Nitrogen cycling in Indian terrestrial natural ecosystems

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Nitrogen (N) is essential to the survival of all life forms and often limits productivity, decomposition and the long-term accumulation of carbon in terrestrial ecosystems. Soil and vegetation are the respective primary and secondary sinks for N in terrestrial ecosystems. Litter production determines the amount and quality of N returned to the forest floor and mineral soil. Decomposition of litter is crucial for N recycling and is influenced by a number of factors, including litter concentrations of N and lignin, C : N and lignin : N ratios, moisture and temperature. In many ecosystems, soil microbial biomass acts as a source and sink of plant-available N. Retranslocation of N during leaf senescence could also be a significant source of plant nutrient supply and is likely to meet a significant proportion of N demand of the developing leaves of forest tree species. Ecosystem transboundary exchanges of N are little understood for Indian terrestrial biomes. Indian studies show that landuse change, slash and burn agriculture, pollution and species invasion are some of the important drivers altering natural N cycle in many ecosystems, but we know little about the impact of anthropogenic N input.

Keywords: Nitrogen dynamics, landuse, pollution, savanna, slash and burn agriculture, species invasion.

IN most ecosystems, the supply of plant-available N has been one of the limiting factors that controls the nature and diversity of plant life, the population dynamics of organisms at higher trophic levels and ecosystem processes such as primary productivity and the cycling of carbon and soil minerals. N is usually acquired by plants in greater quantity from the soil than any other element and its relative availability in adequate amounts can frequently determine the type of vegetation that can grow and survive in a certain area. An understanding of the N cycle in natural terrestrial ecosystems is becoming crucially important for a tropical country like India. A coordinated study and analysis of the N cycle and the assessment of N fluxes will make it possible to develop country and region-specific solutions to local N-related environmental problems and ultimately to apply the appropriate scientific, engineering and policy tools to implement these solutions. This article analyses the current knowledge of N cycling in terrestrial natural ecosystems of India and identifies future research directions.

Vegetation N pools

In forest ecosystems, tree leaves generally exhibit maximum N concentration, followed by shrub leaves and the herb biomass (Table 1). In the aboveground tree, N concentration follows the order: leaf > twig > branch > bole and in belowground components: fine root > lateral root > stump root[1–4]. Bole bark has higher N concentration than bole wood, and leaf N concentration may be as high as eight times that of bole wood[2]. Leaf N concentration of mature leaves varied from 0.86 to 4.11% among 90 species of dry tropical forest[5]; both N concentration and N mass also vary during the life span of foliage as the leaves emerge, grow, mature and senesce[6,7]. Leaves from both evergreen and deciduous species in the Himalaya contain more N on a leaf-area basis than leaves of tropical dry forest trees[8]. The N content of Himalayan deciduous

Table 1. N concentration (%) in different vegetation components of a temperate maple forest in central Himalaya (based on Garkoti and Singh[2]) and a dry tropical forest of Vindhyan Highlands (Singh and Singh[4])

	N concentration (%)	
Component	Temperate forest	Dry deciduous forest
Tree layer		
Bole wood	0.39	0.60[a]
Bole bark	0.78	–
Branch	0.47	0.71
Twig	0.84	–
Foliage	2.71	2.04
Stump root	0.51	–
Lateral root	0.54	0.82[b]
Fine root	0.78	1.05
Shrub layer		
Stem	0.64	0.77
Foliage	1.18	2.34
Root	0.52	0.79[b]
Herb layer		
Aboveground	1.21	1.54[c]
Belowground	1.16	–

[a]Wood + bark; [b]Coarse root; [c]Total herb.

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leaves is 2.87 g/m^2, whereas that of tropical dry forest leaves is 1.65 g/m^2. Similarly, Himalayan evergreen leaves have N content of 3.47 g/m^2, compared with 2.50 g/m^2 in evergreen leaves from tropical dry forest[8].

