Impact of environmental nutrient loading on the structure and functioning of terrestrial ecosystems

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Wet and dry depositions of essential elements (e.g. N, P, S) in different terrestrial ecosystems have been rapidly increasing in recent years due to perturbations of biogeochemical cycles of these elements by different anthropogenic activities. It is expected that the increased deposition of these elements over a period of time will have dramatic effects on natural and modified terrestrial ecosystems. An important task ahead is to understand the early signs and predict the impact of nutrient loading on the structure and functioning of terrestrial ecosystems. In this review we discuss the emerging trends of possible nutrient loading effects on terrestrial ecosystem components and processes, and suggest major research objectives.

ANTHROPOGENIC activities have dramatically altered the global cycles of carbon and other essential elements. Although the significance of biogeochemical cycles of these elements has been recognized for long, until recently much less attention has been paid to evaluate the ecological consequences of perturbations of these cycles by human activities[1]. Bulk of information regarding the potential ecological effects of these perturbations is available with respect to carbon. However, the changes in biogeochemical cycling of several other elements essential for plant growth (such as N, P and S) have been recently considered to be more dramatic. Solid particles containing fractions of these elements may be suspended in rain (wet deposition), mist or snow, or may be carried as separate dry particles (dry deposition) to be continuously deposited from the atmosphere to the terrestrial ecosystems. There has been a growing ecological concern from the deposition of N (e.g. NO_3^- and NH_4^+), P (PO_4^{---}) and S (SO_4^{--}) on terrestrial ecosystems.

The recent global annual conversion rate of unreactive nitrogen to its reactive forms is about 145 Tg, of which 55% is associated with fertilizer production, 31% is derived from legume and rice cultivation, and the remaining 14% from fossil fuel combustion[2]. It is estimated that these practices are now releasing more combined nitrogen into the terrestrial environment than that due to N-fixation by micro-organisms in natural and semi-natural ecosystems[3]. This estimate also includes a doubling of the natural rate of N-fixation and an increase of atmospheric N-deposition rates by more than 10-fold over the last 40 years to the current values of 5–25 kg N ha^{-1} $year^{-1}$ in eastern USA and 5–60 kg N ha^{-1} $year^{-1}$ in Northern Europe[4]. Further increase in fossil fuel burning and fertilizer use is projected to lead to a 60% increase in combined annual N-release by the year 2020. About two-thirds of the increase will occur in Asia which will account for more than half of the global anthropogenic nitrogen fixation by 2020. In many terrestrial ecosystems, N deposition rates range from 2.5 to 20 kg N ha^{-1} yr^{-1}; however, in several other ecosystems increased N deposition levels (30–64 kg N ha^{-1} yr^{-1}) have been reported to cause imbalances in mineral nutrition[5,6]. In comparison to the information on the deposition of N, much less information is available on the deposition of P in different ecosystems. Most reports of total P deposition range from 0.07 to 1.7 kg P ha^{-1} yr^{-1}, although exceptional values as high as 27 kg P ha^{-1} yr^{-1} have been reported[7].

The Industrial Revolution, particularly the smelting of sulphur-containing ores, led to an increase in the burning of fossil fuel (coal) which became the major anthropogenic source of highly phytotoxic SO_2 gas and its solution products. The increased wet and dry depositions of sulphur have been reported to cause a wide range of changes in the structure and functioning of terrestrial ecosystems. For example, total sulphur deposition has been reported to have increased from about 2.5 kg ha^{-1} $year^{-1}$ in 1880 to about 15 kg ha^{-1} $year^{-1}$ in 1990 in southern Sweden[8].

