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Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems

Cory C. Cleveland,[1,2] Alan R. Townsend,[1,2] David S. Schimel,[3] Hank Fisher,[3] Robert W. Howarth,[4] Lars O. Hedin,[4] Steven S. Perakis,[4] Erika F. Latty,[4] Joseph C. Von Fischer,[4] Adrien Elseroad,[4] and Matt F. Wasson[4]

Abstract. Human activities have clearly caused dramatic alterations of the terrestrial nitrogen cycle, and analyses of the extent and effects of such changes are now common in the scientific literature. However, any attempt to evaluate N cycling processes within ecosystems, as well as anthropogenic influences on the N cycle, requires an understanding of the magnitude of inputs via biological nitrogen fixation (BNF). Although there have been many studies addressing the microbiology, physiology, and magnitude of N fixation at local scales, there are very few estimates of BNF over large scales. We utilized >100 preexisting published estimates of BNF to generate biome- and global-level estimates of biological N fixation. We also used net primary productivity (NPP) and evapotranspiration (ET) estimates from the Century terrestrial ecosystem model to examine global relationships between these variables and BNF as well as to compare observed and Century-modeled BNF. Our data-based estimates showed a strong positive relationship between ecosystem ET and BNF, and our analyses suggest that while the model's simple relationships for BNF predict broad scale patterns, they do not capture much of the variability or magnitude of published rates. Patterns of BNF were also similar to patterns of ecosystem NPP. Our "best estimate" of potential nitrogen fixation by natural ecosystems is ~195 Tg N yr^{-1}, with a range of 100-290 Tg N yr^{-1}. Although these estimates do not account for the decrease in natural N fixation due to cultivation, this would not dramatically alter our estimate, as the greatest reductions in area have occurred in systems characterized by relatively low rates of N fixation (e.g., grasslands). Although our estimate of BNF in natural ecosystems is similar to previously published estimates of terrestrial BNF, we believe that this study provides a more documented, constrained estimate of this important flux.

1. Introduction

In the absence of human influence, two major processes "fix" atmospheric N_2 into biologically available forms: lightning [*Liaw et al.*, 1990; *Logan*, 1983] and biological nitrogen fixation (BNF). In the pristine biosphere, it is generally believed that nitrogen (N) fixation by terrestrial BNF was roughly an order of magnitude greater than that by lightning [*Galloway et al.*, 1995] and that it was therefore the dominant source of newly fixed N to the landscape. However, in recent decades human activities have caused dramatic alterations of the terrestrial nitrogen cycle, and analyses of the extent and effects of such changes are now common in the scientific literature [e.g., *Hedin et al.*, 1995; *Vitousek*, 1994a; *Galloway et al.*, 1995; *Townsend et al.*, 1996; *Howarth et al.*, 1996; *Vitousek et al.*, 1997]. Three of the major anthropogenic changes are the production of nitrogen fertilizer, widespread cultivation of legumes, and incidental N fixation in internal combustion engines. *Vitousek et al.* [1997] estimate that these three processes together now more than double the total natural rate of N fixation and highlight this comparison as "the most fundamental human-caused change to the global N cycle."

While it is unquestionable that humans have sharply increased the rate at which atmospheric N_2 is fixed into reactive forms, the comparison between anthropogenic sources and BNF is tenuous. Prior estimates of BNF in terrestrial ecosystems range from ~40-200 Tg N yr^{-1} (1 Tg = 10^{12} g; [*Soderland and Rosswall*, 1982; *Stedman and Shetter*, 1983; *Paul and Clark*, 1989; *Schlesinger*, 1991]), which appears relatively constrained; yet the data from which all of these estimates were obtained are difficult to discern as few present a list of data sources for their global number. At best, the global value is broken down into a few very broad components (e.g., forest, grassland and other [*Soderlund and Rosswall*, 1982]), but such a division averages enormous land areas that contain significant variation in both BNF data sets and biome types. These poorly documented, spatially unresolved estimates of BNF represent a sharp contrast to the estimates of anthropogenic sources of N, which can be derived for much of the developed world by county, state, and/or country [e.g.,

[1]Department of EPO Biology, University of Colorado, Boulder.
[2]Also at Institute for Arctic and Alpine Research, Boulder, Colorado.
[3]National Center for Atmospheric Research, Boulder, Colorado.
[4]Department of Ecology and Systematics, Cornell University, Ithaca, New York.

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Matthews, 1996; *Boden et al.,* 1995]. As suggested by *Hedin et al.* [1995], estimates of the degree to which the global N cycle has changed depend on a good understanding of baseline conditions (i.e., conditions prior to human influences). A primary determinant of that baseline is the rate of biological N fixation; therefore a more robust estimate of this value at both global and biome-specific scales is critically needed.

While changes in the N cycle can be summarized in global terms, reactive and biologically available forms of nitrogen do not truly cycle globally. Rather, their transport occurs over distances of tens to many hundreds of kilometers [*Logan,* 1983; *Vitousek,* 1994a]. Consequently, alteration of the global nitrogen cycle results from changes in cycling at the scale of large regions [*Townsend et al.,* 1996; *Asner et al.,* 1997]. At the global scale, N fixation may have roughly doubled; however, in heavily industrial and/or agricultural regions of the world anthropogenic sources of nitrogen may be orders of magnitude greater than the natural inputs [*Chameides et al.,* 1994; *Howarth et al.,* 1996], while in more pristine regions natural processes may still dominate [*Hedin et al.,* 1995]. Thus the focus on changes in the N cycle must be at the regional scale, and such analyses will depend on estimates of BNF that are regionally specific.

Our main objectives in this study were to assemble a global database of BNF in terrestrial biomes derived from a compilation of all available data, which was linked to the spatial scale of currently available databases on land cover and land use [*Schimel et al.,* 1997]. We present that database here, along with tables detailing the original sources of all the data from which it is derived, and discuss the difficulties in translating plot- and laboratory-level BNF data to biome-scale averages. We also use estimates of net primary productivity (NPP) and evapotranspiration (ET) from the Century ecosystem model [*Parton et al.,* 1987; *Schimel et al.,* 1997] to examine the relationships between those variables and BNF. Models such as Century have proven to be a valuable tool in large-scale analyses of terrestrial ecosystems and their response to global environmental change, but none of the major simulation models have robust, predictive relationships addressing N fixation and its response to a changing N cycle [*Vitousek and Field,* 1999]. Century predicts BNF from crude relationships with climate; we also use the database presented here to evaluate the general accuracy of this approach at the scale of large regions.

2. Methods

2.1. Symbiotic versus Nonsymbiotic N Fixation

Symbiotic N fixation provides the dominant input of nitrogen in many ecosystems, although it is probably most important during early successional stages (especially in temperate ecosystems), with inputs tending to decrease as succession proceeds [*Gutschick,* 1981, 1987]. The majority of symbiotic BNF occurs via a root-nodule symbiosis. Root nodules are structures on roots inhabited by specific N fixing microorganisms [*Akkermans and Houwers,* 1983]. In this relationship, the N fixer is maintained by the plant and uses the plant as a carbon source, while excreting fixed nitrogen for the benefit of the plant. Nonsymbiotic nitrogen fixation includes fixation by the true free-living N_2 fixers, as well as by autotrophic and heterotrophic organisms not in direct symbioses with vascular plants, including cyanobacteria symbiotic in lichens, bryophytes, or associative N_2 fixing systems. In addition, it is worth noting that many filamentous actinomycetes (e.g., *Frankia)* can fix nitrogen as free-living microorganisms or in symbiosis with a number of nonleguminous vascular species.