N accumulates both in short-lived and long-lived components of the forest vegetation. Quite disproportionate to their structural role (relative storage), the short-lived components of the ecosystems (foliage, fine roots and herbs) play a dominant role in the functioning (relative contribution to nutrient cycling) of the forest ecosystems. For example, N storage in the short-lived components of a dry tropical forest is quite low compared to their share in the total nutrient uptake and return (Table 2)[9]. The reverse is true for the long-lived components. These studies indicate the occurrence of two kinds of mineral turnover: a rather rapid cycle through short-lived ecosystem components and a slower cycle of minerals incorporated into larger woody axes.

Litter pool

Plant litter production above and below the soil surface determines the amount and quality of N returned to the forest floor and mineral soil, and therefore is an important process controlling the N cycling within natural terrestrial ecosystems. Leaf litter serves as a temporary sink for N and functions as a 'slow-release' nutrient source in forest ecosystems.

N concentration in litter

The range of N concentration in total litter fall from tropical forests is 1.2–26.0 mg/g dry matter[10]. In rainforests of Karnataka[11], annual variations in the concentration of litter-fall N was in the range 3.9–20.3 mg/g. In Shiroy hill forests of northeast India[12], N content of leaf litter varies from 9.5 to 27.3 mg/g.

Generally, the woody litter has lower N concentration than leaf litter[13–15]. Seasonal variations in litter N content

Table 2. Per cent contribution of short- and long-lived components in N economy of dry deciduous forests (based on Singh and Singh[9])

Component	N storage	Annual N uptake	Annual N return
Short-lived			
Foliage	18.3	25.2	38.5
Fine roots	5.8	30.5	34.9
Aboveground herbs	0.9	10.9	12.6
Total	25.0	66.6	86.0
Long-lived			
Branch	25.8	20.8	14.0
Bole	31.2	8.9	NA
Coarse roots	12.3	3.6	NA
Total	69.3	33.3	NA

NA, Not available.

are also reported for many ecosystems. For example, in northeast forests, N concentration was generally greater during autumn (0.6–1.3%) and lowest during the rainy season (0.4–0.9%) in all forest stands[14]. However, in a study from Kerala, no distinctive seasonal variation was discernible, except that the concentrations were generally lower during summer[16]. Khiewtam and Ramakrishnan[17] reported uniformly low values for N, P and K of litter samples during the wet season. N concentration in the pine or pine-dominated forests[18] is relatively low compared to the oak-dominated or mature oak forest ('sacred grove') in the same locality[13].

N input through litterfall

On an average, Indian forests receive about 54–93 kg N/ha/yr in litter fall (Table 3). In four rainforests of Karnataka, it is reported[11] that litterfall deposits 25.2–67.3 kg N/ha/yr to the forest floor. However, in 7–13-year-old humid subtropical forest stands of northeastern India[14], annual input of N through litter may reach up to 106–153 kg/ha. Although underestimated, contribution of belowground litter input in various forests may range from 5 to 21 kg N/ha/yr (Table 3). Conservative estimates indicate that total N return (aboveground and belowground litter) in forests of India is in the range 63–101 kg N/ha/yr (Table 3).

N dynamics during litter decomposition

Decomposition of litter, mediated primarily by soil biota, is crucial for nutrient recycling and long-term productivity of the forest ecosystems, where vegetation depends mainly on the nutrients recycled from plant detritus. Extensive studies are available on litterfall and litter decomposition in several forest ecosystems of India (see Singh and Singh[7] for review).

N dynamics during the course of litter decomposition has been studied for several central Himalayan forest tree species, indicating differential immobilization release phases[19,20]. In subtropical grasslands at Cherrapunji, there was significant increase in N concentration in grass litter over that in the dead shoot[21]. A net gain of N of up to 160% during the first few months of litter decomposition on the soil surface at Cherrapunji has been reported[22]. The immobilization and mineralization rates differ among species; the marked immobilization of available N by microbes during decomposition of pine litter may in fact intensify the N shortage in nutrient-poor soils and may be inimical to oaks which have heavy N demand[23].

