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Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis

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Abstract. The relative importance of nitrogen inputs from atmospheric deposition and biological fixation is reviewed in a number of diverse, non-agricultural terrestrial ecosystems. Bulk precipitation inputs of N ($1\text{–}12\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) are the same order of magnitude as, or frequently larger than, the usual range of inputs from nonsymbiotic fixation ($<1 - 5\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$), especially in areas influenced by industrial activity. Bulk precipitation measurements may underestimate total atmospheric deposition by 30–40% because they generally do not include all forms of wet and dry deposition. Symbiotic fixation generally ranges from $\cong 10\text{–}160\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ in ecosystems where N-fixing species are present during early successional stages, and may exceed the range under unusual conditions.

Rates of both symbiotic and nonsymbiotic fixation appear to be greater during early successional stages of forest development, where they have major impacts on nitrogen dynamics and ecosystem productivity. Fates and impacts of these nitrogen inputs are important considerations that are inadequately understood. These input processes are highly variable in space and time, and few sites have adequate comparative information on both nitrogen deposition and fixation.

The existing information on N inputs is deficient in several areas:

- more intensive studies of total atmospheric deposition, especially of dry deposition, are needed over a wide range of ecosystems;
- additional studies of symbiotic fixation are needed that carefully quantify variation over space and time, examine more factors regulating fixation, and focus upon the availability of N and its effects upon productivity and other nutrient cycling processes;
- process-level studies of associative N-fixation should be conducted over a range of ecosystems to determine the universal importance of rhizosphere fixation;
- further examination of the role of free-living fixation in wood decomposition and soil organic matter genesis is needed, with attention upon spatial and temporal variation; and
- investigations of long-term biogeochemical impacts of these inputs must be integrated with process-level studies using modern modelling techniques.

Introduction

Although a vast quantity of nitrogen is stored in the atmosphere, terrestrial ecosystems receive relatively small natural inputs with which productivity and other processes are maintained. The element is also unique due to the number of biological transformations which may result in its loss from the time that it enters in an inorganic form until it is mineralized from decomposing organic matter. Its dynamic nature and usual deficiency have influenced species within terrestrial ecosystems to evolve diverse means of acquiring, efficiently utilizing, and retaining these smaldl quantities of nitrogen. As a result, nitrogen input and availability are key factors regulating the organization and metabolism of terrestrial ecosystems.

Two major pathways of nitrogen input to terrestrial ecosystems occur: atmospheric deposition and biological fixation. Atmospheric deposition includes several forms of nitrogen in both dry and wet deposition modes. Both symbiotic and nonsymbiotic nitrogen-fixing organisms are responsible for the biological fixation of atmospheric nitrogen. Within any single ecosystem, our understanding of the relative magnitudes of these nitrogen inputs and their impacts on terrestrial nutrient cycling is incomplete. Furthermore, an understanding of these fundamental processes is prerequisite to accurate predictions of the potential significance of atmospheric pollution and long-term inorganic fertilizer subsidies in managed ecosystems.

In this paper we review the relative importance of nitrogen inputs from atmospheric deposition and biological fixation in a number of diverse non-agricultural terrestrial ecosystems. Since Clark & Rosswall's (1981) summary of nitrogen cycling processes in terrestrial environments, additional studies have refined both our understanding of these processes and our definition of research priorities. Our approach here is not to present an exhaustive list of data for all potential terrestrial ecosystems, but rather to concentrate on locations where detailed information on nitrogen cycling complements new research results on atmospheric deposition or biological nitrogen fixation. Our discussion is organized into three main areas:

- Comparison of the relative magnitudes of nitrogen inputs via atmospheric deposition, and symbiotic and nonsymbiotic fixation,
- Review of current knowledge regarding ecosystem fates and impacts of these N inputs.
- Recommendations for future research.

Table 1. Major forms of atmospheric nitrogen deposition.

Form	Deposition state
Nitrate, NO_3	Dissolved and aerosol
Ammonium, NH_4	Dissolved and aerosol
Nitric oxide, NO	Gas
Nitrogen dioxide, NO_2	Gas
Nitric acid, HNO_3	Gas
Ammonia, NH_3	Gas

Relative magnitudes of nitrogen inputs

Atmospheric deposition

Because of current interest in the impacts of air pollutants on ecosystems, a rapidly expanding literature exists on the formation, long-range transport, and deposition of nitrogenous compounds. As this literature grows, new insights are accumulating regarding the magnitude and regulation of these processes. It is beyond the scope of this paper to review atmospheric deposition processes from all these perspectives. We have selected very specific studies which illustrate key points regarding the forms of and mechanisms responsible for nitrogen deposition to terrestrial ecosystems. Current estimates of the magnitude of deposition inputs of N are presented, and methodological problems inherent in these estimates are also treated. Data from forest ecosystems play a prominent role in our analyses since most current studies emphasize atmospheric deposition as a pollutant impact on forests. Comparable data on total deposition inputs of N to other types of terrestrial ecosystems are not extensively available.

Nitrogen forms and deposition processes

By the mid-19th century, NO_3^- and NH_4^+ in rain were recognized as potential sources of plant N, preceding the discovery of biological nitrogen fixation in the soil (Junge 1963). However, only in the past decade have research efforts focused on improving estimates of precipitation deposition of the various inorganic nitrogen forms. A variety of forms exist in the atmosphere (Table 1), some of which can be rapidly incorporated into terrestrial nitrogen cycles after deposition. The transfer of other atmospheric nitrogen constituents in aerosal and gaseous forms to vegetation surfaces has been theorized, but field experiments and estimates at an ecosystem level are rare. In comparison to other surfaces, deposition in forests is particularly complicated because of complex physicochemical processes, a three-dimensional and non-uniform surface, and seasonal variation within and among forest types.

The removal of substances from the atmosphere can be separated into wet and dry deposition processes. Wet deposition includes two processes: rainout, where the constituent is incorporated into droplets within the cloud; and washout, where the constituent is removed by falling precipitation below the cloud (Rodhe & Grandell 1972). Precipitation is usually regarded as the most important and efficient mechanism of particulate, aerosol, and gas removal from the atmosphere (Junge 1963), but exceptions can occur for some constituents (Lindberg et al. 1979). The efficiency of these scavengng processes has been described and summarized by numerous investigators (US Energy Research and Development Administration 1977, McMahon & Dennison 1979), and is related to constituent properties such as particle size, solubility, and chemical activity. Condensation, a process of rainout, is most efficient for removing aerosols between 0.1–1.0 μm radius, while Brownian motion and/or water vapor gradient transfer are more important for constituents concentrated on particles less than 0.1 μm (Junge 1963). Washout, or impaction scavenging, is important in removing particles greater than 1 μm radius. Nitrate can be associated with both large and small particles while the ammonium ion is usually associated with particles $< 2\,\mu$m diameter (Soderlund 1981; Wolff 1984).

Dry deposition includes processes of gravitational sedimentation of large particles ($> 3\,\mu$m diameter), aerosol impaction, and gaseous absorption. Deposition velocity, a simplified concept for estimating the scavenging efficiency of a forest canopy, is defined as the vertical flux of a substance divided by the mean concentration of the substance at a specified height above the canopy. Based on laboratory and field studies, McMahon & Dennison (1979) determined the relationship between deposition velocity and particle size and concluded that the minimum deposition velocity occurs in the 0.1 to 1 μm particle diameter range. However, the authors point out, as have others (Slinn 1982), that "typical" deposition velocities can vary by at least an order of magnitude. Aerosols and gases which originate from combustion processes and contain various forms of N are composed of small particles; thus, dry deposition is potentially a major process of N deposition. A thorough review of forest canopy interactions with particles and gases is provided by Hosker & Lindberg (1982).

Deposition inputs to forest ecosystems

Estimates of all of the potential forms of N deposition are unavailable for any terrestrial ecosystem. Although conservatively estimated, N inputs measured in bulk precipitation provide some measure of the relative importance of atmospheric deposition to forests (Table 2). Selected sites represent

Table 2. Annual nitrogen inputs in bulk precipitation for ecosystems in selected regions of the United States.