2.2. Nitrogen Fixation Rate Estimates: Review of Methodology

2.2.1. Nitrogen accumulation method. The simplest method of estimating BNF, the nitrogen accumulation method, involves comparing the total nitrogen content of an ecosystem at two points in time. Increases in N in all system components (soil and vegetation) or differences in N accumulation between nitrogen fixing and nonfixing species over time are measured to determine nitrogen fixation rates [*Warembourg,* 1993]. A variation of this method involves using a sequence of plots at different locations to approximate the accretion that would occur in a single site over time [*Roskowski,* 1980]. However, estimating the actual gain of nitrogen from BNF using this method is difficult because it does not account for other inputs (e.g., atmospheric deposition) or losses of nitrogen from the system (e.g., via N leaching, denitrification). In some systems, mass balance studies have been used to determine nitrogen accumulation [*Likens et al.,* 1977; *Swank and Waide,* 1987]. However, estimates of BNF using this approach are relatively difficult to obtain, as they require a precise quantification of all N inputs and outputs. Mass balance estimates of N fixation have been used successfully in temperate forest ecosystems in the United States and Europe [*Silvester,* 1983], but this approach has not been widely used in other ecosystems.

2.2.2. Acetylene reduction method. The most common method used to determine BNF rates is the acetylene reduction assay (ARA). This method relies on the fact that the nitrogenase enzyme, the enzyme primarily responsible for N fixation, has a high preference for acetylene (C_2H_2) over N_2, and the product of acetylene reduction (ethylene, C_2H_4) is easy to measure. Samples are amended with C_2H_2 and incubated; a gas sample is removed; and ethylene (C_2H_4) concentrations are evaluated using gas chromatography. A rate of N fixation is calculated by dividing the rate of C_2H_2 reduction by a factor that accounts for the greater electron requirement of N fixation per mole of atmospheric nitrogen [*Binkley et al.,* 1994]. In most studies, a 3:1 (C_2H_2:N_2) conversion ratio is used, representing the theoretical stoichiometric relationship between C_2H_2 reduction and N fixation [*Roskowski,* 1981; *Hardy et al.,* 1968]. However, there is evidence that experimental ratios may vary from the theoretical 3:1 ratio. Therefore, literature estimates that were not converted using a 3:1 ratio are also included and reflect the actual conversion ratio used in these studies [e.g. *Vitousek,* 1994b]. A detailed explanation of the acetylene reduction method is provided by *Hardy et al.* [1968, 1973].

2.2.3. ^{15}N methods. Other techniques to estimate N fixation rates utilize the stable isotope ^{15}N. The ^{15}N natural abundance method [*Shearer and Kohl,* 1986] uses differences in naturally occurring ^{15}N signatures of plants reliant on soil N

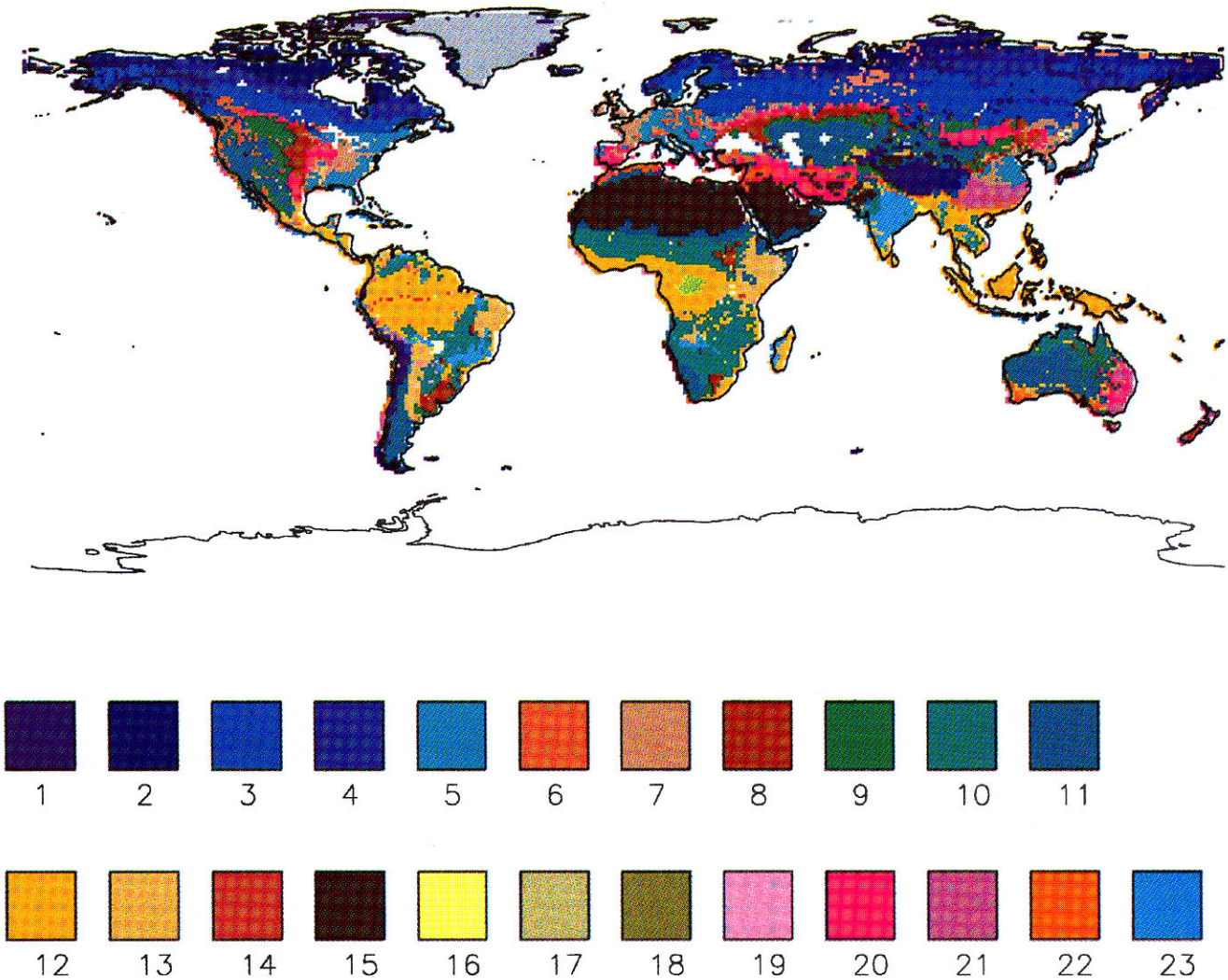

Plate 1. Map of the 23 major ecosystems used in the current study and classified under the IGBP GAIM Potsdam model intercomparison. Color numbers correspond to the ecosystem types in Table 1.

relative to plants which utilize N derived solely from atmospheric N_2 through fixation. The ^{15}N abundance of fixing plants, reference plants, and symbiotic plants grown in the absence of inorganic N can be used to provide an integrated estimate of symbiotic N fixation in the field.

The ^{15}N enrichment technique entails enriching the soil with ^{15}N [*Silvester,* 1983]; over time, ^{15}N:^{14}N ratios in N fixing plants will be lower relative to nonfixing species, and these ratios can be used to calculate N_2 derived from the atmosphere. In some cases, the natural ratio of ^{15}N:^{14}N in soil is sufficiently different from that of the atmosphere, thus enabling a calculation of N fixation by comparing ratios of N fixing species and nonfixing species. A detailed description of ^{15}N methods of estimating N fixation is provided by *Warembourg* [1993].