Nutrient release through litter decomposition is influenced by a number of factors, including concentrations of N and lignin, C : N and lignin : N ratios, moisture and temperature[24]. The periods of active mineralization and

Table 3. Nitrogen budget for tree layer of certain Indian forests (data source given in Singh et al.[68])

	Forest type			
	Dry deciduous	Sal	Pine	Oak
Compartment pools (t/ha)				
Vegetation	0.656	4.45	1.108	3.299
Litter	0.036	0.05	0.131	0.094
Soil	2.970	4.01	3.964	5.820
Total	3.662	8.51	5.203	9.213
Accumulation in net production (t/ha/yr)	0.141	0.154	0.139	0.185
Retranslocation from senescing leaves (t/ha/yr)	0.033	0.034	0.046	0.018
Net uptake from soil (t/ha/yr)	0.011	0.120	0.092	0.167
N return* (t/ha/yr)				
Litter fall (leaf + wood)	0.063	0.074	0.054	0.093
Root mortality	0.021	0.005	0.009	0.008
Total	0.084	0.079	0.063	0.101
Retention in vegetation (t/ha/yr)	0.057	0.075	0.071	0.078

*N return does not include canopy throughfall and stem flow.

immobilization coincided with minimum and maximum soil microbial biomass[25]. Singh and Gupta[26] have suggested that N-rich, broadleaf litter seemed to decompose at a faster rate than those of narrow-leaf litters. In dry tropical environments, N mineralization rate is best predicted by lignin content and is positively correlated with litter mass loss.

Fine-root mortality and decomposition may represent an important pathway for N cycling in dry deciduous forest due to its high root biomass and high fine-root production. In Indian forests conservative estimates show that root turnover may contribute 8–25% to the total vegetation nutrient return (Table 3). In northeast Indian forests[27], total input of N to the soil by roots ranges from 42.2 to 52.5 kg/ha. Annually, around 58% of N content of the roots was mineralized in the forest stands. These values are comparable with those obtained for semi-evergreen broadleaved forest of Meghalaya[18]. The mean N storage[4] in the root compartment of a dry tropical forest was 102 kg/ha. However, it should be noted that methods often underestimate root turnover and decomposition patterns of roots may differ from the aboveground litter due to the differences in the resource quality of the two types of litter and differences in the environmental conditions under which they decompose[27].

Soil N pools

Soil organic N

Soil organic matter (SOM) is the largest N pool within terrestrial ecosystems accounting for more than 90% of total ecosystem N. It is formed from recalcitrant components of the detritus, and also from dead microbes. On average, dry tropical forests have lower soil N compared to Himalayan temperate forests, but as much as 81% of the
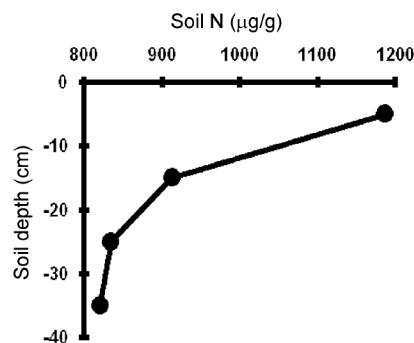
Figure 1. Depth distribution of N in dry tropical forests of India.

ecosystem N pool is in the soil (Table 3). Within ecosystem variability in the soil N stocks may be high due to influence of vegetation and topography. For example, soil N in dry tropical forests may vary from 0.84 to 1.58 t/ha in its 0–10 cm profile[24]. Most of the N in forest soil is confined to 0–20 cm horizon (Figure 1).