Location	Inorganic N	Organic N $\mathrm{kg\,ha^{-1}\,yr^{-1}}$	Total N
Temperate deciduous forest Walker Branch, Eastern Tennessee[1]	8.4	4.0	12.4
Temperate deciduous forest Coweeta, Mountains of North Carolina[2]	4.9	4.3	9.2
Temperate coniferous forest Lower Coastal Plain, Northern Florida[3]	3.8	2.8	6.6
Temperate coniferous forest H.J. Andrews, Western Cascade Mountains, Oregon[4]	0.7	1.5	2.2
Temperate coniferous forest Santee watershed, Lower Coastal Plain, South Carolina[5]	2.6 a	2.5	5.1
Temperate coniferous forest Tesuque watershed 4, Sangre de Cristo Mountains New Mexico[6]	4.5	1.7	6.2
Temperate deciduous forest Hubbard Brook, New Hampshire[7]	6.5		
Chaparral Santa Ynez Mountains, Southern California[8]	1.2		
Temperate coniferous forest Clemson Forest, Piedmont of South Carolina[9]	6.2		
Temperate coniferous forest Thompson Research Center, Western Cascade Mountains, Washington[10]			1.1
Temperate coniferous forest Duke Forest, Piedmont of North Carolina[11]			5.4

[1] Kelly & Meagher (1986); [2] Swank & Waide (1987); [3] Riekerk 1983; [4] Grier et al. 1974; Fredriksen 1975; [5] Richter et al. 1983; [6] Gosz, JR 1980; [7] Likens et al. 1977; [8] Schlesinger & Hasey 1980; [9] Van Lear et al. 1983; [10] Grier et al. 1974; [11] Wells & Jorgensen 1975.

locations with either long precipitation chemistry records, inorganic plus organic analyses, and/or biological fixation data. Deposition of inorganic N (NO_3^- + NH_4^+) ranges from about 1 kg ha^{-1} yr^{-1} for some western locations in the United States to 5 kg ha^{-1} yr^{-1} or more for sites under the influence of industrial emissions; relatively unpolluted eastern sites show intermediate deposition rates. Higher values at the Walker Branch site result from its close proximity to coal-fired power plants in the Tennessee Valley.

The magnitude of inputs is related to washout and rainout processes and is partially a function of precipitation amounts. Normalization of wet deposition of inorganic N for rainfall amounts can be derived for regional assessments from several chemistry monitoring networks in the United States (Wilson et al. 1982). Estimates of organic N inputs are less often measured, but frequently accounts for 50 percent or more of the total N in bulk precipitation (Table 2). Sources of organic nitrogen include particulates generated from agricultural activities and combustion processes. The availability of organic forms to vegetation will depend on mineralization, but microbial transformations of particular nitrogen pollutants to NH_4^+ and NO_3^- have been observed (Wainwright & Killham 1982). Thus, total atmospheric N inputs to temperate forest ecosystems frequently exceed 5 kg ha^{-1} yr^{-1}.

The relative importance of wet and dry processes of N deposition can differ substantially. For example, at Coweeta, dryfall (as estimated from open collectors) accounts for less than 20 percent of the NO_3^- and NH_4^+ inputs (Swank & Waide 1987) in contrast to more than 50 percent estimated from open collectors at Walker Branch (Kelly & Meagher 1986). Dryfall data represent input primarily from large particles deposited by the sedimentation process and are not representative of small particulate and gaseous deposition.

Comparative analyses of N inputs must also consider other factors which regulate the gross deposition of the various forms of nitrogen to terrestrial ecosystems. Particularly for nitrogenous compounds generated by human activities, proximity to nitrogen source (e.g. marine aerosols, industrial emissions) is a primary factor. Also important are the total amount, form, and distribution of precipitation, and the meteorological and other factors which regulate constituent transport and transformations within the relevant airshed. Of secondary importance, especially for dry deposition inputs, are the surface area and distribution of aboveground plant parts available to filter particulates or aerosols from air masses as they pass over or through the ecosystem of interest. Temporal trends in deposition inputs are related to season and longer-term changes in precipitation amounts, canopy structure, meteorological conditions, and the strength of the nitrogen source.

Table 3. Summary of annual deposition inputs for various forms of nitrogen in a deciduous forest at Walker Branch watershed in Tennessee.

Deposition form	Input kg $ha^{-1} yr^{-1}$
Wetfall[a]	
NO_3-N	2.8
NH_4-N	1.7
Dryfall	
Particulate NO_3-N[a]	1.2
HNO_3 vapor NO_3-N[a]	3.6
NH_4-N[a]	0.8
NO-N[b]	0.7
NO_2-N[b]	1.7
Total	12.50

[a] Lovett & Lindberg (1986); [b]Kelly & Meagher (1986).

Problems with measurement

Methods for measuring atmospheric deposition to forests have been slow to develop (Galloway & Likens 1976, 1978). Bulk samples that combine precipitation and some components of dry deposition in the same container are most frequently used in ecosystem studies. Another commonly used method is an automated collector, such as that used in the National Atmospheric Deposition Program network (Bigelow 1982), which is open only during rainfall events and excludes dryfall. Methods for routine measurement of dry deposition are not well established and include a diversity of approaches such as micrometeorological methods, comparison of inert surfaces in combination with foliar extraction of deposited constituents, and statistical analysis of individual rain and throughfall events (Lindberg & Lovett 1985; Lovett & Lindberg 1984).

More recent studies at Walker Branch provide improved estimates of deposition to a deciduous forest for most sources of N. Lovett & Lindberg (1986) used three separate methods to estimate dry deposition of NO_3^-. A best estimate was obtained by combining the advantages of each method for estimating the various forms of dry deposition (Table 3). Annual dry deposition of NO_3-N was estimated to be 4.8 kg ha^{-1} with 75 percent deposited as nitric acid vapor. Kelly & Meagher (1986) estimated direct deposition of NO and NO_2 at the same site as 2.4 kg $ha^{-1} yr^{-1}$ (Table 3). These investigators point out the need to view some of the values provided in Table 3 with caution due to methodological uncertainties and assumptions. The magnitude of gaseous NH_4^+ absorption is unknown, but several studies have demonstrated the potential of plant leaves to absorb NH_4^+ (Hutchinson et al. 1972; Pang 1984).

It is clear that dry deposition is the dominant process of N input at Walker Branch and that estimates based on conventional measurements (bulk precipitation) may underestimate total N inputs by 30–50 percent or more. The inadequacy of bulk measurements of total inorganic N inputs has also been clearly shown by Lovett et al. (1982) for subalpine balsam fir in the White Mountains of New Hampshire. Cloud droplet deposition accounted for 46 percent of the water input to the forest. This was associated with inorganic N deposition of $39\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ which was more than four-fold larger than the quantity measured in bulk precipitation. Evaluations of the relative magnitude of N inputs via atmospheric deposition versus nitrogen fixation must take these methodological inadequacies into account.

Nitrogen fixation

Within the past three years, several volumes on specialized aspects of symbiotic nitrogen fixation have been published. Two of these specifically address microbiological, physiological, and biochemical perspectives (Alexander 1984; Veeger & Newton 1984). For forest ecosystems, other works have recently addressed the diversity of nitrogen-fixing organisms or their present and potential uses in silvicultural systems (Dawson 1983; Gordon & Wheeler 1983; Binkley 1986). Two points are clear from these reviews. First, most of the information on symbiotic nitrogen fixation comes from studies of agronomic legumes; controls of N fixation unique to forest and arid environments are poorly understood. Second, although intensive research has recently been conducted on a small number of woody leguminous and actinorhizal nitrogen-fixing species in some desert and forest ecosystems, large gaps still exist in our knowledge of this process in many ecosystems.

Considerable data also exist on nonsymbiotic fixation for a wide variety of terrestrial ecosystems. We have a general understanding of the most active sites for fixation, the organisms primarily responsible for nonsymbiotic fixation, and the major factors influencing rates. Much of this information was summarized in Paul (1978), Waughman et al. (1981), and Clark & Rosswall (1981), primarily in the chapter by Granhall (1981) and the section on "Ecosystem strategies". We now understand a great deal about the nitrogen fixation process, but we still have an inadequate knowledge of its quantitative, long-term importance to the nitrogen cycle of many terrestrial ecosystems. Here we review aspects of both symbiotic and nonsymbiotic

Table 4. Estimated symbiotic N fixation rates for diverse terrestrial ecosystems. ARA indicates measurement by acetylene reduction assay, and N gain indicates measurement by gains in total stand N by summing soil, litter, and biomass increases over age sequences.

