 1975; Peterson & Bazzaz, 1978; Bell et al., 1979).

Mc Arthur and Wilson (1967) pointed out that organisms in an open environment are selected for greater reproductive potential (r-selection) where as organisms in a closed environment are selected for greater competitive ability (k-selection). Gadgil and Solbrig (1972) expanded the concepts of r- and k-selection in plants and tried to formulate them more rigorously. They emphasized on the r-strategy in invoking patterns of mortality rather than fullness of habitat. The central idea of r- and k-selection has been considered from a number of other aspects like duration of life cycle and propagation ability in a crowded or uncrowded environment (Fischer, 1958; Williams, 1966; Gadgil & Bossert, 1970; Pinaka, 1970; Wilber *et al.*, 1974). Abrahamson and Gadgil (1973) suggested that the reproductive effort should decrease under shaded condition as more emphasis is given for the vegetative growth, for survival of the plants here. Similar resource patterns have also been shown by a number of other workers (Abrahamson & Gadgil, 1973; Gaines *et al.*, 1974; Roos & Quinn, 1977; Saxena & Ramakrishnan, 1984).

Species growing in poor soil sites allocate much biomass toward roots and rhizome than those which are found in nutrient rich soils and therefore have lower shoot: root ratio (Nye, 1977; Nye & Tinker, 1977). The low shoot:root ratio found in the field in many infertile soils (Denis & Johnson, 1970) is part of the phenotypic response to reduced nutrient availability (White, 1972; Christie & Moorby, 1975). Rapidly growing species from high nutrient habitats show considerable phenotypic plasticity in shoot:root ratio and generally have a lower ratio at lower availability and a higher ratio at higher availability (Christie & Moorby, 1975; Grime & Curtis, 1976).

Grime (1974) considered the importance of stress and disturbed conditions in the allocation of biomass. He defined 'distrubance, as any factor that limits and cause distruction of biomass like herbivory, pathogenicity and human activities. Thus, Grime (1974; 1979) recognized stress tolerance as a strategy of plants under unproductive environments.

Considerable work has been done on the allocation of biomass or energy to different life purposes (Harper & Ogden, 1970; Hickman & Pitelka, 1975; Hickman, 1975; Peterson & Bazzaz, 1978; Bell et al., 1978; Augspurger et al., 1985), but very few studies are available on the allocation of nutrients which is also equally important in the evolution of reproductive strategy, particularly in situations with limited supply of nutrients (Harper & Ogden 1970; Van Andel & Vera, 1977). Saxena and Ramakrishnan (1983) studied the growth, allocation pattern and nutritional status of some dominant annual weeds under successional environment and nutrient allocation pattern. Reproductive allocation of nitrogen and phosphorus was higher than that of biomass and potassium in these annuals. They further showed that allocation of biomass and nutrients to leaves decrease during growth and this was more pronounced at the time of reproduction. Saxena and Ramakrishnan (1983) also studied the growth and allocation pattern of biomass in important perennial weeds and concluded that the perennials often tend to allocate more to vegetative reproduction compared to sexual reproduction. Adams and Wallace (1985) also found similar results in case of C_4 species in tall grass prairie. Further, Saxena and Ramakrishnan (1983) observed that the C_4 perennials like Imperata cylindrica and Thysonolenna maxima are well adapted for nutrient poor soils, and C_3 species are generally confined to nutrient rich microsites.

FIRE AS ECOLOGICAL FACTOR

Fire is an ecological factor in terrestial environment especially in the temperate and tropical regions where the deciduous habit of the trees permit accumulation of a thick litter deposit on the forest floor. In grasslands also the dead leaves and plant parts are deposited year after year and provide inflammable materials. The effect of fire is to damage a plant community to a greater or lesser degree, after which the community may escape similar disturbance for sufficient time to allow a restoration of its former structure and composition.

Fire affect on both structural as well as functional attributes of ecosystems.

On community structure:

Fire occurring frequently in grasslands play an important role in the regulation of population and species composition. A fire of mild intensity may stimulate high seedling establishment and growth by raising the soil temperature and nutrient status by removal of plant litter and vegetation cover (Buell & Cantlon, 1953; Shaw 1957; Mark, 1965; Old, 1969; Sharp, 1970; Whelan & Nain, 1979; Gartner et al., 1983; 1986; Mallik & Gimingham, 1985). Toky & Ramakrishnan (1983a), Saxena and Ramakrishnan (1984b) had observed in successional environment that fire had promotory effect on flowering of a successional grass, Imperata cylindrica.