Information on nutrient deposition in natural or man-made ecosystems is extremely scanty in India. Khemani et al.[9] have reported the following ionic concentrations (mg l^{-1}) in rainwater: For $NH_4^+ + NO_3^-$, coastal locations 0.84–0.91; urban 0.58–3.7; non-urban 1.45–2.71; for SO_4^{--}, coastal 1.11–2.58; urban 1.78–2.73; non-urban 1.53. Exceptionally high values of SO_4^{--} have been reported from industrial areas in Kalyan (5.2 mg l^{-1})[9] and Chembur (20.2 mg l^{-1})[10]. Assuming an annual rainfall of 1000 mm, the range of concentrations reported above, i.e. 0.58 to 20.2 mg l^{-1}, corresponds to a deposition of 5.8 to 202 kg ha^{-1} yr^{-1}. In the Chandraprabha Sanctuary

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supporting dry tropical forests, Singh and Misra[11] esti-mated an annual wet deposition of: NO_3-N, 9.1; organic-N, 14.1; and PO_4-P, 4.2 kg ha^{-1} yr^{-1}. In different Central Himalayan forests, Mehra et al.[12] have reported annual wet deposition values 8.5 to 11.4 kg ha^{-1} for N and 1.4 to 2.1 kg ha^{-1} for P.

Continued addition of N, P and S over prolonged periods of time is expected to radically change the structure and functioning of natural and modified terrestrial ecosystems. As nutrient loading increases positively during the course of time, its effect becomes more pronounced but difficult to predict. Thus, there is an urgent need to analyse the effect of nutrient loading on terrestrial ecosystems. The main aim of this paper is to bring out the emerging trends of the effect of nutrient loading on terrestrial ecosystems and to suggest future research needs. For the sake of convenience the impact of nutrient loading has been considered under three sections – ecosystem structure, function and soil processes.

Possible impact of nutrient loading on ecosystem structure

Increased nutrient loading is expected to substantially elevate the nutrient level of the soil. While the elevated nutrient levels may prove advantageous to many species, the same levels may become deleterious to several other species leading to their disappearance from the ecosystem. Disappearance of some species may disturb the ecosystem equilibrium because the survival of some species is often dependent on the survival of many other species present within the same ecosystem. If the increased nutrient level adversely affects the plant species diversity in an ecosystem, the same ecosystem may collapse in the coming decades because a certain threshold level of biodiversity may be required for the proper functioning of every ecosystem[13].

Many tropical forests, grasslands and shrublands showing high diversity occur in relatively low-nutrient habitats. In such ecosystems, plant species diversity is generally not a single increasing function of productivity or nutrient supply rate. While some studies indicate greater diversity in low-nutrient supply habitats, several other studies suggest higher diversity in intermediate nutrient level habitats. It has been suggested that the low soil fertility reduces diversity through nutrient stress and that high soil fertility removes the limitations imposed by nutrient stress, resulting in simplified communities as the outcome of competitive exclusion. Tilman and Pecala[14] have concluded that peak diversity is obtained in habitats with soils of low to intermediate levels of nutrient supply, although they have not considered the extreme environments such as tundra and desert where diversity might be expected to be low because few species are adapted to these conditions.

Deleterious environmental effects of S compounds were noticed much before those of N and P. Direct phytotoxic effects of SO_2 emanating from coal-burning industries in Manchester and Shaffield, UK were reported in the surrounding area during the 19th century. For instance, decline in lichen species was attributed due to coal smoke pollution[15]. Presence of acid in rainwater and its possible harmful effects were reported by Smith[16] who also listed SO_2 sensitive higher plant species, suggesting that the difference in sensitivity may cause changes in species composition of vegetation with continued phytotoxic S load. Later in the same region evidence was presented to show that composition of peat vegetation changed due to disappearance of Sphagnum species due to air pollution effects[17]. The same effect was demonstrated by spraying dilute solution of bisulphite ions (a solution of SO_2 at rainwater pH) on a Sphagnum-rich bog in North Wales, resulting in the elimination of Sphagnum within a year, but the survival of angiospermous Eriophorum species[18]. The adverse effect of acidic deposition on forest trees in Sweden is well known[19] and may even lead to the replacement of understory species with acidophillous species[20]. However, effects of low concentrations of sulphur dioxide and its solution products are difficult to quantify in semi-natural ecosystems and may be much more widespread than currently realized.

In recent years, in developed nations like North America and Western Europe, research emphasis has shifted from sulphur pollutants to nitrogen. The effect of sulphur deposition on biodiversity may be slow, but in the long term, the sulphur deposition in association with nitrogen may have a tremendous effect[1]. Nitrogen deposition is expected to have a greater effect than sulphur because the former is required in larger amount by plants than the latter, and often nitrogen limits plant growth in many ecosystems. A large number of plant species in natural and semi-natural ecosystems are adapted to grow in oligotrophic (nutrient scarcity) conditions and can compete successfully with other species only in nutrient-deficient soil. Plant species restricted to low nutrient status soils and those dependent on the atmospheric solute supply are likely to be the most susceptible to enhanced nitrogen deposition. About 65–80% of central European Red list endangered species occurring on nutrient-poor soils may be at risk from increased nitrogen loading[21].