Ecosystem	Species	Rate kg ha^{-1} yr^{-1}	Method	Reference
Pacific northwest conifer forest	*Ceanothus velutinus*	0–100	ARA & N gain	Tarrant 1983
Pacific northwest conifer forest	*Alnus rubra*	40–160	N gain	Luken & Fonda 1983
Alaskan boreal forest	*Alnus incana*	156–362	N gain	Van Cleve et al. 1971
Appalachian oak forest	*Robinia pseudoacacia*	30–75	N gain & ARA	Boring & Swank 1984a,b
SE Coastal plain *Pinus elliottii* forest	*Myrica cerifera*	< 2–11	N gain & ARA	Permar & Fisher 1983
Massachusetts peatland	*Myrica gale*	35	ARA	Schwintzer 1983
Australian Jarrah forest	*Acacia pulchella* and others	< 1–6	ARA	Hingston et al. 1982
New Zealand *Pinus radiata* forest	*Lupinus arboreus*	160 160	N gain ARA	Gadgil 1971b Sprent 1973
Sonoran desert	*Prosopis glandulosa*	25–35	N gain	Rundel et al. 1982

nitrogen fixation that relate to their long-term importance in non-agricultural terrestrial ecosystems, focusing upon:

- amounts of nitrogen fixed,
- factors regulating fixation over space and time, and
- problems with measurement of nitrogen fixation.

Symbiotic fixation

Symbiotic nitrogen-fixing species frequently grow on sites where nitrogen is limiting or subject to substantial loss, including:

- primary successional sites,
- sites with rapid mineralization accompanied by high leaching rates,
- alkaline soils with high rates of mineralization and NH_3 volatilization,
- areas where frequent fires release large amounts of organic nitrogen, and
- sites with high C:N ratios and substantial N immobilization (Reiners 1981).

Symbiotic nitrogen fixation has been documented to be a dominant input to a number of diverse terrestrial ecosystems (Table 4). Most of this research has centered around a small number of non-agricultural woody nitrogen-fixing plants in the temperate zone, including *Alnus rubra* in Pacific northwest coniferous forests, *Prosopis glandulosa* in southwestern USA deserts, *Robinia pseudoacacia* in southern Appalachian deciduous forests, and *Lupinus arboreus* in New Zealand coastal plantations of *Pinus radiata.* Estimated values for fixation range up to 362 kg N ha^{-1} yr^{-1}, although most values are from 30 to 160 kg N ha^{-1} yr^{-1}. Note that there are problems in directly comparing some of these studies since they measured different variables or used different techniques.

In Australian jarrah forest, intense fire stimulates regeneration of several understory legumes, including *Acacia* spp., which subsequently fix < 1–6 kg N ha^{-1} yr^{-1} (Hingston et al. 1982). In chaparral of the southwestern USA, symbiotic fixation by dominant *Ceanothus* spp. is apparently low, but fixation by herbaceous legumes (*Lotus* spp.), following fire may result in locally large N inputs (Schlesinger et al. 1982; Ellis et al. 1983). In such habitats, nitrogen-fixing species have a considerable nutritional advantage since fire not only decreases N pools through volatization, but also releases other nutrients previously immobilized in biomass and litter.

In North American temperate forest ecosystems, nitrogen-fixing species are most common in early successional stages but are not restricted to burned sites or primary successional seres (Permar & Fisher 1983; Tarrant 1983; Boring & Swank 1984a). Many early successional forest sites contain abundant woody debris, including dead roots, with high C:N ratios which might result in temporary N immobilization and provide a competitive advantage to nitrogen-fixing species. Fixation rates for *Robinia pseudoacacia, Myrica cerifera, Alnus* spp., and *Ceanothus* spp. (Table 4) are high during early forest succession, comprising the dominant N input to these ecosystems (Boring & Swang 1984b). Nitrogen-fixing species may also contribute important nitrogen inputs to *Pinus taeda, P. palustris* and *P. elliottii* forests of the southeastern USA, particularly following fire or on nitrogen-depleted sites (Haines & DeBell 1979; Permar & Fisher 1983; Gholz et al. 1985; Jorgensen & Wells 1985). Unfortunately, most native understory legumes in this region have not been examined in detail for their N fixation potential.

Nitrogen fixation by legumes and actinorhizal species may be significant in boreal forest and tundra ecosystems (Van Cleve & Alexander 1981). Low nitrogen mineralization rates due to unfavorable climatic conditions may provide a competitive advantage to nitrogen-fixing species. At a tundra site in the Northwest Territories, herbaceous legume N fixation accounted for

97% of the total fixation (3 kg N ha^{-1} yr^{-1}) on some microsites, but on another tundra site at Barrow, Alaska, legumes accounted for no fixed N (Karagatzides et al. 1985).

Warm desert regions throughout the world may frequently contain drought-adapted tree legumes such as *Prosopis* spp. and *Acacia* spp. A *Prosopis glandulosa* dominated woodland in the Sonoran Desert of the southwestern USA was estimated to maintain unusually high productivity and to accumulate an average of 25–35 kg N ha^{-1} yr^{-1} (Rundel et al. 1982). This high range of productivity and N accretion is attributable to the species' ability to tap groundwater with exceptionally deep roots, and to maintain substantial nodulation and nitrogenase activity at soil depths exceeding 3 m (Felker & Clark 1982).

In grasslands, legumes may fix significant quantities of nitrogen during early periods of recovery from disturbance. However, such inputs are extremely variable in both space and time, ranging up to 25 kg N ha^{-1} yr^{-1} in some seasons and sites but being absent in others (Woodmansee et al. 1981).

Although less information is available on symbiotic nitrogen fixation rates in tropical forests, recent studies are rapidly expanding our perspectives on woody legume biology and potential uses in agroforestry and silviculture (Roskoski 1981b; Halliday 1984; Dommergues et al. 1984). Woody legumes are common in many tropical forest types, and estimated fixation rates in mixed stands appear to be similar to those shown in Table 4 for predominantly temperate species. However, dense, managed stands of tropical N-fixing species such as *Casuarina equisetifolia* and *Leucaena leucocephala* have potential fixation rates exceeding 250–500 kg N ha^{-1} yr^{-1} (Dommergues et al. 1984). It is likely that tropical trees maintain the highest symbiotic nitrogen-fixation rates in the world, and that fixation in tropical forests may be relatively more important than in most temperate ecosystems.

Many studies have quantified fixation rates on one site at one time, ignoring both spatial and temporal variation. The spatial distribution of nitrogen-fixing species may be highly variable within both managed and unmanaged ecosystems. This variation makes it difficult to quantify a species' contribution of fixed nitrogen over a given land area. For example, *Myrica cerifera* has been shown to accumulate 24 kg N ha^{-1} yr^{-1} beneath its own canopy, but this amounted to only 2 kg N ha^{-1} yr^{-1} on a stand basis (Permar & Fisher 1983).

Symbiotic N fixation is strongly influenced by time-dependent biological and environmental factors. These effects are generally manifested by variable diurnal and seasonal patterns of nitrogenase activity and nodulation

(Sprent 1979). Additional research is needed on numerous perennial species to understand relationships among symbiotic nitrogen fixation, carbon gain, nutrient and water availability, and external stress (Dixon & Wheeler 1983). Although other factors may limit fixation under a given circumstance, critical controls likely to regulate fixation in wood plants include:

- age-dependent changes in overall carbon status as influenced by factors affecting light levels, leaf area, or net photosynthesis;
- stand density and competitive interactions;
- the influence of soil moisture, temperature, and phenological development upon diurnal and seasonal patterns of carbon gain;
- nutritional status, often related to mycorrhizal symbionts, soil nitrogen availability, pH or the long-term insufficiency of phosphorus or trace elements (e.g. Co, Mo) as necessary cofactors in the nitrogen fixation process;
- stress induced by grazers or pathogens; and
- the availability, compatibility and efficiency of the nitrogen-fixing microsymbiont and mycorrhizae.

Nitrogen fixation may vary during successional development due to changes in stand structure, nitrogen availability, and resultant changes in vigor and abundance of N-fixing species. Both *Alnus rubra* and *Robinia pseudoacacia* are dominant in early- and mid-successional forests in the Pacific northwest and the southern Appalachians, USA, respectively. Assuming that nitrogen accretion rates in stands reflect nitrogen fixation, both species have greater fixation rates associated with early-to-intermediate stages of stand development (Table 5). Nodule biomass of *Robinia pseudoacacia* parallels the pattern of nitrogen accretion (Boring & Swank 1984a), and similar observations have been made for Sahelian *Acacia* spp. (Dommergues et al. 1984). With subsequent successional development, most of these species become less important stand components, and cease to fix significant amounts of nitrogen. With the possible exception of savannahs and tropical forests on infertile or highly leached soils, high rates of symbiotic N fixation (by plants) are generally restricted to early- and mid-successional seres of forest development.

During stand development, any external factor (such as shading) which alters the long-term availability of photosynthate should indirectly regulate N-fixation (Pate 1977). Bormann & Gordon (1984) found a high correlation between N fixation and leaf mass per tree in *Alnus rubra* plantations of different densities, and concluded that the leaf area per tree regulated photosynthate availability for nodules. With pasture legumes, shading or defoliation may reduce N-fixation (in short-term), and in the long-term

Table 5. Comparison of nitrogen accretion rates of different-aged nitrogen-fixing forest stands.