Microbial biomass N

The microbial biomass in soil is both a major sink for plant-available nutrients (immobilization) and a source (mineralization)[28]. In dry tropical forests, soil microbial biomass N ranges from 20 to 72 µg/g dry soil, accounting for 1.7–9.6% of the total soil N and probably a greater fraction of the labile nutrient pools[29,30]. Similarly, for subtropical humid forest of northeast India, soil microbial N was 42–124 µg/g, showing[25,31] a share of about 2% of the total soil N. Microbial N values for Indian savanna are lesser than forests and range from 30 to 68 µg/g (3.2–3·6% of the soil N)[32].

In the dry tropical forest and savanna ecosystems, the principal function of the microbial biomass is to accumulate and conserve nutrients in a biologically active form

during the dry period and then to release them rapidly during the wet period to initiate plant growth. Therefore, microbial immobilization may be the main source of nutrients for the plants and may lead to nutrient conservation by reducing nutrient loss. Reduced microbial biomass and increased microbial turnover in the wet period may result from feeding by expanded microbivore populations[28,33]. Therefore, periodic crashes in microbial populations may release nutrients from microbial biomass. The pulsed turnover of microbial biomass in the early part of the rainy season (first four weeks) contributes about 32 kg/ha N in the forest soils and about 25 kg/ha N in savanna soils. Compared to this, total rainy season (12–14 weeks) litter decomposition releases only about 22 and 19 kg/ha N in the forest and savanna respectively[33].

In the subtropical humid forest in northeast India, microbial biomass N was highest during the winter and lowest during the rainy season[25]. The lower values of microbial biomass during the rainy season when temperature and soil moisture conditions were favourable for microbial activity, indicated a period of rapid mineralization in soil[25]. In other studies of the region, similar dynamics was reported[34,35].

N mineralization

Dry tropical forests of India are extremely nutrient-poor because of low N pools and low N mineralization rates. Inorganic N in the forest soil ranges from 4.5 to 5.2 $\mu g/g$, whereas annual N mineralization[24] ranges from 125 to 203 $\mu g/g$. In these forests, even peak N mineralization rates (33 $\mu g/g$/month) are substantially lower than the values reported for other tropical ecosystems[24]. The N mineralization rates are maximum during the rainy season and minimum during the summer season, indicating a close link to seasonal variations in moisture as temperature is seldom limiting. The flush of N mineralization observed at the onset of the rainy season following the summer is consistent with several reports of increased N mineralization of dry soils after rewetting[28,36].

In the humid subtropical forest ecosystem of northeast India, the mean monthly N mineralization rate in the upper soil layer was 13.8–14.1 and 11.4–11.9 $\mu g/g$/month in the protected and unprotected stands respectively. The low and high N mineralization rates observed during the dry and wet periods respectively, coincided with the lean and peak periods of fine-root mass[37]. Rapid mineralization of N in the disturbed plots signals potential loss of available N from the system, and may result in a lower concentration of ammonium-N in soils of the tree-cut stand and soil heaps[18].

Studies indicate that the N mineralization process is regulated by soil properties, such as quality of soil organic matter, microbial biomass and activity, and soil temperature and moisture. The importance of soil moisture (dry–wet cycle) on N mineralization has been reported from dry tropical savanna[32] and subtropical humid forest of northeast India[38]. Nutrient availability is strongly regulated by soil-water availability. Reports[39,40] suggest that habitat heterogeneity in forest ecosystems leads to patchy distribution of N availability. In such SOM-rich patches microbial biomass and N mineralization rates are higher and fine roots are concentrated.

