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Nutrient cycling in an excessively rainfed subtropical grassland at Cherrapunji

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Abstract. Cycling of six mineral elements (N, P, K, Na, Ca and Mg) was studied in a humid subtropical grassland at Cherrapunji, north-eastern India during 1988-1989. Elemental concentrations in the shoot of four dominant grass species, *viz., Arundinella khaseana, Chrysopogon gryllus, Eragrostiella leioptera* and *Eulalia trispicata* were very low, and none of the species appears suitable for fodder use. Among different vegetation compartments, live root was the largest reservoir of all the nutrients (except Ca) followed by live shoot, dead shoot, litter and dead root. For Ca, live shoot was the major storage compartment. The total annual uptake (kg ha^{-1}) was 137·3, 10·4, 51·1, 5·5, 8·7 and 18·2 for N, P, K, Na, Ca and Mg, respectively. In an annual cycle 98% N, 77% P, 49% K, 109% Na, 87% Ca and 65% Mg returned to the soil through litter and belowground detritus. A major portion of N, P and Na was recycled through the belowground system, whereas nearly half of K, Ca and Mg was recycled through the shoot system. Precipitation acts as the source of N and P input, but at the same time causes loss of cations.

Keywords. Humid grassland; nutrient concentration; nutrient cycling.

1. Introduction

Humid grasslands of north-eastern India owe their origin to indiscriminate tree felling, burning and grazing and have many features in common with several other tropical grasslands, such as low species diversity, poor representation of legumes and dominance of a few perennial graminoides (Ramakrishnan and Ram 1988; Uma Shankar *et al* 1991). At Cherrapunji, a spot which has the distinction of receiving the highest annual rainfall in the world, vast tracts of degraded land are covered by *Arundinella* type of grasslands (Dabadghao and Shankarnarayan 1973) with *Osbeckia* spp., *Carex* spp., *Fimbristylis* spp. and *Arisaema echinatum* Roxb. occurring in different proportions at different sites. These grasslands are being maintained by biotic stresses and show poor growth due to soil nutrient depletion caused by heavy precipitation. Interspersed amidst these grasslands, are found the patches of relict evergreen broad-leaved forest dominated by *Ligustrum robustum* L., *Castanopsis* spp., *Syzygium cumini* (*L.*) Skeels, *Quercus dealbata* L. and *Engelhardtia spicata* Roxb.

In India, nutrient cycling has been studied extensively under arid, semiarid and subhumid ecoclimates (Billore and Mall 1976, 1985; Yadava 1980; Mishra 1979; Agrawal and Tiwari 1987; Chaturvedi *et al* 1988), but has received little attention in humid, especially excessively rainfed grassland at Cherrapunji (Ram and Ramakrishnan 1992). Ram and Ramakrishnan (1992) examined the effect of fire on nutrient cycling especially through aboveground herbage and run of and leaching.

However, recent investigations on phytomass cycling in this grassland system show that belowground components (roots and rhizomes) play a major role in accumulation, decomposition and recycling of phytomass (Uma Shankar 1991; Uma Shankar *et al* 1993). Also, although the run off and leaching losses of nutrients have been measured for these grasslands (Ram and Ramakrishnan 1988b), the inputs through rainfall, which is substantially higher at this site, have not been measured. And therefore, the understanding of nutrient cycling in Cherrapunji grasslands remains incomplete.

We in this paper address the following questions: (i) whether belowground system plays a major role in the cycling of nutrients as it does for phytomass recycle, and (ii) how does excessive rainfall regulate the cycling process? A study of cycling of six mineral elements (N, P, K, Na, Ca and Mg) was carried out by quantifying (i) standing state and distribution of nutrients in different components of the producer subsystem and soil, (ii) annual input of nutrients through rainfall and output through run off and percolation, and (iii) annual uptake of nutrients from soil, their transfer to various vegetation compartments and return to the soil.

2. Materials and methods

2.1 *Climate, soil and vegetation of study area*

The study was conducted at Cherrapunji (25° 14' N, 91° 42'E, 1300m asl) in Meghalaya, north-eastern India. The climate is monsoonic with a relatively long rainy season (mid-May to mid-October). Winter (November to February) is severe and relatively dry and spring (March to mid-May) is bright and warmer than winter. Long-term average annual rainfall is *ca.* 12500 mm. During the study period (August 1988 to July 1989), however, it was greater than normal, *i. e.,* 16247 mm, and 95% of it occurred during rainy season. Relative humidity was quite high during rainy season (>90%) and declined through spring (80–90%) and winter (60–70%). The mean monthly maximum and minimum temperatures in the coldest month (February) were 14·2 and 11·5°C and in the hottest month (May) were 21·7 and 18·7° C, respectively. Seasonal variability in temperature was low (figure 1). Average wind speed which is generally high during spring, varied between 3 and 5 km h^{-1}.