Species and location	Age during accretion (years)	N Accretion kg N $ha^{-1} yr^{-1}$	Reference
Alnus incana – Alaskan boreal forest	0–5	362	Van Cleve et al. 1971
	0–10	170	
	0–20	156	
Alnus rubra – PNW coniferous forest	0–14	163	Luken & Fonda 1983
	14–24	81	
	24–65	40	
Robinia pseudoacacia – Appalachian oak-hickory forest	0–4	48	Boring & Swank 1984a
	0–17	75	
	0–38	33	

cause nodule shedding. With *Lupinus arboreus*, shading reduced nodule biomass and nitrogenase activity (Sprent 1973). These factors are likely to be important for most N-fixing species, and the ratio of leaf tissue to total biomass may serve as an important indicator of a tree's carbon status as it ages. Stand competition and shading may be manifested in older trees by decreases in crown leaf area and pose physiological problems for early successional, shade-intolerant species. *Robinia pseudoacacia* and *L. arboreus* are also normally subject to high levels of insect-caused defoliation and stem-borer attack (Hoffard & Anderson 1982; Gadgil 1971b), which could cause further decreases in carbon gain and N-fixation, resulting eventually in death in older trees already succumbing to competition.

Nonsymbiotic nitrogen fixation

For the purposes of this review, this section will summarize information on the fixation of atmospheric nitrogen by autotrophic and heterotrophic organisms not living in direct symbiotic relationships with vascular plants. Along with fixation by true free-living N-fixers, here we will also consider fixation via lichens, cyanobacteria in association with mosses, and associative N-fixing systems. Detailed information on the biochemistry, physiology, and taxonomy of these highly diverse N-fixing organisms has been reviewed extensively (Hardy & Silver 1977; Newton et al. 1977; Broughton 1981; Clark & Rosswall 1981; Gordon & Wheeler 1983; Alexander 1984) and will not be detailed here.

Table 6. Nonsymbiotic nitrogen fixation inputs to terrestrial ecosystems.

Ecosystem type and location	Nonsymbiotic fixation ($kg\,N\,ha^{-1}\,yr^{-1}$)	Source
Tundra		
Range of sites	0.2–2 (3)[a]	Paul 1978; Van Cleve & Alexander 1981, Waughman et al. 1981
Boreal forest (taiga)		
Range of sites	0.1–4 (17)	Paul 1978, Van Cleve & Alexander 1981
Desert		
Range of sites	1–30 (100)	Paul 1978, Skujins 1981; Waughman et al. 1981
Grassland		
Relict prairie site, Ohio	8.2	DuBois & Kaputska 1983
Arapaho prairie, Nebraska	4.3	Kapustka & DuBois 1987
Range of US-IBP grassland sites	< 0.5–2.5	Woodmansee 1978
Range of sites	1–5 (90)	Paul 1978; Waughman et al. 1981, Woodmansee et al. 1981
Savanna		
Range of sites	2–30 (90)	Bate 1981
Chaparral		
Ceanothus spp. Santa Ynez Mountains, California	1.0	Schlesinger et al. 1982 Ellis et al. 1983
Temperate coniferous forests		
Old-growth Douglas-fir, H.J. Andrews Forest, Oregon	4.2	Sollins et al. 1980 Silvester et al. 1982
Lodgepole pine forest Southeastern Wyoming	0.3	Fahey et al. 1985
Loblolly pine plantation, Duke Forest, North Carolina	1.7–2.2	Jorgensen & Wells 1984
Loblolly pine forest, Clemson Forest, South Carolina	3.7	Van Lear et al. 1983
Slash pine plantation, North Florida Coastal Plain	3.0	DiStefano 1984, Gholz et al. 1985
Mixed coniferous forests, Tesuque Experimental Watershed, New Mexico	0.1–3.3	Gosz 1980

Table 6. (continued).

Ecosystem type and location	Nonsymbiotic fixation ($kg\,N\,ha^{-1}yr^{-1}$)	Source
Range of sites	< 1-5 (28)	Gosz 1981, Waughman et al. 1981
Temperate deciduous forests		
Oak hickory, University Forest, Missouri	0.1	Vance et al. 1983
Oak hickory, Coweeta Hydrologic Laboratory, North Carolina	4-6	Waide et al. 1987
Range of sites	< 1-6 (12)	Melillo 1981, Waughman et al. 1981
Tropical rain forests		
Rio Negro, Venezuela	16	Jordan et al. 1983
Range of sites	2-20 (90)	Herrera & Jordan 1981, Jordan et al. 1983

[a] Values within parentheses represent extreme maximum values reported for the indicated ecosystem type. Other values shown reflect a typical range of inputs.

Estimates of typical nonsymbiotic nitrogen fixation inputs range from near 0 to 30 $kg\,ha^{-1}$ annually (Table 6). Extremely large inputs (90–100 $kg\,N\,ha^{-1}yr^{-1}$) have been reported for desert, tropical grassland and savanna sites (Bate 1981; Skujins 1981; Dobereiner 1978; Paul 1978), but inputs of this magnitude are not common. Much of the high fixation input to deserts is quickly lost via volatilization or denitrification (Skujins 1981), whereas the geographic extent and significance of the large apparent N inputs to natural grasslands and savannas is uncertain (Hubbell & Gaskins 1984). A generalized progression from low to high input rates for different ecosystems would be: Chaparral $\cong$ Tundra $\leqq$ Boreal forest $\leqq$ Temperate coniferous forest $\leqq$ Temperate deciduous forest $\leqq$ Grassland $\leqq$ Savanna $\leqq$ Tropical rain forest $\leqq$ Desert. However, data available for such a generalization are limited and estimates within an ecosystem type are often highly variable.

Our understanding of how environmental factors influence nonsymbiotic nitrogen fixation within natural ecosystems is incomplete. Van Cleve & Alexander (1981) suggest that low precipitation, cold temperatures, and restricted biological activity contribute to low annual nonsymbiotic N inputs in tundra and boreal environments. However, fixation rates may be quite high during the short tundra growing season (Barsdate & Alexander 1975), and some productive deciduous forests in the boreal zone may exhibit substantial N-fixing activity (Van Cleve et al. 1971; Van Cleve & Alexander 1981). In deserts, reduced temperatures and light intensity together with favorable soil moisture conditions have resulted in some of the highest measured rates of nonsymbiotic nitrogen fixation (Skujins 1981). Heterotrophic fixation is typically restricted by low soil carbon availability in deserts. High rates of nonsymbiotic fixation may also occur in grasslands when light, temperature, and moisture conditions are favorable (Paul et al. 1971; Vlassak et al. 1973; Woodmansee et al. 1981; Kapustka & DuBois 1987). In savanna and tropical grasslands, fixation appears to be greatest where *Azospirillium* and *Azotobacter* bacteria are associated with the rhizosphere of grasses such as *Paspalum*, *Digitaria*, and *Panicum* (Dobereiner et al. 1972; Dobereiner & Day 1976; Dobereiner 1978). Significantly lower rates of fixation by associative diazotrophs have been reported in temperate grasslands (Kapustka & DuBois 1987). In coniferous and deciduous forests, environmental factors such as low light, soil pH and availability of readily mineralizable carbon may contribute to low nonsymbiotic fixation (Melillo 1981; Dawson 1983; DiStefano 1984), but little detailed research has been conducted on this subject.

Spatial and temporal variation in nonsymbiotic nitrogen fixation has been more intensively studied than has environmental control *per se*, although the two subjects are obviously related. In arid and semi-arid desert and grassland ecosystems (also probably chaparral and savanna), nonsymbiotic fixation activity predominates in bare soil areas between vegetation and in association with crusts composed of either free-living blue-green algae or blue-greens growing in association with lichens or phyllosphere mosses (Paul 1978; Skujins 1981; Kapustka & DuBois 1987). Extensive surface crusts are typically associated with leaf area indexes of less than one in grasslands (Paul 1978). Allelochemical inhibition of crusts may occur under shrub canopies in deserts (Skujins & Klubek 1978).

In tundra, fixation is restricted to the short growing season (Barsdate & alexander 1975). Moisture availability, as regulated by microtopography, has also been shown to influence nitrogen-fixing activity (Barsdate & Alexander 1975; Van Cleve & Alexander 1981; Karagatzides et al. 1985). Activity generally increases from dry to wet sites and is associated with a shift from blue-green algae in lichen associations (dry sites) to free-living blue-greens associated with mosses (wet sites).