Internal cycling of N

For nutrient-poor habitats, it is demonstrated that the vegetation has developed the nutrient conserving strategy of withdrawing substantial amounts of N before senescence, so that each unit of nutrient absorbed from the soil is used for the development of successive generations of foliage. For woody species of dry tropical species, N retranslocation during senescence varies from 26 to 83% (mean 58%), indicating that the species resorb N in substantial amounts to support new growth (Table 4)[5]. In dry tropical teak plantations it was found[41] that withdrawal of N from senescing leaves may be in the range 53–65%. Measured range[42] of N retranslocation during senescence for temperate Himalayan species is 33–75%. Withdrawal of N from senescing leaves to the extent of 51–52, 39–41 and 8–13% respectively, for pine, sal and oak forests has been reported[7]. Values indicate that resorbed N could be a significant source of plant nutrient supply and is likely to meet a significant proportion of N demand of the developing leaves of forest tree species[6]. Thus the retranslocated N becomes a major source to support the initial demand of newly emerging leaves during the dry period, when nutrient uptake from the soil is hindered due to very low soil moisture. A strategy that drops nutrient-rich litter exposes those nutrients to competition from other individuals and from the soil microbial biomass and therefore, it is advantageous for plants to depend more on internal nutrient recycling in general, and nutrient resorption in particular[13]. However, not all dry deciduous species are equally efficient in N resorption.

Species and habitat differences have been demonstrated in central Himalayan forests also. For example, the percentages of retranslocation of N from senescing leaves of chir pine were significantly greater (53) than from oak leaves (22–25)[43]. The former is adapted to infertile habitats and the latter to fertile habitats[7]. This observation is consistent with the suggestion that species of infertile

Table 4. Leaf N retranslocation in different dry tropical plant groups (based on Lal et al.[5]). Resorption efficiency is ratio of resorbed N pool and peak N mass

Species group	Resorbed N pool (μg cm^{-2})	Resorption efficiency (%)
Deciduous ($n = 35$)	120.0	65.8
Evergreen ($n = 33$)	91.8	54.7

sites show greater proportional retranslocation of N than do the species adapted to fertile sites. Overall, the deciduous shrubs showed greater percentages of retranslocation than did the evergreen shrubs. There was also a limited increase in N resorption with altitude[2]. Experiments by Singh et al.[44] on Himalayan tree seedlings also demonstrated that in nutrient-limited conditions, internal nutrient conservation via efficient nutrient resorption as well as use is advantageous and these processes are linked to the availability of this nutrient in soil.

Ecosystem N inputs

The forest cover over India receives its N input through atmospheric deposition, biological N fixation and to a lesser extent from stream flow and weathering of N containing rocks and minerals. Nothing is known about the extent of N deposition in various terrestrial ecosystems of India.

Almost no information exists on rates and extent of both symbiotic and asymbiotic N fixation in the natural terrestrial ecosystems of India. In one study, in different age monoculture stands of eastern Himalayan Alnus nepalensis, the total N_2 fixation ranged from 29 to 117 kg/ha, the highest values being recorded from youngest stands. Similarly, in Alnus–cardamom plantations of the same region, annual N fixation increased from 52 kg/ha in the 5-year-old stand to a peak value of 155 kg/ha in the 15-year-old stand. Annual N fixation was essentially static (58 and 59 kg/ha respectively) in 30- and 40-year-old plantations[45].

N inputs through canopy wash (throughfall and stem flow) can be substantial. An input of 3.8–6.3 kg N/ha/yr for four forest types of central Himalaya was reported[46]. These values are substantially lower than the quantities returned through litter fall (48–70 kg/ha/yr), but N from canopy wash is in plant-available form, while that in litter has to be released in available form through decomposition.

N budgets in selected ecosystems

Forests

The mean standing state and net annual flux of N for dry deciduous forests (Figure 2) have been described earlier[4]. Aboveground N storage in these forests is 82% of that stored in vegetation and 21% of that stored in the stand (including soil). About 52% N of the net uptake by the aboveground vegetation is returned to the forest floor in litterfall. Litter turnover recycles about 56 kg N/ha/yr. Fine-root turnover contributes 40 kg/ha/yr N to the soil pool which amounts to 42% of the total N released from the soil for vegetation uptake, making it an important component of N cycling in dry tropical forests.