The soil, grouped under latosol (oxisol) type, is derived from the underlying gneisses, schists and granite rocks of Archaean age. It is a loamy sand with particles >2mm comprising three-fourth of the total substratum. Physico-chemical properties, given in table 1, indicate that the soil is poor in N, P and exchangeable cations.

In the grassland under study, *Arundinella khaseana* Nees, *Chrysopogon gryllus* (L.) Trin, *Eulalia trispicata* (Schult.) Henr. and *Eragrostiella leioptera* (Stapf.) Bor were the abundant species with an importance value of 92·0, 60·6, 48·9 and 52·7, respectively (Uma Shankar *et al* 1991).

2.2. *Sampling of vegetation and soil*

Samples of vegetation and soil were drawn from a 3 hectare grassland fenced by the State Forest Department three years before commencement of the study in August

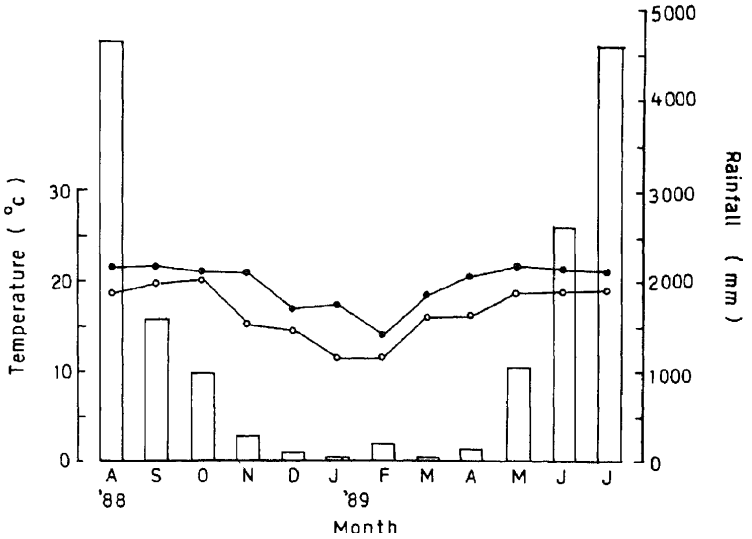

Figure 1. Ombrothermic diagram for Cherrapunji during August, 1988 to July, 1989. Bars represent rainfall. (●) Maximum temperature; (O) minimum temperature.

Table 1. Physico-chemical properties of grassland soil down to 30 cm depth at Cherrapunji.

Parameter	Value
Soil substratum composition (%)	
Stone (>5 mm)	48·0±4·1
Gravel (5–2 mm)	28·1±1·9
Mineral particles (<2 mm)	23·9±2·0
Texture (% of mineral particles)	
Sand	80·7±6·8
Silt	10·3±0·7
Clay	9·0±0·8
Water holding capacity (% dry wt. soil)	41·9±1·6
pH	5·5±0·03
Organic matter (mg g^{-1})	25±4
Total nitrogen (mg g^{-1})	1·5±0·2
C/N ratio	9·7
NH_4–N (μg g^{-1})	1·2±0·3
NO_3–N (μg g^{-1})	4·1±0·8
Extractable phosphorus (mg kg^{-1})	1·25±0·21
Cation exchange capacity (meq 100 g^{-1})	8·1±1·3
Exchangeable potassium (meq 100 g^{-1})	0·07±0·01
Exchangeable sodium (meq 100 g^{-1})	0·06±0·004
Exchangeable calcium (meq 100 g^{-1})	1·13±0·21
Exchangeable magnesium (meg 100 g^{-1})	0·21±0·03

Values are means ±SE.