Variability associated with forest ecosystems is vertical as well as hor-

Table 7. Comparison of rates (kg N $ha^{-1} yr^{-1}$) of nonsymbiotic nitrogen fixation associated with different components of forest ecosystems.

Ecosystem	Ecosystem component					Source
	Phyllo-sphere epiphytes	Bole epiphytes	Leaf and needle litter	Decaying wood	Mineral soil	
Old-growth Douglas fir, H.J. Andrews Forest, Oregon	2.8	–[a]	–	1.4	–	Sollins et al. 1980; Silvester et al. 1982
Slash pine plantation, Northern Florida Coastal Plain	–	–	0.1	0.1	2.8	DiStefano 1984
Northern hardwoods, Hubbard Brook Experimental Forest, New Hamp[shire	0	0	0	0.3	0	Roskoski 1977
Oak hickory, Coweeta Hydrologic Laboratory, North Carolina	0.2	1.0	1.7[b]	0.6	8.6[b]	Todd et al. 1978; Swank & Waide 1980
Oak maple, Harvard Forest, Massachusetts	0	0	0	0	1	Tjepkema 1979
Beech forest, Mirwart, Belgium	4.7	–	–	3.6	–	Remacle 1977
Tropical rain forest, Rio Negro, Venezuela	< 1	< 1	8	–	7	Jordan et al. 1983

[a] Indicates fixation rate for this component not measured.

[b] These rates represent a potential input based on laboratory incubations at optimal temperatures. Recent analyses indicate that actual rates may be only 20–40% of those listed here (Waide et al. 1987).

izontal and is related primarily to nonsymbiotic fixation occurring in the crown and boles of trees (Table 7; Melillo 1981; Dawson 1983). In old-growth Douglas fir stands, Sollins et al. (1980) reported that 67% of the nonsymbiotic fixation could be attributed to canopy epiphytic lichens. Denison (1973) and Larsen et al. (1978) reported even greater phyllosphere fixation. In addition, the large surface area associated with dead and down trees in these ecosystems is also a site of significant fixation (Silvester et al. 1982; Dawson 1983). In southeastern (USA) coniferous forests, temperate deciduous forests, and tropical forests, nonsymbiotic fixation is generally centered in decaying wood and in both organic and surface mineral soil horizons (Todd et al. 1978; Melillo 1981; Jordan et al. 1983; DiStefano 1984; Jorgensen & Wells 1985). Exceptions exist to this general trend, and selected sites have reported considerable fixation on boles and within the canopy (Mellilo 1981). In a recent report, van der Kamp (1986) reported measurable rates of nonsymbiotic N fixation in the sapwood of living cottonwood (*Populus trichocarpa*) growing in western Canada. This may represent a previously overlooked source of N inputs to forest ecosystems.

Successional influences on rates of nonsymbiotic nitrogen fixation have been documented for deciduous forests at both Hubbard Brook and Coweeta (Roskoski 1977, 1981a; Waide et al. 1987). At Hubbard Brook, annual N-fixation rates in decaying wood were measured at 2 kg ha^{-1} in a 4-year-old stand, 0.1 kg ha^{-1} in an 18-year-old stand, 0.3 kg ha^{-1} at 40–57 years of age, and finally 2 kg ha^{-1} in 200-year-old stands. These changes were directly related to the standing crops of decaying wood. At Coweeta, nonsymbiotic fixation in the soil and forest floor (excluding coarse woody litter) increased to maximum potential rates of 14–16 kg N $ha^{-1} yr^{-1}$ in the first three to five years following clearcutting (Waide et al. 1987), a presumable response to large carbon transfers to the forest floor in the form of dead roots and small fractions of logging debris.

Problems with measurement of N fixation

Ecosystem estimates of nitrogen fixation inputs have largely been dominated by the application of N balance techniques and by the extrapolation of acetylene reduction assays. However, the reliability of these techniques to approximate actual N fixation may often be questionable. As a result, several variations of ^{15}N analysis are becoming more widely used. Although these may result in more accurate measures of N fixation, some limitations must still be placed on these techniques. Knowles (1980) correctly summarized the problems of fixation measurement with three comments:

- The great variety of natural systems requires the use of varied methods.
- Low nitrogenase activity may result in poor accuracy and precision of quantitative estimates.
- Due to the diversity of nitrogen-fixing systems and procedures one should utilize two or more methods whenever possible.

Nitrogen balance calculations, comparing stands with and without symbiotic N-fixing plants, are often used to estimate N accretion over time, but they provide only indirect estimates of the actual N fixed and are subject to error from site differences (Knowles 1980). Such calculations usually provide no estimates of the amount of fixed N lost by processes such as nitrification and subsequent leaching (Binkley et al. 1982; Montagnini et al. 1986), denitrification (Virginia et al. 1982; Davidson & Swank 1986), or NH_3 volatilization (Farquhar 1979). Although some of these losses may be generally shown to be small, volatilization from fire may represent sizeable losses of N (Reiners 1981). The measured accretion is also partially the result of atmospheric deposition and nonsymbiotic nitrogen fixation; thus the approach does not permit partitioning for N inputs or outputs.

Since it is simple and inexpensive, the acetylene reduction assay has been extensively used for in situ field studies of nitrogen fixation (Hardy et al. 1973). With proper quality control and verification, it has been a useful tool to determine nitrogenase activity (McNabb & Geist 1979), but too often it is used as a laboratory potential assay which is extrapolated directly to field conditions without careful evaluation of possible sources of error. In the case of symbiotic fixation assays, it should be combined with seasonal nodule biomass measurements which adequately assess total nitrogenase activity over space and time. In field assays of both symbiotic and nonsymbiotic studies, emphasis should be devoted to diurnal and seasonal variation in nitrogenase activity and encompass in situ measurements over a range of environmental conditions (Boring & Swank 1984b). For estimates of free-living N fixation, the necessarily long incubation times (Roskoski 1981a), the natural formation of ethylene in forest soils (Nohrstedt 1983a), and the differential solubility of acetylene and N_2 in soil water (Nohrstedt 1983b) all pose formidable but surmountable problems.

Acetylene reduction assays are of the greatest value when they are calibrated against actual nitrogen fixation rates using $^{15}N_2$ (Silvester 1983). However, only a few studies of nonsymbiotic fixation (e.g. Paul et al. 1971; Vlassak et al. 1973; Roskoski 1981a; Silvester et al. 1982) have verified estimates with $^{15}N_2$ methods. These confirmation studies have frequently yielded $C_2H_2:N_2$ ratios which depart markedly from the theoretical 3:1 conversion ratio. These differences are attributable to the greater solubility of C_2H_2 than $^{15}N_2$ or C_2H_4, the absence of end-product feedback of C_2H_4 upon N metabolism, and decreased H_2 evolution in the presence of C_2H_2, which masks the actual N-fixing efficiency of the study system. As a result, many studies which have not utilized $^{15}N_2$ verification have likely overestimated actual fixation.

Nitrogen-15 may be utilized with different techniques to quantify nitrogen fixation, including natural abundance measurements, acetylene/^{15}N verification, and several variations upon isotope dilution procedures. These uses in the field and laboratory are discussed from different perspectives by Knowles (1980), Silvester (1983), Witty (1983), and Chalk (1985).

Nitrogen-15 natural abundance measurements have been useful presumptive indicators of nitrogen fixation for broad surveys or for symbiotic systems of unusual difficulty for study (Shearer et al. 1983; Virginia et al. 1984). However, isotopic discrimination of ^{15}N during microbial transformations may invalidate natural abundance techniques as useful quantitative tools for measuring and tracing fixed nitrogen in the soil (Turner et al. 1983; Binkley et al. 1985).

The ^{15}N isotope dilution procedure depends upon differences in isotopic composition of the sources of N available for plant growth — i.e. the ^{15}N experimentally enriched soil pools, versus the relatively ^{15}N depleted source fixed from the atmosphere. This permits partitioning of plant-immobilized nitrogen into fixed versus soil-acquired proportions. The validity of the procedure is dependent upon having a stable labeled pool of soil-available nitrogen, and upon using a reliable non-nitrogen-fixing reference plant to assess ^{15}N availability in the experimentally labeled soil. Chalk (1985) has reviewed the development, application, and current limitations of these techniques, and Gauthier et al. (1985) have compared the results from two variations of this procedure with a direct N difference method on an actinorhizal tree species, *Casuarina equisetifolia.* These isotope dilution methods are proving to be increasingly useful research tools, and concurrently decreasing costs of isotope purchase and analysis are making them universally available.

Summary of patterns of nitrogen inputs

Based upon our diverse information base, several general conclusions may be drawn about the magnitudes of nitrogen inputs to terrestrial ecosystems. However, we stress that few sites still have adequate information on both nitrogen deposition and fixation, and that methodological problems are inherent in many of the studies which have been conducted in the past.