2.3. Statistical Analysis and Calculations

We estimated current rates of terrestrial biological nitrogen fixation by conducting a thorough review of the literature. Much of our current knowledge of nitrogen fixation is derived from work in agricultural systems, and large gaps still exist in our knowledge of the quantitative, long-term importance of the process in many natural ecosystems [*Boring et al.,* 1988]. The majority of studies on rates of N fixation in natural systems available in the literature are from North America, with fewer contributions from Europe and Australia. Estimates of N fixation from Asian, South American, and African ecosystems are extremely rare.

Our estimates of N fixation are the means of the available published estimates of both symbiotic and asymbiotic components of N fixation measured for each ecosystem, using the ecosystem classification from *Schimel et al.* [1996] developed for the International Geosphere-Biosphere Programme (IGBP) Global Analysis and Modeling (GAIM) Potsdam model intercomparison (Plate 1). Attributes of each ecosystem are depicted in Table 1. In some cases we applied an arithmetic mean to represent a "component average," and in others we applied a geometric mean [*Parkin and Robinson,* 1993], depending on the distribution of the published data.

Table 1. Average Net Primary Productivity, Evapotranspiration, and Mean Annual Temperature by Ecosystem Type.

Color Number*	Potsdam Vegetation Type†	Average NPP, g C m^{-2} yr^{-1}	Average ET, cm yr^{-1}	Mean Annual Temperature, °C
1	polar desert/alpine tundra	144	17	-2
2	moist tundra	197	18	-8
3	boreal borest	271	45	-2
4	boreal woodland	216	32	-6
5	temperate mixed forest	478	78	11
6	temperate coniferous forest	646	53	10
7	temperate deciduous forest	484	66	9
8	tall/medium grassland	304	59	10
9	short grassland	130	34	8
10	tropical savanna	180	89	24
11	arid shrubland	77	23	16
12	tropical evergreen forest (rain forest)	945	136	25
13	xeromorphic forest	187	60	21
14	tropical forested floodplain	1123	148	26
15	desert	31	7	24
16	tropical non-forested floodplain	542	114	26
17	temperate forested floodplain	508	58	9
18	temperate non-forested floodplain	241	50	9
19	wet savanna	411	115	22
20	temperate savanna	194	43	11
21	temperate broadleafed evergreen forest	702	84	17
22	mediterranean shrubland	151	37	17
23	tropical deciduous forest	395	104	24

*Color numbers correspond to those depicted in Plate 1.
†The ecosystem classification was developed for the IGBP GAIM Potsdam model intercomparison [*Schimel et al.*, 1996].

Specifically, in cases where the distribution of the published N fixation rates were not symmetric (i.e., the mean and the median had vastly different values), a geometric mean was applied to temper extremely high rates of fixation which would otherwise inflate an arithmetic mean [*Parkin and Robinson*, 1993]. In cases where the distribution of rate frequencies of N fixation were symmetric with no obvious outliers, the arithmetic mean was used to represent the N fixation rate.

More than 75% of the published papers used in this study utilized the ARA method to determine nitrogen fixation rates. In most cases, rates of N fixation in the literature were expressed in molar units (C_2H_2 g^{-1} d^{-1}) and were converted by the original investigators to more standard units (g N m^{-2} yr^{-1}; kg N ha^{-1} yr^{-1}) to account for growing season length within each ecosystem. Owing to the variability in other conversion factors used in the published studies (e.g., depth of active soil nitrogen fixation), we made no attempt to normalize the published estimates, but rather assumed that "site specific" conversion factors used by the authors were accurately assessed and applied to derive each estimate. Estimates of N fixation obtained using other methods were not normalized or rescaled in any way but were assumed to accurately reflect the individual attributes of the study site being investigated.

Estimates of N fixation that did not explicitly report the contribution of symbiotic and not symbiotic fixers, but rather only reported a total N fixation value at a site were not used to generate our "total" estimates of N fixation. However, where these estimates are available, they are included in the tables for comparison to our total estimate. It should also be emphasized that N fixation rates reported in the tables are extracted from plot-scale studies of either symbiotic or nonsymbiotic N fixation and as such may not represent N fixation rates for an entire ecosystem. In addition, symbiotic N fixation estimates reported in the tables represent temporally averaged contributions of symbiotic fixers, although there is clear evidence from many ecosystems that N fixation rates vary with successional status and ecosystem age [*Vitousek*, 1994; *Blundon and Dale*, 1990; *Boring and Swank*, 1984; *Gorham et al.*, 1979].

For each biome, we provide three estimates of N fixation which differ only in the possible contribution of symbiotic fixation to the total estimate. We refer to these as our "conservative," "central," and "upper-bound" estimates. This was done to account for the heterogeneous distribution of symbiotic nitrogen fixers (e.g., leguminous species) over large landscapes [*Johnson and Mayeux*, 1990; *Piccolo et al.*, 1994]. In this study, we located a total of 46 estimates of symbiotic N fixation in natural ecosystems. Of these, 11 studies (24%) included estimates of legume cover at the study sites from which rates of N fixation were obtained. For ecosystems in which some literature rates of symbiotic N fixation were associated with published estimates of N fixer coverage, a coverage is calculated that represents the average of all cover estimates for that ecosystem. We then assume that this coverage is associated with our calculated rate of N fixation. Unless otherwise indicated, "conservative" and "upper-bound" estimates are +/- 2/3 of the empirically derived coverage value. This range was chosen because it captures +/-

2 standard errors (SE) from the geomean of all coverage estimates (geomean = 15.5; SE = 5.7). Since several coverage estimates for individual ecosystems were <10%, using a range of +/- 10% in all cases would produce negative values. Thus we scaled the range to the magnitude of the coverage estimate by using +/- 2/3.

For ecosystems that did not include any coverage estimates of N-fixing species, we calculated an average N fixation rate and assumed that this was associated with an average coverage of 15%, which represents the geometric mean of all available coverage estimates from all ecosystems combined *(n=11)*. For consistency, "conservative" and "upper-bound" estimates are based on a hypthetical range of coverages +/- 2/3 of this value. Each estimate of N fixation also includes a value that represents nonsymbiotic fixation, and we assume that this value does not vary within individual systems (i.e. coverage of nonsymbiotic fixers over the landscape is relatively homogeneous). Although this may be unrealistic, for our purposes we believe it is reasonable considering the low contribution of nonsymbiotic N fixation relative to symbiotic N fixation in systems where both components have been studied.

2.4. Modeling Methods

Data on fluxes of and controls over BNF in natural ecosystems are fairly sparse, and data that give ecosystem-average fluxes (as opposed to data from stands containing symbiotic fixers or on a species basis) are even more rare. In addition, we had no site-level data on potential correlates and controls of BNF across sites from the N fixation literature. Therefore we compared our compilation of measurements to estimates of BNF (symbiotic plus nonsymbiotic) generated by a global model of terrestrial biogeochemistry, the Century model, and we used estimates of NPP and ET from this model in analyzing the literature results [*Ojima et al.*, 1994; *Schimel et al.*, 1997; *Parton et al.*, 1987]. Century, to our knowledge, is the only ecosystem model that explicitly computes the principal input and loss fluxes for N. A full description of Century is found in the literature by *Parton et al.* [1987, 1993] and *Schimel et al.* [1996, 1997], and is available at (http://www.nrel.colostate.edu/PROGRAMS/MODELING/CENTURY/CENTURY.html). In Century, N fixation is computed using very simple routines, reflecting the sparse data and low degree of synthesis in BNF studies. The first fixation flux is computed by a simple regression on evapotranspiration (Nfix = 0.006 × (ET - 40)). This allows high fixation in moist, warm regions or periods and provides the bulk of N inputs in rain forest ecosystems. This relationship is not derived from any thorough, mechanistic understanding but captures phenomenologically the assumption that most observations of high rates of BNF are from humid settings with relatively high evapotranspiration [e.g., *Boring and Swank*, 1988]. The second fixation flux built into Century is estimated by computing a potential rate of fixation, using ecosystem-specific maximum rates of N fixation per unit NPP (based on literature values), multiplied by the amount of NPP. Thus, in Century, as NPP increases, potential N fixation increases, leading to a codependency with carbon uptake. However, in this second equation, N fixation decreases as N available from other sources increases [*Vitousek and Howarth*, 1991; *Ojima et al.*, 1994; *Eisele et al.*, 1989], reflecting the energetic expense of BNF relative to root uptake. This second equation provides substantial N inputs in frequently burned savanna and shrubland/chaparral ecosystems but fails in rain forests where large amounts of N circulate, causing this equation to reduce N fixation. The two equations are added together in Century to compute the BNF flux.