Inorganic fertilizers, particularly nitrogen compounds, can cause significant changes in species composition when applied to mixed grasslands. Such applications usually increase the dominance of a few species but cause overall loss of species richness[22]. N loading has been recognized by Morecraft et al.[23] as a major threat to grassland ecosystems and may cause loss of diversity, increased abundance of non-native species and the disruption of ecosystem functions.

The species composition of the vegetation has been reported to be affected by the nature of nutrient limitation

(e.g. N or P limitation). It has been observed that the addition of P in the absence of N encourages particularly the growth of leguminous species that are capable of nitrogen fixation. In contrast, application of N in the absence of P has been observed to stimulate the growth of grass species in particular[24]. In different parts of Europe atmospheric N deposition has resulted in increased abundance of nitrophilous herbs (e.g. *Rubus idaeus, Chamaenerion angustifolium, Urtica dioca*) in ground flora in different forests[25]. It is expected that the sites dominated by N deposition will be dominated by species of grasses and those with greater P deposition may show enhanced proportion of leguminous species. But overall the species richness and species diversity will be decreased with the replacement of few sensitive species after the addition of both nutrients.

As a result of atmospheric N deposition in the Netherlands, many heathland communities dominated by species such as *Calluna vulgaris* and *Erica tetralix* have been replaced by grasses such as *Molinia caerulea, Deschampsia flexuosa* and *Festuca ovina*[26]. Nitrogen fertilization experiments simulating enhanced atmospheric deposition may lead to the invasion of rough grasses in *Calluna* heathland and lichen-rich grass heath[26,27]. In the Netherlands and Southern England, loss of species diversity and conservation value due to increase in the rough grass (e.g. *Brachypodium pinnatum)* are ascribed to atmospheric nitrogen deposition[28]. Atmospheric nitrogen deposition is also suspected to be the cause of losses in bryophyte and lichen species at high altitude sites in Britain; particularly sensitive species are *Sphagnum* species[29] and the moss *Racomitrium lanuginosum*. Tundra vegetation has been found to be potentially sensitive to atmospheric nitrogen deposition in fertilizer experiments in Alaska[30].

Extra supply of nutrients may affect the vegetation in different ecosystems differently. For instance, N seems to be more influential in causing changes in species composition and plant growth at certain sites while P exerts a greater effect than N in certain other sites. Certain species may favour N but the same may be affected by the application of P, whereas the reverse may be true in other cases. Kirkham *et al.*[31] concluded that phosphorus was the most effective nutrient causing botanical changes at Tadham and Tealham moors site in the south-west of England. The species diversity was found to be significantly lower in May 1990 on plots which had received high rates of both N and P with only replacement rates of K, compared to those which had received the same rates of N and P, but with a high rate of K (200 kg ha^{-1}). At the time of discontinuation of nutrient additions in 1990, species numbers per plot differed little between treatments. But the recovery of species richness after 1990 was much more marked on plots which had received a high rate of K than those where replacement rates had been applied[32]. These results support the suggestion by Tilman[33] that the ratios in which nutrient resources are available to plants

may be as significant as their absolute levels in determining vegetation composition and species diversity.

Possible impact of nutrient loading on ecosystem function

In several countries (e.g. Austria, Finland, France, Germany, Sweden and Switzerland) forest stocks have shown a general increase in recent decades[5]. Besides favourable climatic conditions (such as high temperature and high precipitation), the increasing effect of nitrogen deposition has been mentioned as a possible cause of such an increase[34]. Atmospheric nitrogen deposition generally favours increase in tree growth if other nutrients are not limiting. Vitousek[35] has suggested that forest productivity increases along a gradient of increasing P availability, but experiments have failed to support the idea that juvenile tropical plants are limited by P supply, except in the special case of those lacking mycorrhizas[36,37].