1988 to exclude grazing and burning. Aboveground vegetation was harvested by species at monthly intervals from ten randomly laid quadrats of 50 cm ×50 cm size each and litter was picked up from the ground following the harvest. In order to

sample the belowground parts, two soil monoliths of l0 cm × 10 cm × 30 cm were excavated from the centre of each harvested quadrat. Similarly, one monolith from each quadrat was taken for soil analysis. No quadrat was reharvested. The samples were packed into polythene bags and transported to the laboratory. The aboveground, herbage was sorted into live and dead parts for each species. Soil monoliths were soaked overnight in a water-filled bucket and then washed under a jet of water over a 0·5 mm sieve. The roots (roots and rhizomes) retained in the sieve were sorted into live and dead fractions on the basis of pliability and degree of cohesion between cortex and periderm (Singh and Srivastava 1984). Dead roots were often dark in colour and wrinkled in contrast to the smooth and light coloured live roots. The plant samples were oven-dried at 65±5°C to constant weight, weighed, ground and stored in polythene bags for chemical analysis. Soil samples were air-dried, passed through a 2 mm sieve and used for chemical analysis.

2.3 *Chemical analyses*

Stones and gravels in the soil were separated by passing it successively through 5 and 2 mm sieves. Texture was determined by hydrometer method (Kanwar and Chopra 1967). Bulk density, water holding capacity and organic carbon (by Walkley and Black's rapid titration method) were determined according to Piper (1942). pH was determined electrometrically, total nitrogen by micro-Kjeldahl digestion-distillation method, ammonia and nitrate nitrogen by KCl extraction-Kjeldahl distillation method, and exchangeable cations (K, Na, Ca and Mg) and cation exchange capacity (CEC) using ammonium acetate (pH 7) as an extractant (Allen *et al* 1974). Extractable phosphorus was determined by phosphomolybdo blue colour method (Jackson 1958). Nitrogen in plant samples was determined using Tecator's Kjeltec auto 1030 analyzer. Subsequent to mixed acid digestion (Allen *et al* 1974), phosphorus in plant samples was determined by vanadomolybdo-phosphoric yellow colour method (Jackson 1958) and cations (K, Na, Ca and Mg) by a Perkin-Elmer 2380 atomic absorption spectrophotometer. Belowground plant samples were ashed at 600°C for 5 h for correcting contamination caused by adhered soil particles.

Rainwater samples were collected in three rain gauges in August, 1988 and July, 1989, the peak months of rain. Since more than 50% of the rain falls during these two months, the sampling intensity was considered adequate. These water samples were used for elemental analysis following standard methods (APHA 1985). The methods about measurement of nutrient losses through leaching and run off are described in Ram and Ramakrishnan (1988b).

Nutrient concentration in shoot (i.e., live + dead tissues) of each species was determined by multiplying separately the nutrient concentrations of live and dead tissues with dry weights of respective live and dead tissues, which yielded the nutrient contents in the respective tissues. Then these nutrient contents in live and dead tissues were summed, and the sum was divided by the shoot (live + dead) biomass (Woodwell *et al* 1975) to achieve the nutrient concentration in the shoot. Similar approach was adopted to determine nutrient concentration in live and dead shoot compartments of the community.

2.4 *Nutrient transfers between soil and vegetation compartments*

The year-long mean nutrient concentrations in live shoot and live root were multiplied respectively with annual net aboveground and belowground production values, to obtain the estimates of aboveground and belowground nutrient uptake. Nutrient transfers from live shoot to dead shoot and from dead shoot to litter were calculated by multiplying the year-long mean nutrient concentration in dead shoot with the amount of dry mass transferred from live shoot to dead shoot as well as with the amount of dry mass transferred from dead shoot to litter (Bokhari and Singh 1975). Nutrient release from litter was calculated by multiplying the year-long mean nutrient concentration in litter with the quantity of litter that disappeared. Similarly, nutrient transfer from live root to dead root and its release from the latter were calculated by multiplying the year-long mean nutrient concentration in live root with the value of dry mass transfer from live root to dead root, and the year-long mean nutrient concentration in dead root with the quantity of dead root that disappeared during the year. The dry matter production and its transfer between system compartments were calculated following balance sheet approach of Singh and Yadava (1974).

Data were statistically analysed using ANOVA, LSD, Duncan's multiple range test and regression (Kendall and Stuart 1968).