3. Results and Discussion

3.1. Alpine Tundra (1) and Moist Tundra (2)

The low-temperature regimes of high-latitude/high-altitude systems reduce biological processes associated with N fixation compared with rates in temperate ecosystems [*Van Cleve and Alexander*, 1981]. Evidence suggests that free-living bacteria (e.g., *Nostoc commune*, *Gleotrichia* spp.) are the dominant N fixing organisms in tundra ecosystems [*Solheim et al.*, 1996; *Lennihan et al.*, 1994; *Chapin et al.*, 1990]. Rates are extremely variable, ranging from 0.40 to 3.0 kg N ha^{-1} yr^{-1} (Table 2a). In addition, cyanobacteria living as cryptogamic crusts or in association with bryophytes may contribute to N fixation [*Solheim*, 1996].

Table 2a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Moist Tundra (1) and Alpine Tundra (2) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1} Symbiotic (% Cover)	Nonsymbiotic	Method	Source
Marion Island, Antarctica	mire/grassland	-	0.042	C_2H_2	*Smith*, [1988]
Truelove Island, Canada	sedge/moss meadows	-	0.130	C_2H_2	*Babb and Whitfield*, [1977]
Signy Island, Antarctica	mire/grassland	-	0.240	C_2H_2	*Christie*, [1987]
Stordalen, Sweden	mire	-	0.200	C_2H_2	*Rosswall and Granhall*, [1980]
Truelove Island, Canada	sedge/moss meadows	-	0.300	C_2H_2	*Chapin et al.*, [1990]
Alaska, U. S.	wet meadow tundra	-	0.070	unspecified	*Van Cleve and Alexander*, [1981]
Alexandra Fjord, Sweden	arctic sedge meadow	-	0.080	C_2H_2	*Henry and Svoboda*, [1986]
Niwot Ridge, CO (U. S.)	sedge/moss meadows	0.490 (9)	-	^{15}N	*Bowman et al.*, [1996]

Table 2b. Data-Based Estimates of N Fixation in Moist Tundra (1) and Alpine Tundra (2) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	0.490	0.152		
Standard deviation	-	0.097		
Geometric mean	-	0.123		
Variance	-	0.009		
3% cover	0.163	0.123	0.286	2.86
9% cover	0.490	0.123	0.613	6.13
15% cover	0.817	0.123	0.940	9.40

In local regions, symbiotic N fixation may be important, however actual data-based estimates are extremely rare. *Bowman* [1996] found that *Trifolium* was an important source of N fixation in alpine tundra regions, contributing 5.0 kg N ha^{-1} yr^{-1}, based on *Trifolium* coverage of ~9% (Table 2a). However *Trifolium* abundance in tundra ecosystems is highly variable, ranging from 2 to 20% (*May and Webber*, 1982). Therefore, based on published data, our best estimate of N fixation by symbiotic N fixers is between 1.6 and 8.2 kg ha^{-1} yr^{-1}, and total nitrogen input via biological fixation ranges from 2.8 to 9.4 kg N ha^{-1} yr^{-1} (Table 2b). This compares to inputs of 0.3-2.5 kg N ha^{-1} yr^{-1} in precipitation in many arctic sites [*Van Cleve and Alexander,* 1981]. Thus, in some sites, N fixation may provide the dominant N input, while, in others, the dominant source of N may be precipitation. In any case, N inputs into tundra ecosystems are consistently low relative to many other systems.

3.2. Boreal Forests (3) and Boreal Woodlands (4)

In boreal forest and boreal woodland ecosystems, the majority of nitrogen accretion through BNF is contributed by heterotrophic cyanobacteria, either free-living or symbiotic in lichens, or in association with bryophytes [*Alexander and Billington,* 1986; *Weber and Van Cleve,* 1981; *Hendrickson,* 1990]. There are also some N-fixing higher plants in northern areas such as *Alnus* spp. and *Dryas* spp., as well as a number of indigenous legumes, but these are generally not quantitatively important in true arctic regions or in taiga [*Alexander and Billington,* 1986]. Despite the enormous extent of boreal forest systems, previously measured rates of N fixation from different regions are consistently very low (Table 3a). Nitrogen additions in precipitation are also consistently low, owing to the relative isolation of these systems from areas of industrial activity [*Van Cleve and Alexander,* 1981].

Table 3a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Boreal Forest (3) and Boreal Woodland (4) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}				Method	Source
		Symbiotic (% Cover)	Nonsymbiotic Soil	Nonsymbiotic Lichens	Total		
Central Sweden	spruce/pine	-	0.093	-	-	C_2H_2	*Nohrstedt,* [1985]
Alaska, U. S.	black spruce	-	0.100	-	-	C_2H_2	*Alexander and Billington,* [1986]
Ontario, Canada	jack pine	-	0.025	-	-	C_2H_2	*Hendrickson,* [1990]
British Columbia, Canada	lodgepole pine	-	0.280	-	-	C_2H_2	*Hendrickson and Burgess,* [1989]
British Columbia, Canada	firs/bryophytes/ lichens	0.030 (11)	0.030	0.05	-	C_2H_2	*Blundon and Dale,* [1990]
Umeå, Sweden	pine forest	-	-	0.10	-	C_2H_2	*Huss-Danell,* [1976]
Hardangervidda, Norway	birch forest	unspecified	unspecified	unspecified	0.165*	unspecified	*Van Cleve and Alexander,* [1981]
Hardangervidda, Norway	lichen heath	unspecified	unspecified	unspecified	0.056*	unspecified	*Van Cleve and Alexander,* [1981]
Fairbanks, Alaska (U. S.)	spruce forest	unspecified	unspecified	unspecified	0.007*	unspecified	*Van Cleve and Alexander,* [1981]
Kevo, Finland	pine forest	unspecified	unspecified	unspecified	0.350*	unspecified	*Van Cleve and Alexander,* [1981]
Kevo, Finland	birch forest	unspecified	unspecified	unspecified	0.139*	unspecified	*Van Cleve and Alexander,* [1981]

*Total N fixation estimates reported in the literature, and provided for comparison only.

Table 3b. Data-Based Estimates of N Fixation in Boreal Forest (3) and Boreal Woodland (4) Ecosystems

	N Fixation Rate g N m^{-2} yr^{-1}				N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic Soil	Nonsymbiotic Lichens	Total	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	0.030	0.106	0.075	0.150*	0.150*	1.50*
Standard deviation	-	0.103	0.035	0.132*		
Geometric mean	-	0.072	0.071	0.079*	0.079*	0.79*
Variance	-	0.011	0.001	0.017*		
4% cover	0.011	0.072	0.075	0.158	0.158	1.58
11% cover	0.030	0.072	0.075	0.177	0.177	1.77
18% cover	0.049	0.072	0.075	0.196	0.196	1.96

*Total N fixation estimates reported in the literature, and provided for comparison only.