On the other hand, forest decline has also been associated with increasing atmospheric nitrogen deposition, particularly NO_x. A wide range of interacting factors, including nutrient imbalances, excess foliar nitrogen, increased drought sensitivity and pathogen attack, as well as soil acidification may be involved with forest decline[38]. The response of tree growth to nitrogen deposition depends, in particular, on the balance of soil available nutrients. Tamm[39] found that tissue nitrogen concentration in *Pinus sylvestris* increased from 1 to 2.5% when subjected to 90 kg N ha^{-1} yr^{-1} application in a long-term study in Sweden. Among other reported effects of nitrogen deposition are increased algal and fungal growth on bark and needles which may be related to increased N content of needles[40]; decreased root/shoot ratio and reduced mycorrhizal infection, possibly affecting drought sensitivity and uptake of other nutrients[41,42]; and reduced frost resistance[38]. Nitrogen fertilization may cause reduction in yield in nutrient-limited systems[39], primarily as a result of nutrient imbalance caused by relative scarcity of cations such as K^+, Mg^{++} and Ca^{++} (ref. 43). Uptake of cations can be limited in the presence of excess NH_4^+ due to competition of ions. Shortage of cations may be induced by soil acidification associated with excess NH_4^+ and cation leaching[44].

Differential effects of nutrient enrichment on the growth of pioneer and non-pioneer species in Luquillo Experimental Forest, Puerto Rico have been reported[45]. The pioneer species (*Phytoplacca rivinoides, Cecropia schreberiana* and *Palicourea riparia*) responded significantly with respect to biomass to both N and P enrichment. Non-mycorrhizal *P. rivinoides* was the most responsive to P fertilization because mycorrhiza are especially important for P uptake. However, the biomass of non-pioneer species (*Manilkara bidentata*) responded only to N enrichment; this species is highly dependent on the mycorrhizal

fungi and therefore, would not be expected to respond as strongly to P fertilization. Further, P fertilization was found to increase the foliar P concentration in pioneer species, but foliar N did not increase significantly in response to N fertilization. For non-pioneer species, however, both foliar N and P increased in response to fertilization by N and P, respectively. The positive response of pioneer species to P fertilization reflects the low availability of P in soil in the Luquillo Experimental Forest[46] and the high potential growth and photosynthetic rates of the pioneer species may also provide P limited condition because these characteristics allow the species to use extra P when it was supplied. The slower potential growth rates of non-pioneer species may have reduced demand for P.

Dalling and Tanner[47] also found that addition of complete fertilizer increased the concentration of P in landslide-grown seedlings, but not that of N. Absence of distinct increase in the concentration of N in few species, leaves may be due to dilution of the added N by the rapid growth of these species. Amongst the eight species of *Shorea* at Sinharaja Forest Reserves, Sri Lanka, studied for responses of P and Mg additions[48], two groups on the basis of dry mass yield in response to nutrient enrichment, corresponding to nutrient-rich and nutrient-poor sites were separated. The species with the highest maximum mean dry mass yield in any nutrient addition treatment were *Shorea megistophylla, S. cordifolia, S. trapezipolier* and *S. congestiflora*, and the species with the lowest maximum mean dry mass yield in any nutrient addition treatment was *S. gardneri*. The widely distributed *S. disticha* was intermediate between the two groups. The different rates of growth in response to fertilization primarily reflect differences in the physiology of the plant species.

Nutrient resorption or retranslocation is the process by which nutrients are mobilized from senescing leaves and transported to other plant tissue[49]. Resorption of nutrients from senescing leaves enables plants to re-use these nutrients and this process is a major nutrient conservation mechanism, having important implications at both population and community levels. At the population level, it has been postulated that low nutrient loss rates can increase the fitness of plant populations in nutrient-poor environments[50]. Nutrient resorption from senescing leaves has important implications at the ecosystem level because resorbed nutrients are directly available for further plant growth, making a species less dependent on current nutrient uptake. Nutrients which are not resorbed, however, will be cycled through litterfall which takes a longer time to become available to plants for growth. Various authors have considered the resorption of nutrients from senescing leaves as an adaptation to low soil fertility and different relationships were reported. In some studies, nutrient resorption increased with increasing soil fertility, in some the opposite trend was found and in others there were no relations at all. This is because of two reasons: (a) soil

fertility and nutrient resorption were drawn from the limited data set from only one or a few species studied in a specific plant community; (b) species growing in nutrient-poor habitats were compared with species growing in nutrient-rich habitats. Reviewing the nutrient reabsorption efficiency of 226 evergreen and 278 deciduous species, Aerts[51] concluded that there was a weak response of nutrient resorption to increased nutrient supply. The most clear control in nutrient resorption is, however, found when plants are grown at abnormally high leaf nutrient concentration where nutrient resorption efficiency is low[52].