The total N budget of a number of central Himalayan forests at plot scale has been worked out[3,7,47]. The N budgets of selected forest types are given in the Table 3. In sal forest, the vegetation pool accounted for about half of the N, indicating its resemblance with tropical moist forests, which have high proportion of nutrients in the vegetation compartment. Substantial amount of N was reabsorbed from senescing leaves prior to leaf fall. Pine and dry deciduous forests were more efficient in nutrient withdrawal than sal and oak forests. Considerable amount of N was returned through litterfall and root mortality to the soil compartment in these forests. The proportion of N returned relative to total quantities stored in vegetation compartment was maximum in the dry forests, followed by pine, oak and sal forests. Of the total N contained in the annual litter fall, 92, 92, 68 and 42% N was released annually to the soil compartment of sal, dry deciduous, oak and pine forests respectively.

The N cycle of pine and oak forests of central Himalaya and that reported in the successional pine N cycle were compared and found to be highly conservative compared to the climax oak[23]. This indicates that the climax forest with relatively affluent N cycle may be susceptible to greater N losses through deforestation and gaseous emissions.

Grasslands

In India, grassland nutrient cycling has been studied under different ecoclimates[48–54]. Indian grassland soils contain nutrients several times than that held by plant biomass[49,52]. Mishra[52] studied the distribution of N in different plant compartments and in the top 30 cm soil among
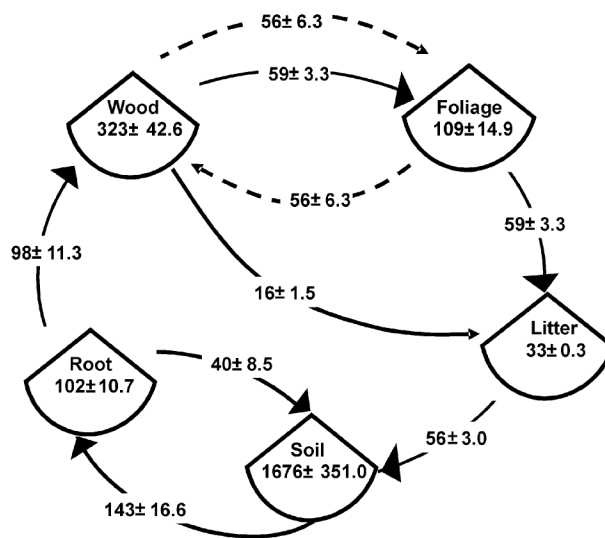

Figure 2. Pools and fluxes of N in dry tropical forests. Tanks, Standing state (kg ha^{-1} ± 1 SE); Solid arrows, Cycling (kg/ha/yr ± 1 SE); Broken arrows, Internal cycling (modified from Singh and Singh[4]).

the protected, semi-protected and open-grazed grasslands. The protected site had greater N pools compared to semi-protected and open-grazed sites. In grasslands investigated by Billore and Mall[49], annually about 58 kg N/ha is taken up by the grasslands, of which 29 kg N/ha is released and about 29 kg/ha is retained in the vegetation compartments. Greater accumulation of nutrients in the shoot, a result of high nutrient concentration and greater biomass, is the characteristic feature of tropical grasslands[48–52], whereas the greater belowground reserve is characteristic of temperate grasslands[55]. Higher allocation of biomass and nutrients to the belowground parts in Indian grasslands at Cherrapunji was shown, which may be due to adverse climatic and edaphic conditions[21]. In these grasslands at Cherrapunji, among different vegetation compartments, live root was the largest reservoir of N followed by live shoot, dead shoot, litter and dead root[21]. The total annual N uptake was 137.3 kg/ha. In an annual cycle, 98% N was returned to the soil through litter and belowground detritus. A major portion of N was recycled through the belowground system.