We estimate that BNF in boreal forest ecosystems contributes between 1.5 and 2.0 kg N ha^{-1} yr^{-1} (Table 3b). This rate is similar to total nitrogen exports in rivers from undisturbed sites in eastern Canada (0.4-1.0 kg N ha^{-1} yr^{-1}, with a median value of 0.8 kg N ha^{-1} yr^{-1} [*Clair et al.,* 1994]), suggesting that our estimate is reasonable. It is likely that cold temperatures and low precipitation during the growing season restricts biological activity in high latitude systems, thus contributing to the observed low N inputs in boreal ecosystems [*Alexander,* 1981].

3.3. Temperate Mixed Forests (5), Temperate Coniferous Forests (6), Temperate Deciduous Forests (7), and Temperate Forested Floodplains (17)

Nitrogen fixation in temperate forests is fairly well studied, owing to the fact that primary productivity in temperate ecosystems is thought to be N limited, [*Vitousek and Howarth,* 1991] and because of the abundance of research institutions located in close proximity to temperate forests. Current data do not show substantial differences in rates of N fixation between coniferous and deciduous forests [*Boring et al.,* 1988], and therefore we have grouped temperate deciduous, temperate coniferous, and temperate mixed forests into one group (temperate forests).

Both symbiotic and asymbiotic forms of N fixation are important in temperate forests. However, published rates of N fixation by overstory woody plants (e.g., *Alnus incana, Robinia pseudocacacia*) and by understory legumes (e.g., *Lupinus* spp.) overestimate the average for all forests, since these species are abundant in only a small percentage of temperate forests or are prominent only in early successional forests [*Fahey et al.,* 1985; *Boring and Swank,* 1984]. When symbiotic N fixing woody plants are present in early successional forests, rates of N fixation in temperate forests can be quite high relative to other potential sources of N fixation in temperate forests. Rates of N fixation estimated from chronosequence studies range from 33.0 to 150.0 kg N ha^{-1} yr^{-1} in pure stands of these species, on the basis of extremely dense coverages of ~60% [*Binkley et al.,* 1994; *Boring and Swank,* 1984]. However, these species are generally abundant only on clear-felled areas, abandoned pastures, and disturbed roadsides [*Boring and Swank,* 1984], all of which are relatively rare over temperate forest ecosystems as a whole. To reflect the scarcity of abandoned lands available for colonization by these species, we calculate N fixation rates by symbiotic overstory species arbitrarily assuming lower coverages of 1, 5, and 10% over these ecosystems, and we suggest that these species fix between 1.08 and 10.83 kg N ha^{-1} yr^{-1} in temperate forested ecosystems.

Rates of N fixation by understory plant genera (e.g., *Lupinus, Ceanothus, Myrica, Bossiaea,* and *Hedysarum*) from a diversity of temperate forest ecosystems range widely from 1.0 to 160.0 kg N ha^{-1} yr^{-1} (Table 4a). Reported coverages of these species range from 5 to 20%, and the average from published estimates is 9.8% (Table 4a). Thus we assume a geometric mean rate of 7.3 kg N ha^{-1} yr^{-1} is distributed over 3, 10, and 17% of the temperate forest landscape to generate rates of N fixation (Table 4a).

The best studied pathway of N fixation in temperate forests is asymbiotic fixation in soils and decaying wood. Several studies have shown rates of asymbiotic nitrogen fixation to increase with accumulations of woody debris [*Harvey et al.,* 1989, *Jurgensen et al.,* 1992] and logging slash [*Waide et al.,* 1988]. However, aside from the relationship with woody debris noted above, there is no clear relationship between asymbiotic nitrogen fixation and forest age across studies [*Grant and Binkley,* 1987; *DiStefano and Gholz,* 1989; *Roskowski,* 1977; *Boring et al.,* 1989]. Therefore we assigned a single mean value 1.48 kg N ha^{-1} yr^{-1} (potential range 1.0 to >25.0 kg N ha^{-1} yr^{-1}) to characterize rates of asymbiotic nitrogen fixation in temperate forest soils and woody debris. This value represents the sum of geometric means of N fixation in litter (0.3 kg N ha^{-1} yr^{-1}), soil (0.64 kg N ha^{-1} yr^{-1}), and decaying woody debris (0.54 kg N ha^{-1} yr^{-1}) (Tables 4a and 4b).

Asymbiotic nitrogen fixation on the bole and in the canopy is perhaps the most poorly studied biological vector of nitrogen inputs to temperate forests. Considerable difficulties exist in both the accurate estimation of rates in the field and in the extrapolation from individual measurements to entire forests [see *Sollins et al.,* 1980]. From *Roskowski,* [1977], *Boring et al.* [1988], *Sollins et al.* [1980], *Todd et al.* [1978], and *Tjepkema* [1979], we estimate an average rate of nitrogen fixation in the phyllosphere of 1.8 kg N ha^{-1} yr^{-1} (1.2-2.8 kg N ha^{-1} yr^{-1}).

Table 4a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Temperate Mixed Forest (5), Temperate Coniferous Forest (6), Temperate Deciduous Forest (7), Temperate Forested Floodplain (17), and Temperate Broadleafed Evergreen Forest (21) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}						Method	Source
		Symbiotic (%Cover)		Nonsymbiotic					
		Trees	Understory	Litter	Soil	Wood	Phyllosphere		
Southeast U. S.	mixed-deciduous forest	4.80 (60)	-	-	-	-	-	N accumulation	*Boring and Swank,* [1984]
Southeast U. S.	mixed-deciduous forest	7.50	-	-	-	-	-	N accumulation	*Boring and Swank,* [1984]
Southeast U. S.	mixed-deciduous forest	3.30	-	-	-	-	-	N accumulation	*Boring and Swank,* [1984]
Northwest U. S.	alder stand	15.00 (NA)	-	-	-	-	-	C_2H_2	*Binkley et al.,* [1994]
Northwest U. S.	alder stand	4.00 (NA)	-	-	-	-	-	C_2H_2	*Luken and Fonda,* [1983]
Northeast U. S.	peat bog	3.50 (NA)	-	-	-	-	-	unspecified	*Schwintzer,* [1983]
Western Australia	eucalyptus forest	-	2.400 (NA)	-	-	-	-	C_2H_2	*Adams and Attiwill,* [1984]
Central Rocky Mountains, U. S.	aspen	-	0.630 (NA)	-	0.390	-	-	C_2H_2	*Skujins et al.,* [1987]
Southwest Australia	eucalyptus forest	-	0.793 (5)	-	-	-	-	C_2H_2	*Grove and Malajczuk,* [1992]
New Zealand	pine forest	-	8.000 (20)	-	-	-	-	N accumulation	*Baker et al.,* [1986]
Canadian Rockies	lodgepole pine forest	-	0.275 (NA)	-	-	-	-	C_2H_2	*Hendrickson and Burgess,* [1989]
Southeast U. S.	slash pine plantatation	-	1.060 (8)	-	-	-	-	N accumulation	*Permar and Fisher,* [1983]
New Zealand	lupin-marram stand	-	16.000 (NA)	-	-	-	-	N accumulation	*Gadgil,* [1971]
Central Rocky Mountains, U. S.	lodgepole pine forest	-	0.100 (5)	0.030	-	-	-	C_2H_2	*Fahey et al.,* [1985]
Western Australia	jarrah forest	-	0.600 (NA)	-	-	-	-	C_2H_2	*Hingston et al.,* [1982]
Canadian Rockies	spruce forest	-	0.165 (11)	-	-	-	-	C_2H_2	*Blundon and Dale,* [1990]
Southeast U. S.	piedmont forst	-	-	0.000	-	-	-	C_2H_2	*Grant and Binkley,* [1987]
Southeast U. S.	slash pine	-	-	0.010	0.250	0.100	-	C_2H_2	*DiStefano and Gholz,* [1989]
Southwest Australia	eucalyptus forest	-	-	0.250	-	-	-	C_2H_2	*O'Connel and Grove,* [1987]
Coastal B. C., Canada	fir/hemlock/cedar	-	-	0.030	-	0.060	-	C_2H_2	*Cushon and Feller,* [1989]
Northeast U. S.	mixed-deciduous forest	-	-	-	0.020	0.004	-	C_2H_2	*Tjepkema,* [1979]
Eastern Austria	alpine vegetation	-	-	-	0.280	-	-	C_2H_2	*Zechmeister-Boltenstern and Kinzel,* [1990]
Northwest U. S.	douglas fir	-	-	0.074	-	-	-	C_2H_2	*Heath et al.,* [1987.
Northwest U. S.	douglas fir	-	-	0.033	0.028	0.500	0.280	N accumulation	*Sollins et al.,* [1980]
Southern Ontario, Canada	mixed deciduous, confers	-	-	-	0.086	-	-	C_2H_2	*Hendrickson,* [1990]
Central Sweden	mixed deciduous, conifers	-	-	-	0.093	-	-	C_2H_2	*Nohrstedt,* [1985]
Northwest U. S.	mixed conifers	-	-	-	-	0.100	-	C_2H_2	*Jurgensen et al.,* [1992]
Northwest U. S.	mixed conifers	-	-	-	-	0.010	-	C_2H_2	*Harvey et al.,* [1989]
Southeast U. S.	mixed deciduous forest	-	-	-	-	0.090	-	C_2H_2	*Cornaby and Waide,* [1973]
Northwest U. S.	mixed conifers	-	-	-	-	0.070	-	C_2H_2	*Larsen et al.,* [1978]
Southeast U. S.	mixed deciduous forest	-	-	-	-	-	0.120	unspecified	*Todd et al.,* [1978]