Litter decomposition rate depends on the combined effects of its chemical quality and the abiotic variables[53,54]. A net increase in N content of decomposing litter is often observed, especially when the initial litter has low N content or high C : N ratio[55]. Although N seems to be a limiting substance for micro-organisms, addition of N to decomposing litter often accelerates the rate of decomposition. A positive effect of N addition seems to occur only if the supply of easily degradable carbon compounds does not limit the decomposition. As a result of increased N supply, the rate of accumulation of organic matter in the soil and the N mineralization rate will change in the long term[56]. But the decomposition and the dynamics of the amount of N in litter may also be affected by the amount of atmospheric N. van Vuuren and van der Eerden[57] have observed that the deposition of ammonium sulphate enriched with ^{15}N in artificial rainwater resulted in marked increase in the ^{15}N values of the leaf litter in different species. This suggests that a part of the supplied N had been absorbed by the litter microbial biomass. While the decomposition rate of the two species was unaffected, the decomposition rate of one species litter increased temporally at the higher N deposition rate.

A number of literature reviews of C/N ratios in plants, litter and soils are available[58]. There is a need for a comprehensive database on the impact of increasing nutrient levels on the C/N ratio in different components of the ecosystems. Also, it is critically important to explore the variability of C/N ratios in plant tissues of various species with respect to nutrient additions. Even if the C/N ratio can be widened only slightly, carbon storage in the soil may increase. It may be argued that the tissue chemical quality of plants grown in high nutrient level conditions could be altered. Probably the C/N ratio of tissues tends to decrease with greater availability of nutrients, particularly N. Since tissues with low C/N ratio (< 20) generally decompose faster, it may be expected that the rate of litter decomposition may increase under high soil–litter nutrient conditions. Also, changed litter quality will have significant effect on plant–herbivore interactions.

Koerselman and Meuleman[59] have postulated that the nature of nutrient limitation can be directly established from the N:P ratio in plant tissues, because this ratio gives an indication of the relative availability of N and P in soil. They assumed that under conditions of relatively low P

supply and high N supply, plants absorb more N than P. Therefore, due to the luxury consumption of N, the N : P ratio in plant tissues will tend to rise. On the other hand, under conditions of relatively high P supply and low N supply, a lower N : P ratio in plant tissues may be expected[60]. These authors have hypothesized that plant species have a critical N : P ratio, indicating whether growth of the species is N-limited or P-limited. On the basis of 40 fertilization studies, Koerselman and Meuleman[59] have generalized that under conditions where either N or P limits plant growth, an N : P ratio > 16 indicates P limitation on a community level, while an N : P ratio < 15 indicates N limitation. At N : P ratios between 14 and 16, either N or P can be limiting, for plant growth is limited by N and P together.