First, bulk precipitation inputs of N to terrestrial ecosystems are the same order of magnitude as, or frequently larger than, N inputs from nonsymbiotic fixation, especially in areas influenced by industrial activity. Symbiotic fixation can greatly exceed bulk precipitation inputs during early successional stages. In deserts and tropical grasslands with high nonsymbiotic fixation, atmospheric deposition is a relatively less dominant form of N input. Since bulk precipitation measurements may underestimate total atmospheric deposition by 30–40%, actual atmospheric deposition may be quantitatively more important than normally stated. Thus, annual deposition inputs of N may range up to 8 kg ha^{-1} for non-forested sites, or even exceed 10 kg ha^{-1} in forests (excluding taiga).

Second, in those ecosystems where symbiotic N-fixation is important during early successional stages, rates of nonsymbiotic fixation are typically much less than rates of symbiotic fixation (e.g. compare rates in Tables 4 and 6). Early successional inputs of N via symbiotic fixation are commonly in the range of 30–100 kg $ha^{-1} yr^{-1}$ in forests, and have less frequently been estimated to exceed 300 kg $ha^{-1} yr^{-1}$ (Tarrant 1983). Thus they are much more important than nonsymbiotic fixation inputs which may occasionally reach early successional maxima of 14–16 kg $ha^{-1} yr^{-1}$ under exceptionally favorable but unusual conditions.

Third, inputs of nonsymbiotically fixed N to undisturbed terrestrial ecosystems are typically less than 10 kg $ha^{-1} yr^{-1}$, and most frequently in the range of 1–5 kg $ha^{-1} yr^{-1}$. Where this is not the case, high N inputs are due to extensive surface crusts of lichens and/or blue-green algae in ecosystems with low leaf area indices, or to associative N-fixing systems involving tropical grasses. In deserts, up to 80% of this high nitrogen input may be quickly lost through volatilization and denitrification, bringing the effective input to a lower level. This pattern may be common to most surface crusts, though it has apparently not been investigated outside of deserts. The high rates of nonsymbiotic inputs observed in associative systems have not been adequately characterized with respect to spatial and temporal extent in natural ecosystems. Thus, annual rates of nonsymbiotic fixation inputs in the range of 1–5 kg N ha^{-1} for mid-to-late successional stages of terrestrial ecosystems seem reasonable. The one exception may be tropical moist forests, where high productivity and carbon availability may combine with a favorable climate to facilitate greater nonsymbiotic inputs.

Fourth, rates of total fixation (symbiotic and nonsymbiotic) in early successional stages of temperate forests following disturbance are substantially higher than in later successional stages. These greater inputs have major impacts on nitrogen dynamics, ecosystem productivity and other processes, both during this period as well as in later stages of ecosystem development. These impacts merit greater attention in a wide array of terrestrial ecosystems.

Fates and impacts of N inputs

Up to this point, our analyses have been based strictly on an evaluation of the relative magnitudes of atmospheric deposition and biological dinitrogen fixation as inputs of nitrogen to natural terrestrial ecosystems. While this is one valid measure of the importance of external N inputs, it is clear that the significance of deposition and fixation can be completely understood only in relation to their immediate and long-term effects on ecosystem biogeochemical processes (Granhall 1981). To fully assess the importance of these external N sources, we need to know their fates (i.e. which ecosystem components they enter), their turnover or residence times in these storage pools, and the extent to which they impact other ecological processes. For example, in those ecosystems with low N availability and with well-developed mechanisms for internal recycling, immobilization and net conservation of N supplies (e.g. coniferous forest, tundra), short-term effects of external N inputs on productivity and N cycling are small (Gosz 1981; Granhall 1981; Van Cleve & Alexander 1981). However, because N availability is low in such ecosystems – due to wide C:N ratios, low rainfall, cold temperatures and permafrost – N inputs may have major impacts on the long-term availability and cycling of N as well as on other ecosystem processes (e.g. Jones 1978). Thus, N inputs must be considered in relation to questions of fate, turnover, and secondary impacts, as well as in comparison with magnitudes of N losses and rates of internal recycling.

In spite of the importance of understanding these factors, our existing knowledge and data base are too scanty to reach many broad generalizations. In the case of symbiotic N fixation, research on coniferous forests of the Pacific Northwest and deciduous forests of the southeastern USA has demonstrated many consequences of N inputs for ecosystem productivity and biogeochemistry (Tarrant 1983; Binkley et al. 1984; Boring & Swank 1984a; Montagnini et al. 1986). Fewer comparative studies exist for other ecosystems. It is equally significant that little is known about specific impacts of N inputs via atmospheric deposition and nonsymbiotic fixation. Moreover, in many instances in which the ecosystem consequences of external N inputs have been considered (e.g. Henderson & Harris 1975; Mitchell et al. 1975; Bormann et al. 1977; Henderson et al. 1978; Sollins et al. 1980; Swank & Waide 1980; Gholz et al. 1985), most analyses have been derived from mass balance calculations, with the magnitude of inputs compared with various ecosystem fluxes and losses. Only a few past investigations (e.g. Jones 1978; Skujins & Klubek 1978) have included detailed process-level studies using specific tracers such as ^{15}N. While the mass-balance approach provides a useful starting point for assessing the significance of N sources (Swank 1984), such studies provide only a preliminary understanding of the true significance of N inputs for internal ecosystem processes.

A summary follows of the existing information on fates and impacts of external N inputs on terrestrial ecosystems. Because of the paucity of specific studies in this area, we recognize that much of this represents tentative generalizations requiring further research. Before focusing on each type of N input separately, we first address two important contrasts in fates and impacts of the various N sources.

First, much of the atmospherically deposited N, particularly the wet fraction, initially enters the ecosystem as highly labile inorganic or organic forms of nitrogen. Nitrogen may subsequently be taken up by biota from these labile nitrogen pools, or may be lost from the system in solution or gaseous form. In contrast, dinitrogen fixation is a biological process, with the fixed N immediately becoming bound with carbon and incorporated into living organic tissues. This form cycles less rapidly and has a longer residence time within terrestrial ecosystems than deposition inputs. As a consequence, fixation inputs of N may have less immediate impact on biogeochemical processes, but also have the potential for affecting ecosystem processes over much longer time frames, than deposition inputs.

A second contrast involves the degree of internal ecosystem regulation over sources and magnitudes of external N inputs. In the case of atmospheric deposition, N inputs are not regulated by ecosystem dynamics and represent an outside subsidy from the physicochemical environment. The possibility exists that large increases in these N inputs may acutely alter the cycling of other elements, as well as damage the state of the entire ecosystem (e.g. the excess ammonium hypothesis for deposition-induced forest decline; Nihlgard 1985). In contrast, N inputs from biological fixation (symbiotic and nonsymbiotic) require carbon and energy subsidies from within the ecosystem, and are highly dependent on the successional state, species composition, energetics, and biogeochemistry of the ecosystem. Numerous potential feedbacks exist between other components of the ecosystem and N inputs from dinitrogen fixation (e.g. successional declines in rates of symbiotic N fixation). Such internal control of N accretion has a much reduced potential for long-term degradation of the ecosystem.

Because of its dependence upon successional status, N fixation has a greater potential for catalyzing or stimulating other ecological processes within terrestrial ecosystems than do deposition inputs. For example, N-fixing organisms contribute to the accretion of nitrogen and organic matter in terrestrial environments during primary and secondary succession; the activities of symbiotic -fixing systems are a major determinant of successional dynamics of community composition, productivity, and C and N cycles in temperate forests (e.g. Tarrant 1983; Boring & Swank 1984a); and nonsymbiotic N inputs to decaying logs may play an essential role in wood decay and soil organic matter genesis in diverse forest ecosystems (e.g. Cornaby & Waide 1973; Silvester et al. 1982; Jurgensen et al. 1984). Deposition inputs may enter the N cycle and be assimilated at various points, but outside of acute pollutant fluxes they probably have less potential for catalyzing other ecosystem processes over long time spans than do fixation inputs.