Table 4b. Data-Based Estimates of N Fixation in Temperate Mixed Forest (5), Temperate Coniferous Forest (6), Temperate Deciduous Forest (7), Temperate Forested Floodplain (17), and Temperate Broadleafed Evergreen Forest (21) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}						N Fixed,	N Fixed,
	Symbiotic (%Cover)		Nonsymbiotic				g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
	Trees	Understory	Litter	Soil	Wood	Phyllosphere		
Arithmetic mean	6.350	2.946 (9.8)	0.099	0.165	0.117	0.200		
Standard deviation	4.505	5.177	0.123	0.118	0.159	0.113		
Geometrric mean	6.497	0.732	0.030	0.064	0.054	0.183		
Variance	202.99	268.03	0.153	0.153	0.254	0.128		
Coverage (Trees/Understory)								
1%/3%	0.108	0.220	0.030	0.064	0.054	0.183	0.659	6.59
5%/10%	0.541	0.732	0.030	0.064	0.054	0.183	1.604	16.04
10%/17%	1.083	1.244	0.030	0.064	0.054	0.183	2.658	26.58

On the basis of estimates of N fixation within each separate component, we estimate that biological N fixation currently contributes between 6.5 and 26.6 kg N ha^{-1} yr^{-1} to temperate forests and temperate forested floodplains, depending on the abundance of canopy and understory symbiotic N fixing species (Table 4b). This range is similar to the range of 1-20 kg N ha^{-1} yr^{-1} reported by *Todd et al.* [1978] and reflects the notion that peak rates of N fixation (i.e. 10-30 kg N ha^{-1} yr^{-1}) occur in early to intermediate stages of forest and may decline thereafter to much lower values (i.e., 1-3 kg ha^{-1} yr^{-1}) [*Waide et al.*, 1988; *Likens et al.*, 1977; *Boring et al.*, 1988].

3.4. Tall/Medium Grasslands(8), Short Grasslands (9), Temperate Nonforested Floodplains (18), and Temperate Savannas (20)

Leguminous species are not a dominant component of the vegetation in most grasslands, frequently accounting for between 1 and 5% of the primary productivity, and therefore contributing little nitrogen via N fixation to grassland ecosystems [*Woodmansee et al.*, 1981]. Also, legumes that are present may not be nodulated or may be only sparsely nodulated [*Woodmansee et al.*, 1981]. However, following disturbances in unimproved annual grasslands, N fixation by legumes may be large. Nonetheless, such inputs are extremely variable in space and time, with large inputs (i.e. >50 kg N ha^{-1} yr^{-1}) in some sites and insignificant inputs in others [*Woodmansee et al.*, 1981]. Rates of symbiotic N fixation range from 0.1 to 10.0 kg N ha^{-1} yr^{-1} [*Woodmansee et al.*, 1981; *Robertson and Rosswall*, 1986].

The principal contributors of biologically fixed N in grasslands appear to be asymbiotic bacteria and heterocystous bacteria [*DuBois and Kapustka*, 1983]. *Eisele et al.* [1989] reported high rates of nonsymbiotic fixation corresponding to higher phosphorus (P) availability following prairie burning.

Table 5a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Tall/Medium Grassland (8), Short Grassland (9), Temperate Nonforested Floodplain (18), and Temperate Savanna (20) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}			Method	Source
		Symbiotic (% Cover)	Algal Nonsymbiotic	Other Nonsymbiotic		
North America	shortgrass steppe	0.025 (NA)	-	0.025	unspecified	*Whitehead*, [1995]
North America	mixed prairie	0.025 (NA)	-	0.025	unspecified	*Whitehead*, [1995]
North America	tallgrass prairie	0.025 (NA)	-	0.025	unspecified	*Whitehead*, [1995]
Unspecified	annual grassland	0.01 (NA)	0.010	-	unspecified	*Woodmansee et al.*, [1981]
Unspecified	annual grassland	0.01 (NA)	0.020	-	unspecified	*Woodmansee et al.*, [1981]
North America	short- tall-grass prairie	-	0.350	0.080	C_2H_2	*Kaputsa and DuBois*, [1987]
West Africa	subdesert grassland	-	0.100	0.600	literature review	*Robertson and Rosswall*, [1986]
United Kingdom	upland pasture	0.8 (NA)	-	-	unspecified	*Whitehead*, [1995]
North America	tallgrass prairie	-	0.820	-	C_2H_2	*DuBois and Kaputsa*, [1983]
North America	tallgrass prairie	-	2.100	-	nitrogenase activity	*Eisele et al.*, [1989]
West Africa	subdesert grassland	1.000 (NA)	1.000	1.000	literature review	*Robertson and Rosswall*, [1986]

Table 5b. Data-Based Estimates of N fixation in Tall/Medium Grassland (8), Short Grassland (9), Temperate Nonforested Floodplain (18), and Temperate Savanna (20) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}			N Fixed,	N Fixed,
	Symbiotic	Algal Nonsymbiotic	Other Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	0.271	0.629	0.251		
Standard deviation	0.434	0.758	0.393		
Geometric mean	0.053	0.198	0.019		
Variance	0.188	0.575	0.155		
5% cover	0.018	0.198	0.019	0.235	2.35
15% cover	0.053	0.198	0.019	0.270	2.70
25% cover	0.088	0.198	0.019	0.305	3.05

DuBois and Kapustka [1983] also reported high rates of asymbiotic fixation. An estimate of N fixation in grasslands is complicated by the fact that tropical grasslands are often managed and contain N fixing forage plants [*Cadisch et al.*, 1994]. In addition, fire greatly affects the abundance of N fixing species in grasslands, with symbiotic nitrogen fixation being more important immediately following a fire. We estimate that symbiotic species may contribute between 0.2 and 0.9 kg N ha^{-1} yr^{-1} to grasslands, and that an additional 2.2 kg N ha^{-1} yr^{-1} is added via nonsymbiotic N fixation to grasslands worldwide. Thus between 2.3 and 3.1 kg N ha^{-1} yr^{-1} are added to grassland via biological fixation (Tables 5a and 5b). These rates are also used to represent N fixation in temperate savannas and temperate nonforested floodplains because data in these ecosystems are unavailable and because they are likely similar in composition to temperate grasslands.