Impact of nutrient enrichment on soil microbial processes

Increased acidic pollutants resulting in enhanced deposition of H^+, SO_4^- and NO_3^- have accelerated acidification of soil in many terrestrial ecosystems of the world. The acidification of forest soils over recent decades in Sweden has been particularly well documented[61], and this is reported as one of the major factors that may substantially contribute to forest decline in Europe[62]. Several reports suggest a strong interaction between atmospheric nitrogen deposition and nitrogen mineralization processes which results in enhanced nitrogen availability in soil. In *Kobresia* meadow soils receiving fertilizer inputs of 250 kg N ha^{-1} over 2 years, nitrogen mineralization rate increased more than 10-fold compared to control plots in the year following the second fertilizer treatment. Morecraft *et al.*[23] found that annual net nitrogen mineralization rates showed little change at low N input rates, but increased linearly with N input above 50 kg ha^{-1} yr^{-1}; the N mineralization rates increased 4-fold over control with a deposition of 140 kg N ha^{-1} yr^{-1}, and the elevated N mineralization rate persisted for 7 years. Vinton and Burke[63] found that even 20 years after the termination of treatment, enhanced nitrogen mineralization rate persisted in the nitrogen-added (50 kg N ha^{-1} in 1971 and 1974) plots in Central Plains Experimental Range, Colorado. Hence it is obvious that the nitrogen enhancement in semi-natural ecosystems potentially had large and long-lasting effects on the soil processes. In an investigation on N and P enrichment effects on soil nutrient availability in one open and two edge plots on a landslide in Puerto Rico, Fetcher *et al.*[45] found that addition of N enhanced total soil N, ammonium and nitrate in the open plots, but not in the edge plots. Enrichment after P caused increases in extractable P in both sets of plots.

Factors regulating nitrification in forest soil are complex and not fully known. Several reports suggested that forest soils incubated without added nitrogen show little or no nitrification[64], indicating that the rate of ammonification may be a limiting factor. Also, the role of soil acidity is suggested by the observation that nitrification in forest soil is often stimulated by liming[65]. In addition to their effect through nutrient supply, fertilizers may affect nitrification indirectly, e.g. hydrolysis of added urea increases soil pH.

Changes in N-mineralization rate following nitrogen enrichment occur as a result of major changes in the activity of microbial community in soils. In response to long-term (7 years) nitrogen addition large increase in utilization in an upland *Calluna* heathland soil became evident; primarily the change was related to the ability of the microbes to utilize organic phosphates as nitrogen deficiency was removed. At the same site, Capron *et al.*[66] recorded the effect of N enrichment on micorrhizal infection in *C. vulgaris*. Several workers have reported reduction in mycorrhizal infection in response to atmospheric N deposition[66,67]. Nutrient enrichment effects on soil microbial communities need to be intensively investigated to analyse the ecological significance of associated changes.

Soil microbial biomass is an important source of labile nutrients, and controls available N both by net mineralization from soil organic matter and also by N immobilization and subsequent re-mineralization from the biomass[68]. Microbial biomass has been shown to immobilize available N at times of low plant uptake[69], and to release N during times of greatest plant demand[70]. The microbial biomass thus mediates the effects of added N to some degree, however, actual responses have varied among different ecosystems. In grasslands, for instance, microbial N increased with N addition[71], whereas microbial activity and biomass N were the same or smaller in fertilized compared to unfertilized forest and clear cuts[72]. Melany and Schmidt[73] have indicated that microbial biomass has the potential to immobilize the present amounts of atmospheric N deposition in alpine tundra soil.

Nutrient loading may have possible impact on the emission of methane, a major greenhouse gas, from the soil by affecting the process of methanogenesis. Investigating the effect of nitrogen fertilization on methane uptake in temperate forest soils in Harvard forest and mixed black oak/red maple stand in Massachusetts, USA, Steudler *et al.*[74] found that increased soil nitrogen content resulted in lower CH_4 uptake rates. Methane consumption in the fertilized plots was reduced by 15–24% relative to control after only four months of fertilization in the hardwood and pine stand, but the reduction increased to 33% after six months of fertilization. Singh *et al.*[75] have shown (21–69%) greater methane flux from urea-fertilized different Indian irrigated rice fields compared to control. The stimulatory effect of ammonium-based fertilizer on CH_4 production is understandable because methanogens use NH_4^+ as nitrogen source[76]. Further N fertilization decreases the soil C/N ratio and increases the activity of soil micro-organisms which consequently increases CH_4 produc-

tion[77]. In natural ecosystems, loading of essential nutrients (like N and P) may enhance organic matter additions into the soil through litterfall and root mortality, which might cause higher CH_4 production rates in these ecosystems. Thus, long-term measurements are required to elucidate the nitrogen–methane interaction in natural and man-made ecosystems which are under the impact of nitrogen deposition. Besides the greater emission of methane from the soil, nutrient loading, especially of N, may lead to greater production of other biogenic gases (like N_2O, NH_3 and NO) from the soil, which may affect several ecosystem processes. The tropical forest and savanna ecosystems, generally showing rapid decomposition and high nutrient turnover rates, deserve special attention with respect to the impact of N loading on their biogenic gas flux. Such information would be especially useful in the context of contribution of biogenic gases, including methane to global warming and global N and C budgets because in many ecosystems, the storage of C is thought to be limited by a lack of N.