3. Results

3.1 *Nutrient concentration and accumulation in dominant species*

The concentration of all elements, except Na, varied widely among shoots (live + dead) of four dominant as well as 'other species' (table 2). It ranged between 4·8 and 8·5mg g^{-1} for N, 0·5 and 1·0 mg g^{-1} for P, 2·4 and 5·7 mg g^{-1} for K, 0·18 and 0·27 mg g^{-1} for Na, 1·0 and 3·6 mg g^{-1} for Ca and 0·7 and 3·4 mg g^{-1} for Mg. In general, the dominant species *viz., A. khaseana, C. gryllus, E. trispicata* and *E. leioptera* had higher N concentration than other elements. Na was present at the lowest concentration. In *E. leioptera,* concentrations of all the elements, except N, were at a minimum, while concentration of N, P and Ca in *E. trispicata* were significantly greater than in the other species. Concentrations of K and Mg were significantly higher and that of N was lower in *A. khaseana* than other three species. The pattern of K and Mg accumulation in the four species was *A. khaseana* > *C. gryllus* > *E. trispicata* > *E. leioptera,* but N, P, Na and Ca accumulation was greater in *C. gryllus* than *A. khaseana* (table 2).

3.2 *Seasonal dynamics of nutrients in vegetation compartments*

The seasonal dynamics of nutrients in the live shoot was characterised by an increase in storage from April to August, a decline from August to December, and insignificant variation between December and April (figure 2). The seasonal trend in dead shoot and litter compartments was not prominent, but an increase in nutrient accumulation in the former compartment was marked by a concomitant decrease in

Table 2. Concentration (mg g^{-1}) and accumulation (mg m^{-2}) of six mineral elements in shoots of dominant grasses in Cherrapunji grassland.

Mineral element	*A. khaseana*	*C. gryllus*	*E. trispicata*	*E. leioptera*	Other species
Nitrogen					
Concentration	$4{\cdot}80 \pm 0{\cdot}24^{a}$	$5{\cdot}97 \pm 0{\cdot}30^{b}$	$8{\cdot}19 \pm 0{\cdot}46^{c}$	$6{\cdot}65 \pm 0{\cdot}31^{b}$	$8{\cdot}47 \pm 0{\cdot}55^{c}$
Accumulation	604 ± 82^{a}	903 ± 118^{b}	405 ± 32^{c}	263 ± 48^{d}	159 ± 34^{d}
Phosphorus					
Concentration	$0{\cdot}72 \pm 0{\cdot}04^{a}$	$0{\cdot}79 \pm 0{\cdot}05^{a}$	$0{\cdot}80 \pm 0{\cdot}05^{a}$	$0{\cdot}48 \pm 0{\cdot}03^{b}$	$1{\cdot}01 \pm 0{\cdot}06^{c}$
Accumulation	90 ± 11^{a}	119 ± 16^{b}	40 ± 4^{c}	19 ± 4^{d}	19 ± 4^{d}
Potassium					
Concentration	$5{\cdot}72 \pm 0{\cdot}60^{a}$	$3{\cdot}80 \pm 0{\cdot}38^{cb}$	$3{\cdot}06 \pm 0{\cdot}30^{b}$	$2{\cdot}43 \pm 0{\cdot}30^{db}$	$3{\cdot}12 \pm 0{\cdot}22^{b}$
Accumulation	740 ± 130^{a}	633 ± 129^{b}	153 ± 17^{c}	85 ± 16^{c}	68 ± 17^{c}
Sodium					
Concentration	$0{\cdot}24 \pm 0{\cdot}02^{a}$	$0{\cdot}25 \pm 0{\cdot}01^{a}$	$0{\cdot}27 \pm 0{\cdot}02^{a}$	$0{\cdot}18 \pm 0{\cdot}01^{b}$	$0{\cdot}24 \pm 0{\cdot}01^{a}$
Accumulation	30 ± 4^{a}	37 ± 4^{a}	13 ± 1^{b}	7 ± 2^{b}	5 ± 1^{b}
Calcium					
Concentration	$1{\cdot}02 \pm 0{\cdot}04^{a}$	$1{\cdot}66 \pm 0{\cdot}10^{b}$	$2{\cdot}66 \pm 0{\cdot}18^{c}$	$1{\cdot}85 \pm 0{\cdot}14^{b}$	$3{\cdot}64 \pm 0{\cdot}44^{d}$
Accumulation	125 ± 14^{a}	247 ± 28^{b}	125 ± 5^{a}	72 ± 14^{c}	72 ± 16^{c}
Magnesium					
Concentration	$3{\cdot}39 \pm 0{\cdot}23^{a}$	$1{\cdot}00 \pm 0{\cdot}17^{b}$	$1{\cdot}31 \pm 0{\cdot}10^{cb}$	$0{\cdot}68 \pm 0{\cdot}08^{db}$	$2{\cdot}19 \pm 0{\cdot}35^{d}$
Accumulation	448 ± 83^{a}	139 ± 24^{b}	64 ± 6^{c}	26 ± 6^{c}	39 ± 9^{c}