3.5. Tropical Savannas (10) and Wet Savannas (19)

In tropical savannas, N fixation by legume nodules probably provides the major input of nitrogen fixed per unit area annually, although there is also evidence of fixation by soil algae [*Bate and Gunton,* 1982; *Stewart et al.,* 1978]. These systems contain a high proportion of trees in the genus *Acacia* or other members of the Mimosaceae family [*Schulze et al.,* 1991]. Therefore it is possible that N fixation in these systems could be very high. However, many nitrogen fixers in this system show large species specific variation in N fixation rates, and species distribution and abundance varies widely over large areas of savannas [*Schulze et al.,* 1991].

Assuming asymbiotic N fixation contributes 9.5 kg N ha^{-1} yr^{-1} and rates of symbiotic N fixation range from 0.7 to 34.5 kg N ha^{-1} yr^{-1} [*Stewart et al.,* 1978; *Bate and Gunton,* 1982], we estimate that N fixation in tropical and wet savannas ranges from 16.3 to 44.0 kg N ha^{-1} yr^{-1} (Tables 6a and 6b). These estimates are greatly influenced by the high rates of symbiotic N fixation commonly observed in tropical savannas; however, these estimates, particularly the upper-bound estimate, may overestimate N fixation over the entirety of these systems.

Although N inputs from atmospheric deposition vary widely in tropical savannas, the amount of N entering them via N fixation appears to greatly exceed atmospheric inputs, which typically range from 2 to 5 kg N ha^{-1} yr^{-1} depending on the total amount of rainfall [*Bate,* 1981]. This suggests that biological N fixation may be the largest source of N in savanna ecosystems.

3.6. Arid Shrublands (11)

The N fixing genus *Prosopis* (mesquite) is the dominant vegetation on millions of square kilometers of arid woodlands in North and South America [*Rundel et al.,* 1982; *Johnson and Mayeux,* 1990]. *Rundel et al.* [1982] reported that net nitrogen uptake by above ground *Prosopis* is 69.8 kg N ha^{-1}

Table 6a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Tropical Savanna (10) and Wet Savanna (19) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate (g N m^{-2} yr^{-1})		Method	Source
		Symbiotic (% Cover)	Nonsymbiotic		
Nigeria	unspecified	-	3.000	C_2H_2	*Stewart et al.,* [1978]
Nigeria	tallgrass savanna	3.800 (NA)	-	C_2H_2	*Bate and Gunton,* [1981]
South Africa	unspecified	9.000 (NA)	-	C_2H_2	*
Nigeria	unspecified	0.300 (NA)	0.300	C_2H_2	*Bate and Gunton,* [1981]
West Africa	unspecified	3.000 (NA)	-	C_2H_2	*Stewart et al.,* [1978]
Brazil	*Paspalum* spp.	2.850 (NA)	-	unspecified	*Dobereiner,* [1977]
Ivory Coast	unspecified	0.900 (NA)	-	unspecified	*Balandreau and Villemin,* [1973]

*N. Grobbelaar and M. W. Rosch, unpublished data, 1979.

Table 6b. Data-Based Estimates of N Fixation in Tropical Savanna (10) and Wet Savanna (19) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	3.308	1.103		
Standard deviation	3.092	1.649		
Geometric mean	2.071	0.208		
Variance	9.558	2.719		
5% cover	0.690	0.949	1.639	16.39
15% cover	2.071	0.949	3.020	30.20
25% cover	3.451	0.949	4.400	44.00

yr^{-1} on a system wide basis, and of that, as much as 50% may come from N fixation. In addition, *Jarrell and Virginia* [1990] have shown that *Prosopis* dominated communities can accumulate very large quantities of soil N. However, *Johnson and Mayeux* [1990] showed that N fixation in *Prosopis* is extremely variable (range is 30-97.5 kg N ha^{-1} yr^{-1}; Table 7a) and that in some cases nodulation did not result in any measurable fixation [*Shearer et al.*, 1983; *Jarrell and Virginia*, 1990; *Rundel et al.*, 1982; *Johnson and Mayeux*, 1990]. In addition, these values were obtained in extremely densely covered sites (i.e., 30-50%). However, estimates suggest that *Prosopis* coverages over the entire landscape vary from 10-20% [*Johnson and Mayeux*, 1990].

To account for the variability in the abundance of *Prosopis* and the activity of the root nodules, we scaled our estimates of symbiotic N fixation from an empirically derived coverage estimate of 40% and estimate that symbiotic fixation by leguminous species adds 6.11-30.57 kg N ha^{-1} yr^{-1} to arid shrublands (Table 7b). In addition, we estimate that nonsymbiotic fixation by *Azospirillium* and/or *Azotobacter* associations in the rhizosphere of grasses such as *Paspalum*, *Digitaria* and *Panicum* contributes 3.4 kg N ha^{-1} yr^{-1} to these systems, for a total input of 9.4 to 33.9 kg N ha^{-1} yr^{-1} (Table 7b).

3.7. Tropical Evergreen Forests (12)

Despite the vast area of tropical forests, estimates of N fixation (particularly rates of symbiotic N fixation and legume abundance) in these systems are extremely rare, and those that are available are highly variable. Many studies have investigated individual components in selected ecosystems, but few have attempted to categorize the total input of nitrogen due to N fixation in a site or to investigate N fixation on a variety of sites characterized by different soil types or biomass and nutrient regimes [*Vitousek and Sanford*, 1986]. However, the few studies that do address N fixation over a variety of landscapes and soil types report an extremely wide range of rates from 1 to > 240 kg N ha^{-1} yr^{-1} [*Sylvester-Bradley et al.*, 1980; *Bruijnzeel*, 1991].

Most current evidence suggests that both symbiotic and asymbiotic nitrogen fixation are important in tropical evergreen forests. Reports of nonsymbiotic fixation by epiphytes and canopy lichens vary from 0.5 to 60.0 kg N ha^{-1} yr^{-1} [*Goosem and Lamb*, 1986; *Edmisten*, 1970]. Fixation of N in the litter and soil layer is also important, with rates ranging from 2.4 to 20.0 kg N ha^{-1} yr^{-1} [*Sylvester-Bradley et al.*, 1980; *Forman*, 1975]. Legumes are not dominant in the Amazonian rain forest, although they are among the five best-represented families [*Sylvester-Bradley et al.*, 1980]. Therefore legumes have been considered an important source of nitrogen in tropical rain forests. The proportion of legume trees growing in tropical forests varies greatly, and, in certain areas, N fixation by legumes may lead to high-nitrogen content in soils [*Jenny*, 1950]. Rates of symbiotic N fixation in tropical forests range from <2 kg N ha^{-1} yr^{-1} in sites on oxisols to >200 kg N ha^{-1} yr^{-1} in sites on alluvial soils [*Salati et al.*, 1982; *Sylvester-Bradley et al.*, 1980].