Human impacts on N cycle

Landuse change

Forests in India are continuously being converted to savanna, cropland and even total destruction is visible in the mined areas. The conversion of dry tropical forest to alternate and simpler landuses significantly reduces soil N (Table 5)[56]. The decrease in soil nutrient stock may be attributed to lower inputs of organic matter in the converted systems due to decline in the plant biomass. In agroecosystems, decomposition is also enhanced because disturbance or tillage physically fragments and redistributes residues. Also, much of the biomass is removed from the agroecosystems for human and animal cultivation[56]. A recent study[57] shows 38% decrease in total N content after conversion of a forest to cropland. The microbial-N declined by 42%, whereas nitrification and net N-mineralization decrease respectively by 51 and 48% after conversion of forest into cropland. Similarly, in the Simlipal National Park area, trends in average soil N content follow the order: evergreen forests (0.49%) > deciduous forests (0.32%) > grassland (0.23%) > cultivated land

Table 5. Per cent decline in soil N pools in derived landuses compared to native forest (based on Srivastava and Singh[56])

	Savanna	Cropland	Mine spoil
Mineral N	13.2*	35.2	37.1
Organic N	52.3	52.8	66.0
Microbial N	41.5	49.2	58.4

*Difference not significant.

(0.16%)[58]. All cultivated areas showed significant lowering of N content compared to the adjoining forest lands. Although reduction of total N in cultivated soils does not seem to be related to the period of cultivation, losses of over 50% N may occur in about 30 years of cultivation[58]. In northeast India, soil N decreased as the duration of cultivation increased[31]. The conversion of natural forest in eastern India has led to a reduction of total N (26–35%) and total microbial biomass N (25–60%) over a period of 30–50 years[59]. Total N values were 2015, 1498, 1304 μg/g in forest, grassland and cropland soils. The ranges of microbial biomass-N in forest, grassland and cropland soils were 65–116, 27–55, 21–43 μg/g soil respectively[59].

Primary soil particles, particularly clays, tend to cohere under natural conditions to form secondary units called aggregates, through the action of temporary and transient binding agents such as microbially derived polysaccharides. Landuse changes (conversion of forest into savanna and cropland) reduce the organic matter input to the soil and the proportion of macroaggregates[60]. The proportion of macroaggegates is highest in the forest followed by savanna and cropland ecosystems (Table 6). Reduction in the proportion of macroaggregates indicates soil deterioration due to ecosystem conversion. Microaggregates in different landuses have higher microbial N compared to macroaggregates, indicating higher N turnover potential in derived ecosystems. Also, food-web in macroaggregates is fungi-dominated, as indicated by higher C/N ratios of microbial biomass associated with macroaggregates, leading to greater conservation of N. In contrast, food-web in microaggregates is bacteria-dominated, thus the microaggregates have lower nutrient conservation potential. This is reflected in the total N values in aggregate fractions of the soil (Table 6).

Slash and burn agriculture

Slash and burn agriculture (jhum) may be an important source of atmospheric N. In slash and burn plots, total soil N declines soon after the fire, with further decline or no significant change subsequently[61]. However, soil N status improves with fallow age. N budgets[62] were prepared under rotational bush fallow agriculture (jhum) at higher elevations of Meghalaya. A shortening of the jhum cycle lowers the N content of the soil. Loss of N through fire was highest (510 kg/ha) in 15-year fallow cycle and lowest (263 kg/ha) in 5-year fallow cycle[62]. During one cropping phase, the agro-ecosystem loses about 600 kg/ha of N. Others[31] recorded that available-N concentrations in the jhum field (20 days after burning) were lower compared to the forest soil. When soils are heated to temperatures as high as 100°C, there may be a large increase in the extractable ammonium-N due to thermal decomposition of organic matter, release of fixed ammonium from soil minerals, and death and subsequent release from micro-

Table 6. Proportion of aggregates and associated N in different landuses in soils of dry tropical zone (data from Singh and Singh[60,69])

Landuse	Macroaggregates (>300 μm)				Microaggregates (≤ 300 μm)			
	Percentage of soil mass	Total N (g kg^{-1})	Microbial N (μg g^{-1})	Microbial C/N	Percentage of soil mass	Total N (g kg^{-1})	Microbial N (μg g^{-1})	Microbial C/N
Forest	65.9	2.44	66.0	7.5	34.1	2.01	72.4	5.3
Savanna	54.6	1.23	36.7	7.5	45.4	1.05	50.5	5.2
Cropland	42.1	1.00	28.2	9.7	57.9	0.45	39.1	4.4

bial biomass. On the other hand, nitrate-N is lost above 150°C as volatilized nitric acid[31].