Values are year-long means ±SE. Values in a row with different superscripts are significantly ($P<0{\cdot}05$) different. In case of two superscripts, second shows no difference from the same single superscript. All Statistical analyses were performed using analysis of variance and Duncan's multiple range test.

nutrient storage in live shoot. Litter generally showed the peak accumulation in November. The dynamics in the live root differed from the live shoot in having peak accumulation in September instead of August. However, N and Na were exceptions in this regard by showing another peak in December-January. Accumulation in dead root compartment remained unchanged all-year-round. The seasonal nutrient dynamics followed the dynamics of dry matter for live shoot, live root and dead root compartments. The seasonal dynamics of dry matter is described in Uma Shankar *et al* (1993) and its correlation coefficients with the nutrient dynamics are given in table 3.

The seasonal dynamics of nutrients in live shoot compartment showed a significant ($P < 0{\cdot}01$) relationship with a linear combination of log of precipitation, soil moisture and soil temperature (table 4).

The concentrations of all the nutrients declined significantly from live to dead shoot stage (table 5), but from dead shoot to litter, the trend varied for different elements. N registered an increase, P, K, Ca and Mg declined and Na showed no variation. From live to dead root stage, nutrient concentration did not change significantly except N which showed a marked decline. A comparison between five shoot and live root showed higher concentration of P, K, Ca and Mg in the latter.

3.3 *Nutrient transfers between soil and vegetation compartments*

The total annual uptake (kg ha^{-1}) was 137·3, 10·4, 51·1 5·5, 8·7 and 18·2 for N, P, K, Na, Ca and Mg respectively. Belowground uptake accounted for N 82%, P 65%, Na 79%, Ca 24% and Mg 45%. K showed nearly equal uptake by both

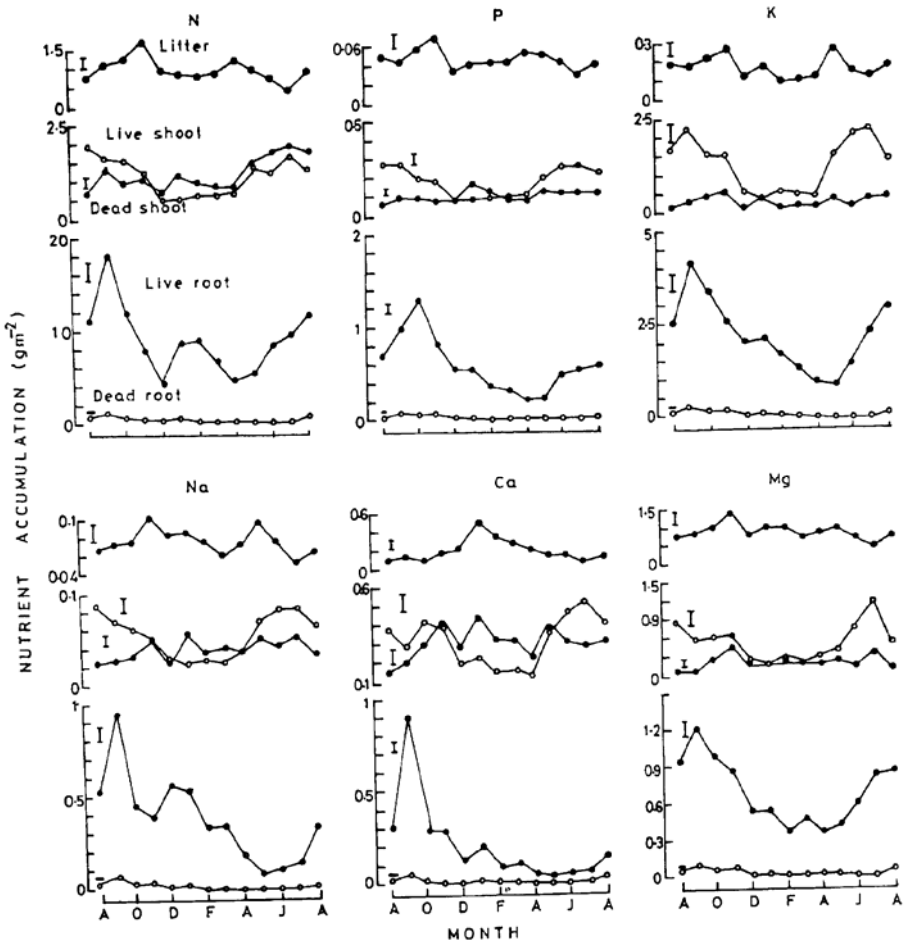

Figure 2. Seasonal dynamics of six mineral elements in live shoot, dead shoot, live root, dead root and litter compartments of vegetation. Vertical lines indicate LSD at 5% level.