Objectives for research

An important task ahead for ecologists is to predict the impact of nutrient loading and changing landscape pattern on the structure and function of terrestrial ecosystems. The following major objectives may be framed to investigate the role of nutrient loading on Indian terrestrial ecosystems:

(a) To document the short- and long-term changes in species composition and relative abundance of species in different regions in relation to nutrient loading, and to understand the impact of nutrient loading on the abundance of rare and key species of different ecosystems.
(b) To find out whether nutrient loading will alter soil nutrient availability in terrestrial ecosystems in different climatic regions.
(c) To investigate the changes in biodiversity in relation to nutrient availability.
(d) To establish the relationships between the biodiversity and the ecosystem functions (e.g. productivity and nutrient cycling) in different ecological regions under increased nutrient level conditions.
(e) To investigate how the reproductive biology and behaviour of individuals of rare and key species (whose presence or absence can critically alter the composition of local communities) respond to nutrient loading, and ultimately to understand the changes in the functioning of these plants in the ecosystems with respect to nutrient loading.
(f) To understand how elevated tissue nutrient concentration of plants affect herbivore interactions, and to find out how these changes are transmitted through higher trophic levels.

(g) To document how the alterations in species composition that accompany land-use changes affect nitrogen, carbon and trace gas emissions to the atmosphere.

Concluding remarks

Nutrient inputs from the atmosphere vary greatly from one ecosystem to another and these inputs can balance or exceed nutrient losses at some sites but are unable to do so at other sites. The rate of nutrient input to a site is likely to be a crucial determinant of whether an ecosystem is sustainable long-term or whether the soil and hence the vegetation will slowly change. The foregoing account indicates that our knowledge about N and P inputs from the atmosphere and their possible ecological effects on the structure and functioning of natural and modified ecosystems is still limited and uneven. Nutrient input may cause long-term effects on site properties (Table 1). Besides the immediate effects on wood productivity, nutrient input may lead to more long-lasting beneficial changes such as an improvement of soil biological activity and an alteration of the humus type.

Nitrogen and sulphur deposition tends to acidify the soil, alter the nutrient supply rate, affect sensitive plant species, decrease mycorrhizal infection in plant species, and contribute to the discoloration and defoliation of trees. Moreover, the N deposition may alter the tissue chemical quality of plants grown in high nutrient level conditions. Probably the C/N ratio of tissues may decrease. It may be expected that the rate of litter decomposition may increase under elevated nutrient level conditions. The increased litter decomposition rate will have considerable effect on soil chemical properties. This will also enhance nutrient mineralization rates which may influence future

Table 1. Likely impact of nutrient deposition on different ecosystem parameters

Ecosystem parameter	Possible impact
Species diversity	Decrease
Species richness	Decrease
Individual species	
Rough grass species	Increase
Sensitive species	Decrease
Rare or key stone species	May disappear
Ecosystem productivity	Increase
Frost resistance	Decrease
Root/shoot ratio	Decrease
Mycorrhizal infection	Decrease
Plant growth	Increase
Nutrient resorption	Marginal increase
Tissue nutrient concentration	Increase
Tissue C/N ratio	Decrease
Tissue N/P ratio	Increase
Nutrient availability in soil	Increase
Nutrient mineralization	Increase
Soil microbial biomass	Increase
Litter decomposition	Increase

plant growth of the terrestrial ecosystems. The changed litter quality will have a significant effect on plant–herbivore interactions. Attention should be focused on such early signs, bearing in mind the irretrievable value of growth potential of different ecosystems.

Note added in proof: Sala *et al.*[78] have identified and ranked drivers for global biodiversity change. For terrestrial ecosystems, they have considered land use change as the most important driver followed by climate change, nitrogen deposition, biotic exchange and elevated carbon dioxide concentration. They speculate that the increased depositions of nitrogen would have the largest impact on the biodiversity in nitrogen-limited areas.

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