Pollution

Very few studies are available which clearly demonstrate the effect of pollution on N economy of Indian natural ecosystems. With the increasing pollution load, foliar N content decreases in selected dry tropical forest tree species[63]. The lower N content in the leaves of trees from polluted sites may be ascribed to unfavourable changes in plant metabolism due to gaseous and particulate pollutants present in the area[64]. Disturbed soil microbial activity may also reduce N availability in soil[65]. Reduction in N content was more during summer in evergreen and during winter in deciduous plants[63].

Species invasions

A study in the dry tropical forests suggests that lantana cover alters soil N dynamics successively with increasing cover[66]. Increasing lantana cover in these forests escalates the nutrient availability. When N returns from the decaying litter of invasive species to the soil, the nutrient pool increases, thus increasing N availability in the soil due to fast N mineralization. Higher turnover rates, which reflect the rate of nutrient cycling, were also reported for lantana in oak forests[3]. The study also showed that high turnover rates, high rates of decomposition of litter and efficient translocation of nutrients result in high production of lantana. N content of lantana is reported[67] to be higher than other native species within its habitat. Superiority in N extraction from the soil along with an efficient retranslocation of N from the senescing leaves enables lantana to perform better as an invasive species[67].

Future research directions

The synthesis of existing knowledge on N cycling in natural terrestrial ecosystems of India shows that there are a number of important uncertainties in our understanding. In order to fill this gap we need to plan biome-level integrated studies on N cycling, covering the areas listed below.

N input

The inability to accurately measure inputs of N is one common research gap to most Indian natural ecosystems. N inputs can mainly come in deposition (wet and dry) and N_2 fixation (both symbiotic and associative). Although a few studies give data on wet deposition, inputs of N via dry deposition are seldom measured.

N uptake

Reliable data on the magnitude, importance and mechanisms of uptake of reactive N by plant canopies are needed from Indian terrestrial ecosystems. A better understanding of physiological controls over and the relative importance of canopy uptake of N is also desired. Secondary chemical reactions and processes occurring inside the leaf, which define the assimilation rate of reactive N into the canopy are also not understood in tropical species. Studies are needed to determine if canopy-derived N has the potential to influence ecosystem function differently than does soil-derived N.

N availability

Abiotic and biotic factors controlling N availability in terrestrial soils need to be understood. Organisms available to assimilate N in an ecosystem need to be identified together with their preferred form of N (NH_4^+, NO_3^-, or dissolved organic N). Data on species-level efficiency of N use is needed for modelling the impact of species changes on N dynamics. Competition among plant species and between plant and microbial communities in N cycling in different ecosystems needs to be understood.

Impact of anthropogenic N input

There are gaps in our knowledge of atmospheric N effects on Indian natural ecosystems. A comprehensive accounting of the N cycle in natural ecosystems together with ecosystem-level fertilization experiments may be designed for major terrestrial biomes of India to identify the direct and indirect effects of N additions. The links between alterations in N cycling and productivity and carbon cycling in these ecosystems need to be understood.

Gaseous N emissions

There is an urgent need to document the spatial and temporal variation in emission of the dominant nitrogen trace gases (N_2, NO, N_2O, and NH_3) from various terrestrial ecosystems of India. Influence of soil moisture on partitioning of gaseous N emissions is an important aspect of research as soil wetting/drying cycle is shown to affect soil N dynamics in many Indian ecosystems. Proper understanding of how whole-ecosystem emissions respond to changes in N inputs will help in understanding vegetation–climate feedbacks.

Finally, as N cycling occurs across atmospheric, terrestrial and aquatic interfaces, the interactions and feedbacks between these systems are also important aspects to be studied.

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