The presence of recurring distrubances such as fire favours grasslands, savannas or park lands in regions with climates capable of supporting bush or forest. Repeated fires generally promote grasses at the expense of woody species (Glover, 1971; Scott, 1971; Van Rensburg, 1971; Vogl, 1974; Sharrow & Wright, 1977). Mallik and Gimmingham (1985) observed the reduction of Juniperus communis in heath land after fire. In dry steppes, annuals may gain at the expense of perennials after fire (Reynolds & Bohning, 1956; West, 1965).

On functional aspects:

Fire has direct effect on the functional aspect of the system like productivity and biomass, nutrient loss and nutrient cycling.

Burning of grassland was found generally to increase the productivity (Lay, 1956; Hughes, 1957; Duvall, 1962; Cushwa & Redd, 1966; Pandey, 1974; San Jose & Medina, 1976), but Grant et al. (1963) did not observe any change in productivity in Molinia caerulea communities after the burn. Cook (1939), Botha(1945) in South Africa, Blydenstein (1963), in Trachypogon savanna in Venezuela, Hilmon and Lewis (1962) in southern Florida, Fridrikson (1963) in Arctic region obtained reduced productivity and biomass after the fire.

Except for volatilization of N,C and S, fire results in no direct loss of nutrients from an ecosystem. However, after the fire, nitrification is enhanced due to increase of pH and temperature and a build up of NO_3-N occur (Christensen, 1976; Sharrow & Wright, 1977). Ramakrishnan & Toky, Mishra & Ramakrishnan (1983) also found a build up of NO_3-N under jhum fallows after the fire. Allelopathy may reduce nitrification (Smith et al., 1968; Rice, 1974) but are either reduced or eliminated after the fire and hence the enhanced nitrification (Moore &

Jaiyebo, 1963; Ahlgren & Ahlgren, 1965; Wells, 1971; Ramakrishnan & Saxena, 1984; Saxena & Ramakrishnan, 1986).

After the fire, a slight increase of available phosphorus often occur. Such a build up of available phosphorus is due to (i) release from the ash after the rainfall and (ii) increase in soil temperature, soil pH and the consequent increase in microbial activity which may result in rapid mineralization of residual humus (Ahlgren & Ahlgren, 1965).

Though there are no obvious mechanisms of volatilization, losses are reported through convection via particulates to the atmosphere (Freedman, 1981). There are conflicting reports on addition of phosphorus through fire. (Nye & Greenland, 1960; Stark, 1971; Stromgaard, 1984); a few suggest some losses from the system (Llyod, 1971; Harwood & Jackson, 1975; Ashton, 1976; Mishra & Ramakrishnan, 1983; Swamy, 1986).

After the fire all the cations are released in a single flush on the soil surface as ash. The increase of cation level is a general phenomenon after the fire and is well documented for grasslands (Heywards & Barnett 1934; Moore, 1960; Metz et al., 1961; Daubenmire, 1968; Vogl, 1974; Kellman et al., 1985). Ramakrishnan and

and Toky (1981) and Mishra and Ramakrishnan (1983b) observed an increase in cation levels after fire under slash and burn agriculture in north-eastern India.

Fire also influences elemental cycling in ecosystems in various ways: from stimulating growth and increasing nutritive value of forage in some grasslands, or by destroying not only vegetation but also entire soil-plant-animal-microorganism systems in some forested lands (Woodmansee & Wallach, 1981). The initial effects of fire on the elemental cycles of ecosystems are: (1) The direct loss of elements to the atmosphere as volatilized compounds or as particulates carried away in smoke, (2) the release and transformation of ions and consequent deposition of ash elements on the surface, (3) the response of individual organisms to the heat generated by fire, and (4) the uptake of nutrients by plants.

Intense fires that kill large portions of whole plants or all vegetation drastically alter cycling pattern. Pioneer species (often annual or short-lived perennials) may become quickly established and immobilize large amount of available nutrients especially nitrogen. Nutrients are initially immobilized, then slowly released as more permanent vegetation becomes established and plant biomass becomes large enough to retain all available nutrients not retained by microorganisms. When vegetation is re-established, leaching losses should be reduced to or below ambient levels (Vitousek & Reiners, 1975) Similar results are available for the north-eastern slash and burn agriculture system (Toky & Ramakrishnan, 1981; Mishra & Ramakrishnan, 1983a; Swamy, 1986). Risser and Parton (1982) in tall grass prairie found a reduction of nutrient uptake both in root and shoot component after repeated fire.