Atmospheric deposition

Deposition inputs of inorganic N may be absorbed and assimilated directly within the vegetation canopy by aboveground plant parts or by resident epiphyte or microbial populations. Alternatively, such inputs may enter labile litter-soil pools, from which N may be taken up by plant roots or micro-organisms, or be lost via leaching, clay fixation, or denitrification. Organic N inputs may be rapidly mineralized and made available as inorganic N for biotic uptake. Based on nutrient budget studies in undisturbed terrestrial ecosystems (e.g. Likens et al. 1977; Henderson et al. 1978; Swank & Waide 1980), it is well established that the majority of atmospheric N inputs are utilized within the ecosystem, with only small amounts being lost via leaching (Vitousek & Melillo 1979; Khanna 1981). Thus, atmospheric inputs of N may contribute substantial fractions of net annual requirements to terrestrial plants, even following management disturbances (e.g. Swank 1984). However, detailed information on the actual fate and effect of N deposition on biogeochemical pathways is not available for any single ecosystem. Nonetheless, deposition sources provide short-term inputs of N for plant and microbial growth.

The burning of fossil fuels in industrialized nations has resulted in large increases of N inputs to terrestrial ecosystems. Current interest in assessing ecosystem impacts of such elevated inputs is providing new information on within-system behaviors and effects as well as insights regarding the threshold between beneficial and detrimental impacts on ecosystem processes. Specifically, NO_3^- concentrations have become elevated in precipitation, and the total deposition of various N species (e.g. Table 4) is continuing to increase in many areas (e.g. Likens et al. 1977; McColl 1982). Such inputs may represent up to 50% of total annual aboveground N uptake in some forests (Johnson & Richter 1984) and other ecosystems, and could have important effects on numerous biogeochemical processes.

In terrestrial ecosystems where elevated N inputs do not exceed biotic uptake by plants and microbes, such N sources may stimulate primary productivity over the short term and accelerate other ecosystem processes (e.g. microbial decay of plant litter having high C:N ratios). However, where inputs exceed biotic uptake, several negative impacts on ecosystem processes are possible (Abrahamsen 1980; Cowling & Linthurst 1981; Johnson & Richter 1984). These include direct physiological impairment of sensitive plant species (Landolt & Keller 1985; Kozlowski & Constantinidou 1986a; 1986b); alterations in microbial processes such as accelerated rates of nitrification and denitrification, reduced rates of N fixation, reduced rates of organic matter decomposition and N mineralization, reductions in microbial respiration and enzyme activities, and reduced levels of mycorrhizal infection (Killham et al. 1983; Stroo & Alexander 1985, 1986; Berg 1986; Bewley & Parkinson 1986; Klein & Alexander 1986; Will et al. 1986), and changes in soil chemical processes such as accelerated leaching of NO_3^- and cations, acidification of upper soil horizons, and declines in nutrient availability and general fertility (Johnson et al. 1983; Heute & McColl 1984; Johnson & Reuss 1984). Some of these impacts result from the confounding of excess N inputs with those of other ions (e.g., H^+, SO_4^{-2}). Excess N inputs, particularly as inorganic NH_4^+, have also been hypothesized to be a significant cause of forest decline in heavily polluted areas (Nihlgard 1985).

Specific information on impacts of elevated deposition inputs of N are just beginning to accumulate. Ecosystem fates and effects of such inputs, as well as the breakpoint between beneficial and harmful impacts, will vary substantially across ecosystems and sites, and over time. Moreover, particularly in studies of deposition impacts on microbial processes, it is difficult to infer actual impacts on natural terrestrial ecosystems over the long-term from even well-controlled short-term experiments in the lab or field (Bewley & Parkinson 1986; Klein & Alexander 1986). Conclusions from such studies are highly dependent on experimental conditions. Also, most previous studies have focused on short-term acute effects rather than longer-term chronic impacts, and have not included spatial heterogeneity and actual resource levels in the experimental design.

Nonsymbiotic fixation

Nonsymbiotically fixed N initially becomes incorporated into microbial tissues and impacts biogeochemical processes over a variety of time scales. This source of N may lead to the long-term accretion of N and organic matter in terrestrial environments and may stimulate various other biogeochemical processes. Although beneficial effects of nonsymbiotically fixed N are frequently discussed, direct evidence of the specific fates and turnover of this N input are rare. Some of the nitrogen fixed nonsymbiotically may be lost via denitrification, either rapidly in the case of desert cryptogamic crusts (Skujins & Klubek 1978) or following cell death and mineralization in the case of both blue-green algae (Jones & Wilson 1978) and free-living heterotrophs (Jones 1978). A large fraction of the fixed N is retained within most terrestrial ecosystems, becoming incorporated into soil organic matter pools or being released extracellularly as labile organic N which is taken up in the phyllosphere by leaves or in the soil by bacteria, fungi, algae, mosses, or vascular plants (Jones 1978; Jones & Wilson 1978). Similarly, N fixed by lichens may be released for biotic uptake via leaching processes (Millbank 1979), or following death and decomposition.

In temperate grasslands, fixation inputs due to associative diazotrophs contribute only small amounts of N relative to atmospheric deposition (0.8 vs 4–8 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$; Kapustka & DuBois 1987). However, this fixed N has been reported to stimulate significant root proliferation by grasses, to promote grass seedling establishment, and to enhance formation of vesicular-arbuscular mycorrhizal associations (Kapustka et al. 1985). Although the amount of fixed N was not sufficient to satisfy N requirements of grass seedlings, it did promote root growth and mycorrhizal infection, and was critical to seedling establishment and survival in this semi-arid environment. Fixation of N also contributed to the growth of cyanolichen crusts on bare soil between grass crowns and has been postulated to stabilize otherwise erosive soils, thereby reducing soil loss (Kapustka & DuBois 1987).

Several studies have documented the importance of nonsymbiotic N fixation to wood decomposition in forests (Cowling & Merrill 1966; Cornaby & Waide 1973; Silvester et al. 1982; Jurgensen et al. 1984). In addition to enhancing the turnover of woody litter, such inputs contribute to the long-term accumulation of both soil N and organic matter within these ecosystems. However, careful analyses of the specific processes which regulate the contribution of N fixation and wood decay to the genesis and subsequent availability of soil N and C reserves over long-term chronosequences are presently lacking (Harmon et al. 1986). This represents a major gap in our understanding of coupled dynamics of C and N in terrestrial ecosystems.

Human activities may substantially alter nonsymbiotic inputs to terrestrial ecosystems, and hence affect the fates and impacts of these inputs. Specifically, it is primarily the way in which site management alters soil, microenvironments and resource levels that determines the magnitude, fates, and impacts of nonsymbiotic N fixation inputs. For example, in the case of forests, whether prescribed burning or intensive site preparation are employed will, in large measure, determine subsequent dynamics of free-living N fixers and hence N inputs. In particular, because decaying wood is an important site of free-living fixation, the decision as to whether to leave logging residue on site will have major, long-term consequences for rates of nitrogen and organic matter accretion within litter-soil horizons (Jurgensen et al. 1984).

Symbiotic fixation

Considerably more research has been conducted on the fates and impacts of symbiotically fixed N than for the other N inputs considered here. Complementing innumerable studies of herbaceous crop plants, most of our past understanding in this area has come from studies in forests dominated by *Alnus* spp., *Lupinus* spp. and *Robinia pseudoacacia*. Results of historically important studies in nonagricultural ecosystems have revealed that nitrogen-fixing species may contribute to the long-term accretion of soil nitrogen and organic matter on infertile sites, enhance nutrition of associated plant species when nitrogen is limiting, stimulate primary production and biomass accretion, and potentially alter a variety of biogeochemical processes (Chapman 1935; Ike & Stone 1955; Trappe et al. 1968; Klemmedson 1979; Tarrant 1983). However, a clear understanding of underlying mechanisms has often been lacking. Recent research on the fates and impacts of symbiotically fixed nitrogen has provided significant new information on:

- conditions and timing for increases in soil nitrogen mineralization and availability,
- relative importance of various nutrient transfers to the soil and forest floor,
- species-dependent impacts upon forest population and community dynamics, and
- effects of elevated N storage and availability upon soil acidity and dynamics of other elements.

Recent studies have shown that the magnitude and timing of increases in N availability are dependent upon plant stress levels, specifics of nutrient transfers to the forest floor and soil, and successional dynamics of nitrogen-fixing species. Early studies of N transfer in crop legumes demonstrated that, following vigorous growth and high rates of N fixation, defoliation or shading induced root and nodule shedding, and subsequently increased N mineralization due to decomposition of N-rich tissues (Wilson 1942; Butler et al. 1959). More recent studies with woody legumes have shown that drought may result in pulses of nodule and fine root shedding (Sprent 1979; Boring & Swank 1984a), potentially resulting in elevated N mineralization in subsequent periods favorable for decomposition. In assessing the influence of damaged tree lupines upon *Pinus radiata* nutrition, Gadgil (1971) concluded that regular insect defoliation and stand senescence increased N availability, although the relative contributions of sloughed root, nodule, and leaf tissues versus insect frass to nitrogen mineralization were not assessed.