Table 3. Relationship (correlation coefficient, *r)* between seasonal dynamics of dry matter and nutrients in different vegetation compartments.

Compartment	N	P	K	Na	Ca	Mg
Live shoot	0·955	0·917	0·851	0·878	0·886	0·811
Dead shoot	–0·161*	0·113*	0·410*	–0·095*	0·354*	–0·011*
Litter	0·025*	–0·694**	–0·619**	–0·689	0·375*	–0·406*
Live root	0·793	0·905	0·936	0·634	0·729	0·981
Dead root	0·956	0·935	0·907	0·943	0·866	0·966

Significance levels: *, Not significant; **, 5%; others significant at 1%.

Table 4. A multiple linear relationship between the seasonal dynamics of nutrients in live shoot and three abiotic variables (log of precipitation, soil moisture and soil temperature).

Dependent variable (mg m^{-2})	Independent variables: Log of precipitation (mm)	Soil moisture (%)	Soil temperature (°C)	Constant	Correlation coefficient (r)
N-dynamics	−2·150	+39·882	+103·455	−1079·547	0·993
P-dynamics	+3·400	+3·063	+20·966	−223·086	0·985
K-dynamics	+60·484	+24·825	+151·635	−1857·281	0·914
Na-dynamics	+3·279	+1·109	+3·533	−41·250	0·980
Ca-dynamics	−10·377	+14·592	+5·943	+27·129	0·883
Mg-dynamics	+31·413	+22·746	+9·417	−205·195	0·861

All correlation coefficients are significant at 1% level (degree of freedom is 11 in all case).

Table 5. Concentrations (mg g^{-1}) of six mineral elements in different vegetation compartments of Cherrapunji grassland.

Element	Vegetation compartment: Live shoot	Dead shoot	Litter	Live root	Dead root
Nitrogen	$7·30 \pm 0·33^{a}$	$5·16 \pm 0·27^{b}$	$6·27 \pm 0·30^{c}$	$7·98 \pm 0·67^{ba}$	$6·99 \pm 0·48^{ca}$
Phosphorus	$1·09 \pm 0·05^{a}$	$0·49 \pm 0·02^{b}$	$0·30 \pm 0·02^{c}$	$0·48 \pm 0·02^{b}$	$0·43 \pm 0·03^{b}$
Potassium	$7·62 \pm 0·46^{a}$	$1·54 \pm 0·13^{b}$	$1·25 \pm 0·10^{b}$	$1·80 \pm 0·09^{b}$	$1·30 \pm 0·15^{b}$
Sodium	$0·30 \pm 0·02^{a}$	$0·18 \pm 0·01^{b}$	$0·18 \pm 0·02^{b}$	$0·31 \pm 0·04^{a}$	$0·33 \pm 0·05^{a}$
Calcium	$1·95 \pm 0·12^{a}$	$1·46 \pm 0·08^{b}$	$1·30 \pm 0·17^{b}$	$0·15 \pm 0·03^{c}$	$0·23 \pm 0·02^{c}$
Magnesium	$2·97 \pm 0·23^{a}$	$0·96 \pm 0·11^{b}$	$0·59 \pm 0·01^{c}$	$0·58 \pm 0·02^{c}$	$0·60 \pm 0·01^{c}$

Values are year-long means ± SE. See table 2 for statistical terms.

aboveground and belowground parts. The annual return of nutrients (relative to the uptake) to the soil through litter and dead root was: N 98%, P 77%, K 49%, Na 109%, Ca 87% and Mg 65%.

The annual inputs of N and P through rainfall litter and root detritus into the system were more than their outputs through run of, percolation and uptake. Conversely, outputs of cations from the system were more than their inputs into the system. Annually, about 20% of N and 6% of P were retained in the system, whereas about 70% K, 51% Ca and 28% Mg were lost from it.

3.4 *Nutrient input through rainfall*

The nutrient concentrations in rainfall when multiplied by the total rainfall during the study year (16247 mm) yielded nutrient input through rainfall. The input amounts (in kg ha^{-1}) are 73·1 N, 6·5 P, 39·0 K, 14·6 Na, 91·0 Ca and 35·8 Mg.