Similar increases in N availability have been documented in insect-stressed stands of *Robinia pseudoacacia* (Montagnini et al. 1986), a species which chronically sustains relatively high defoliation (Seastedt et al. 1983; Hargrove et al. 1984). Although this species transfers large amounts of N in both leaf and fine root litter (White 1986; Grimm 1988), a large fraction is also present in throughfall as dissolved organic N, NH_4^+, and fine particulates. The fine particulate fractions of insect frass and other organic materials in throughfall are subject to dissolution and represent a labile source of N, subject to more rapid mineralization than the lignin-rich leaf, fine root and woody fractions which decompose slowly (White et al. 1988; Grimm 1988).

Most N-fixing perennial species transfer large amounts of leaf litter to the forest floor; however, these species do not share common patterns of substrate quality, litter decomposition, or N mineralization rates. Although many studies have described rapid litter decomposition of N-fixers, very few early studies actually examined this process in detail. *Myrica gale*, an actinorhizal N-fixer, contains high N concentrations and low C:N values in leaf litter. However it also contains 40% lignin and has been shown to release only 10% of its initial N content during a 5-year decomposition study (Schwintzer 1984). Although this species produces the most recalcitrant leaf litter reported for N-fixing plants in the literature, other species also have slowly decomposing litter. *Robinia pseudoacacia* leaf litter has a high lignin content (18–25%) and N immobilization potential in spite of its low C:N ratio (Bartuska & Lang 1981; Hirschfield et al. 1984; White et al. 1988). Other woody N-fixing species, such as *Ceanothus* and *Alnus*, may have a range of lignin values (10–20%) coupled with low C:N ratios, resulting in variable decomposition rates, but generally more rapid mineralization rates (Edmonds 1980; Aber & Melillo 1982). More rapid mineralization rates in *Alnus* may be at least partially attributed to high N concentration due to inefficient N resorption from senescent leaf tissues (Dawson & Funk 1981; Coté & Dawson 1986).

Although *Alnus* spp. root decomposition has apparently not been examined in detail, decomposing *A. nepalensis* root nodules have been shown to release 95% of their initial N within 10–17 months (Sharma & Ambasht 1986). In contrast, tropical agricultural legumes may lose up to 95% of their initial N within 4 months (Chulan & Waid 1981). Substrate quality and decomposition rates of *R. pseudoacacia* roots are similar to those of its leaves, but nodule decomposition has not been examined. A sequence of four- to thirty-eight-year-old *R. pseudoacacia* stands were found to maintain a total nodule biomass much smaller than that reported for *Alnus* (Boring & Swank 1984a). Total N pools in nodules ranged from only 2–9 kg ha^{-1}, indicating that their contribution of N may be much less significant than root and leaf litter, fine particulates, and throughfall fractions, although rapid turnover rates may potentially increase their contribution.

Successional processes in stands of N-fixing species will influence the conditions and timing of increases in soil N availability, as well as spatial and temporal variations in the accumulation of soil organic matter and total N. In an age-sequence of *R. pseudoacacia* stands in the southern Appalachians, although soil NO_3^- availability was elevated in all stand ages, there were significant increases in total soil N and organic matter only in older stands (Boring & Swank 1984a). The slow increases of soil N and organic matter are presumably explained by slow turnover and mixing of recalcitrant leaf and root litter with the mineral soil, combined with eventual black locust stand mortality. The increased NO_3^- availability is likely due not only to the large litter inputs, but additionally to the high flux of labile forms of nitrogen in throughfall and fine particulate (frass) components in all stands (Montagnini et al. 1986; White 1986; Grimm 1988). Studies of mixed stands of *Alnus* spp. and *Populus* spp. have revealed increased N availability and growth responses only two years after planting (Hansen & Dawson 1982), indicating that the relatively rapid decomposition of *Alnus* leaf litter may be a controlling factor for N availability in this species.

Increases in N availability associated with N-fixing plants may stimulate or alter a number of forest and soil processes. *Eucalyptus marginata* leaf litter has elevated immobilization rates of N, P, and S when decomposing beneath the understory canopy of the N-fixing species *Acacia pulchella* (O'Connell 1986). In mixed *Pseudotsuga menziesii* – *Alnus rubra* and *A. sinuata* stands, ecosystem responses include increased aboveground biomass, basal area growth, stem biomass increment, and stem growth per unit leaf area (Binkley 1983; Binkley et al. 1984). Increases in litterfall mass and nutrient content, litter standing stocks, soil extractable Ca and Mg, available soil P, and aboveground vegetation nutrient pools were also measured in these stands. Similar studies with *R. pseudoacacia* have revealed increases in aboveground biomass, net primary production, leaf production, leaf litter mass (Boring & Swank 1984a), elevated forest floor pools of N, reduced C:N ratios in forest floor horizons (White 1986), elevated concentrations of inorganic N, and accelerated leaching of organic and inorganic N (Montagnini et al. 1986).

An additional effect of some nitrogen-fixing species is soil acidification and long-term decreases in the availability of elements other than N. Franklin et al. (1968) described a one unit pH decrease, reduced cation availability and reduced base saturation in soils under *A. rubra* in the Pacific northwest. They attributed these observations to high nitrification rates coupled with cation leaching below a 15 cm depth, and to high net uptake of nutrients other than nitrogen. Van Miegroet & Cole (1985) have confirmed that nitrification exerts a strong influence on soil and soil solution acidity, and Binkley (1986) has described decreased foliar P in *Pseudotsuga menziesii* growing with *A. rubra*. The considerable production of H^+ and NO_3^- causes downward displacement of exchangeable bases and a significant drop in soil and solution pH in upper profiles. In *A. glutinosa* and *Hippophae rhamnoides*, proton excretion associated with N fixation and nutrient uptake is another source of soil acidification (Troelstra & Blacquiere 1986). Although similar nitrification, leaching and nutrient uptake patterns have been described for *R. pseudoacacia*, detailed acidification studies have not been conducted on this species or on other important tree legumes. The impacts of these processes upon the temporal patterns of nutrient availability for both the N fixer and associated species need further examination, especially relative to phosphorus which may limit the productivity of most N-fixing species.

Recommendations for future research

In previous sections we have reviewed existing information concerning the magnitudes and importance of nitrogen inputs to natural terrestrial ecosystems via atmospheric deposition and biological dinitrogen fixation. We have repeatedly stressed that the existing data base is still incomplete in some areas and is beset with difficulties related to sampling intensity, methodology and the limited range of ecosystems studied in detail. Thus, we conclude our analysis by summarizing five areas requiring detailed future research.

It is clear that we do not have complete measures of total deposition inputs to terrestrial ecosystems. Particularly deficient are careful analyses of dry deposition inputs. More intensive studies are needed in a wide range of ecosystems, particularly focusing on dry deposition of N forms to aboveground ecosystem components. Such studies should quantify total deposition inputs as well as assess within-ecosystem dynamics and impacts.

Second, we stress the need for additional quantification of symbiotic N fixation in those ecosystems in which such studies are deficient. Such studies should be designed to sample variation over space and time, and to examine environmental and ecological factors regulating fixation. Moreover, these studies should focus on the retention and cycling of fixed N, on temporal influences upon N availability and ecosystem productivity, on additional impacts upon carbon dynamics and soil acidity, and on secondary influences upon the availability of other essential elements.

Next, one of the major unknowns involving N fixation concerns associative N-fixing systems. What is the magnitude and variability of associative N inputs across the range of non-agricultural terrestrial ecosystems? There is a need for additional process-level investigations of associative N-fixing systems, particularly in rhizospheres of temperate-zone ecosystems.

Fourth, we feel that further evaluation of the quantitative significance and importance of free-living nitrogen fixation within decaying woody substrates is needed in a variety of terrestrial ecosystems. Studies should include process-level investigations of the role of N inputs in wood decomposition and soil organic matter genesis over the long-term. Also, additional attempts to quantify:

— changes in heterotrophic free-living fixation across successional chronosequences, and
— patterns of nonsymbiotic fixation by phyllosphere organisms and the fates of the fixed N are also justified.

Finally, we feel that emphasis should be placed on integrating process-level studies of N inputs, using nitrogen-15 and other tracers, with ecosystem models. Such an integration of process-oriented research and modeling should prove especially useful in enhancing our understanding of the long-term biogeochemical impacts of these N inputs.

These gaps in our knowledge present major research challenges and opportunities. Substantial effort must be continued in these areas if we wish to assess the full significance of nitrogenous atmospheric pollutants, to predict the impacts of land management practices upon ecosystem nitrogen cycles and productivity, or to utilize symbiotic nitrogen fixation to its full potential in managed forest ecosystems.

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