4. Discussion

4.1 *Nutrient concentration, accumulation and seasonal dynamics*

Data on nutrient concentration of important species in Cherrapunji grassland suggest that species markedly differ in their ability to use the available nutrient pool

in soil. For instance, *A. khaseana* had significantly higher concentration of K and Mg, and *E. trispicata* of N and Ca compared to other species. Such a difference in concentration is helpful for the coexistence of species on nutrient impoverished soil of Cherrapunji. On the oligotrophic sites, dominated by a single species, growth of individuals soon declines due to the limitation in the supply of a particular nutrient (Chapin 1980). The co-existence of species specialists in acquisition of different nutrients could be viewed as a conservation mechanism against the nutrient loss from soil-available pool through outflowing water, which is exceptionally high at Cherrapunji.

The concentrations of all the elements in grass species are much lower than those compiled by Wagner and Jones (1968) for some commonly grown forages at the hay stage and also are below the critical levels associated with both deficiency symptoms and dietary requirements of the graziers (Chapman 1966; Anonymous 1971). Thus the grasses of Cherrapunji are unsuitable for cattle feeding.

The decline in concentration of nutrients from live to dead shoot stage is a common phenomenon in temperate (Bokhari and Singh 1975; Callahan and Kucera 1981) as well as tropical grasslands (Mishra 1979; Billore and Mall 1976, 1985; Chaturvedi *et al* 1988). This decline has been attributed to the withdrawal of nutrients from the shoot during senescence (Clark 1977), weathering and leaching processes (Tukey 1970) and activity of decomposer organisms (Nykvist 1959). Also, a decrease from dead shoot to litter stage is invariably found in all these reports. However, Callahan and Kucera (1981) reported an increase in Mg concentration and we too observed a significant increase (P <0·05) in N concentration in litter over that in the dead shoot. Loss of carbohydrates during the early phase of decomposition and/or net immobilization of nitrogen in associated microbial growth during the course of litter decomposition could account for this increase (Mellilo *et al* 1982). Ram and Ramakrishnan (1988a) have reported a net gain of nitrogen of up to 160% during the first few months of litter decomposition on the soil surface at Cherrapunji. Decrease in nutrient concentration from live to dead root stage corresponds to the trend noted in a high altitude grassland in Kumaun Himalaya by Chaturvedi *et al* (1988). Results of a large number of studies reveal that concentration of nutrients in live root or belowground organs is generally less than the live shoot both in temperate (Callahan and Kucera 1981; Ohlson and Malmer 1990) and tropical grasslands (Billore and Mall 1976, 1985; Agrawal and Tiwari 1987; Buschbacher *et al* 1988; Chaturvedi *et al* 1988). Except for N and Na, this trend is true for Cherrapunji grassland as well, but the magnitude of difference varies for different nutrients.

At community level, live root accumulated the major portion of N, P, K, Na and Mg, while live shoot stored more Ca. The greater accumulation of nutrients in shoot, a result of high nutrient concentration and greater biomass, is the characteristic feature of tropical grasslands (Mishra 1979; Billore and Mall 1976, 1985; Agrawal and Tiwari 1987; Chaturvedi *et al* 1988), whereas the greater belowground reserve is characteristic of temperate grasslands (Bokhari and Singh 1975; Callahan and Kucera 1981; Bazilevich and Titlyanova 1980). Higher allocation of biomass and nutrients to the belowground parts at Cherrapunji due to adverse climatic and edaphic conditions such as low winter temperature and high wind speed, decreased soil moisture content (6–7%) during November to March and low pH is the main reason for greater nutrient storage in the belowground

compartment. Greater allocation of resources to the belowground parts is regarded as an adaptive strategy for survival under stress conditions as it maximizes the root surface area for uptake (Chapin 1980).

Nutrient storage in dead root compartment remained small throughout the year; even when large decrease in live root occurred, nutrient accumulation in dead root did not increase. This may be ascribed to the rapid decomposition at this site (Ram and Ramakrishnan 1988a). Additional pathways of nutrient recycle in belowground system like root herbivory (Stanton 1988), exudation (Russell 1977) and phytomass deposition in soil in several forms (root hairs, mucilages, lysates, and sloughed cortical cells) (Singh and Coleman 1977) might be the other probable causes contributing to this phenomenon.

Alternate prolonged wet and short dry periods characterise unimodal dynamics of biomass and nutrients in live shoot and live root compartments, with greater role of temperature than rainfall in regulating seasonal dynamics (Uma Shankar *et al* 1993).

4.2 *Nutrient transfers between soil and vegetation compartments*

Our values of uptake of all nutrients except N are in agreement with those worked out by Ram and Ramakrishnan (1992) for Cherrapunji grassland; N uptake was

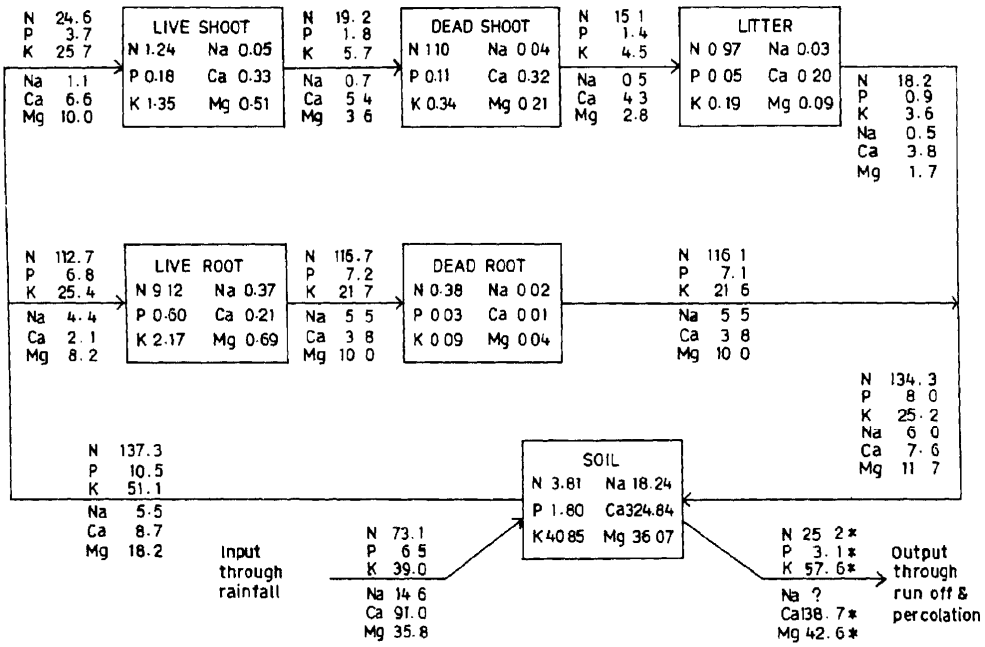

Figure 3. The compartmental model of nutrient cycling in the grassland ecosystem at Cherrapunji. The mean accumulation (kg ha^{-1}) of six nutrients in different vegetation compartments and in available pool in soil down to 30 cm depth is shown in boxes. The flux rates (kg ha^{-1} Yr^{-1}) are indicated on arrows. The amounts of available nutrients in soil have been weighted for particles ≤ 2mm [*data adopted from Ram and Ramakrishnan (1988b)].

higher at our site. Annual uptake of six mineral nutrients was in the order: N > K > Mg > P > Ca > Na. This trend is similar to that noticed in a Himalayan grassland by Chaturvedi *et al* (1988) except Ca, the uptake of which was comparable to N. In semiarid grasslands also, Ca uptake is comparable to N (Billore and Mall 1976, 1985). Lower Ca uptake in the Cherrapunji grassland might be due to high relative humidity which adversely affects Ca translocation within the plant by reducing the transpiration rate (Elgawhary *et al* 1972). Annually, 98% N, 77% P, 49% K, 109% Na, 87% Ca and 65% Mg (of their respective uptake) was returned through litter and belowground detritus in this grassland. Relatively lower return of P, Ca and N to soil indicates the possibility of their retention in vegetation for reuse in the subsequent season (Clark 1977). It is evident from figure 3 that the return of P, K, Na and Mg to soil through litter is much lower than their uptake by aboveground parts, thereby suggesting the possibility of redistribution, *i.e.,* withdrawal during senescence, within the plant for more efficient use in the subsequent growth season.

Input of N and P through precipitation exceeded the losses through run off and percolation, whereas the reverse occurred for cations. This implies that while N and P are either stored geochemically in soil and/or mobilised into vegetation by rapid uptake, cations are leached out of the system. Seastedt (1985) has reported that standing dead vegetation and litter function as a nitrogen filter and a significant portion of nitrogen present in rain water is retained by them.

In conclusion, cycling of mineral elements in degraded grasslands of Cherrapunji is regulated by their greater accumulation in belowground parts, faster recycling through decomposition, and a net gain of N and P through rainfall.

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