On the basis of the geometric means of estimates of symbiotic and nonsymbiotic N fixation in tropical forests, we estimate that biological nitrogen fixation could contribute between 14.7 and 36.1 kg N ha^{-1} yr^{-1} to tropical evergreen forests (Tables 8a and 8b). These values include a nonsymbiotic input of 9.4 kg N ha^{-1} yr^{-1} from soil/litter (6.57 kg N ha^{-1} yr^{-1}) and canopy lichens (2.83 kg N ha^{-1} yr^{-1}), as well

Table 7a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Arid Shrubland (11) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}		Method	Source
		Symbiotic (% Cover)	Nonsymbiotic		
Southwest U. S.	Mesquite (*Prosopis*) woodland	3.00 (30)	-	N accumulation	*Rundel et al.*, [1982]
Southwest U. S.	Mesquite (*Prosopis*) woodland	4.00 (NA)	-	cation accumulation	*Jarrell and Virginia*, [1990]
Southwest U. S.	Mesquite (*Prosopis*) woodland	9.75 (50)	-	nodulation	*Johnson and Mayeux*, [1990]

Table 7b. Data-Based Estimates of N Fixation in Arid Shrubland (11) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	5.583	-		
Standard deviation	3.643	-		
Geometric mean	4.891	0.336*		
Variance	13.271	-		
5% cover	0.611	0.336*	0.947	9.47
15% cover	1.868	0.336*	2.204	22.04
25% cover	3.057	0.336*	3.393	33.93

*Due to a lack of published estimates of non-symbiotic N_2-fixation in arid shrublands, this value is obtained from estimates of N-fixation in desert ecosystems (Tables 11a and 11b).

as symbiotic inputs which reflect possible variability in coverages of symbiotic species. Atmospheric inputs of nitrogen to the Amazon basin have been estimated at 6 kg N ha^{-1} yr^{-1}, and the available data suggest this input is balanced by hydrologic outputs of 5-6 kg N ha^{-1} yr^{-1} [*Lewis et al.,* 1999; *Salati et al.,* 1982]. Thus a balanced N budget requires a total flux of N trace gases (via nitrification, denitrification, and/or volatilization) that is equal to N fixation rates.

3.8. Tropical Forested Floodplains (14) and Tropical Nonforested Floodplains (16)

The Amazon floodplain (várzea) is one of the most fertile and productive regions within the Amazon Basin, and rates of nitrogen fixation by várzea plants, including leguminous and non-leguminous species, emergent, semi-aquatic grasses, and free-living periphyton and plankton, are extremely high [*Martinelli et al.,* 1992; *Doyle and Fisher,* 1982; *Sylvester-Bradley et al.,* 1980]. For example, *Sylvester-Bradley et al.* [1980] noted that nodules on some floodplain trees were so abundant that it was nearly impossible to see the roots. Here N fixation rates in the várzea have been measured as high as 243 kg N ha^{-1} yr^{-1} [*Sylvester-Bradley et al.,* 1980]. However, on the basis of the high variability of nodule abundance and activity of the species investigated, we believe that 243 kg N ha^{-1} yr^{-1} is a maximum (i.e., we assume this rate is based on 100% coverage of N fixing species). Therefore our conservative (5% coverage) estimate of symbiotic N fixation in tropical floodplain ecosystems globally is 12.2 kg N ha^{-1} yr^{-1}; our "best-guess" (15% coverage) estimate is 36.5 kg N ha^{-1} yr^{-1}; and our upper-bound estimate of N fixation in tropical floodplains is 60.75 kg N ha^{-1} yr^{-1}.

The rate of N fixation via periphyton and plankton in tropical nonforested floodplains is estimated at 6.3 kg N ha^{-1} yr^{-1} [*Doyle and Fisher,* 1994]. In addition, N fixing aquatic grasses such as *Paspalum* are abundant in tropical nonforested floodplains, and have been shown to fix 28.5 kg N ha^{-1} yr^{-1} [*Martinelli et al.,* 1992; *Dobereiner,* 1977]. Therefore we estimate that N fixation in these ecosystems contributes between 15.8 (5% coverage of symbiotic N fixers) and 53.8 kg N ha^{-1} yr^{-1} (25% coverage of symbiotic N fixers) (Tables 9a and 9b).

3.9. Xeromorphic Forests/Woodlands (13)

The xeromorphic woodlands that occur in West Africa (e.g., Kenya) and South America (eastern Brazil/northeastern Argentina) are variable in species composition, structure, and density [*Felfili and Da Silva,* 1993]. Nonetheless, legumes and myrtles are abundant in all of these systems, suggesting that rates of N fixation are high [*Sprent et al.,* 1996]. This is supported by ^{15}N data, which showed significant N fixation in species of *Chamaecrista*, *Mimosa*, and *Calliandra*, *Leucaena*, and *Casuarina* spp., which are all abundant in xeromorphic woodlands globally [*Sprent et al.,* 1996].

In spite of the likely importance of N fixation in

Table 8b. Data-Based Estimates of N Fixation in Tropical Evergreen Forest (12) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}			N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic Soil/Litter	Epiphytes/ Lichens	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	1.600	0.886	1.340		
Standard deviation	-	0.716	3.323		
Geometric mean	1.600	0.657	0.283		
Variance	-	0.512	6.803		
5% cover	0.533	0.657	0.283	1.473	14.73
15% cover	1.600	0.657	0.283	2.540	25.40
25% cover	2.667	0.657	0.283	3.607	36.07

Table 8a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Tropical Evergreen Forest (12) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}			Method	Source
		Symbiotic (% Cover)	Nonsymbiotic Soil/Litter	Epiphytes/ Lichens		
New Guinea	tropical rain forest	-	-	0.050	C_2H_2	*Goosem and Lamb*, [1986]
Columbia	tropical rain forest	-	-	0.150	literature review	*Forman*, [1975]
Central Amazonia	tropical rain forest	-	0.245	-	C_2H_2	*Sylvester-Bradley et al.*, [1980]
Sri Lanka	tropical rain forest	-	0.800	-	C_2H_2	*Maheswaran and Gunatilleke*, [1990]
Central Amazonia	secondary forest	-	2.000	-	C_2H_2	*Sylvester-Bradley et al.*, [1980]
Northern Amazonia	tropical rain forest	1.600 (NA)	1.500	0.100	C_2H_2	*Jordan et al.*, [1983]
Kilauea Volcano, Hawaii	tropical rain forest	-	0.280	0.000	C_2H_2	*Vitousek*, [1994]
La Soufriere, Guadeloupe	cloud forest volcano	-	-	0.402	C_2H_2	*Sheridan*, [1991]
Vocanoes NP, Hawaii	tropical dry forest	-	0.490	-	C_2H_2	*Ley and D'Antonio*, [1998]
Unspecified	tropical rain forest	-	-	6.000	unspecified	*Edmiston*, [1970]

xeromorphic woodlands, there are few rate estimates in these systems. Because of the lack of estimates and on the basis of the similarities in species composition between tropical deciduous forests and xeromorphic forests [e.g., *Ambasht and Srivastava*, 1994; *Yoneyama et al.*, 1993], we apply a maximum nitrogen fixation rate of 34.0 and a minimum of 9.4 kg N ha^{-1} yr^{-1} to characterize xeromorphic forests and woodlands (Tables 10a and 10b).

3.10. Deserts (15)

Primary productivity in deserts is generally very low, owing to the limiting factors of water stress and low nitrogen availability [*Rundel et al.*, 1982; *Wallace et al.*, 1978]. Consequently, the largest source of nitrogen in desert systems is provided by biological fixation [*Metting*, 1991]. Both symbiotic and asymbiotic forms of N fixation are important in deserts. Legumes are often present in desert communities and can provide large localized inputs of nitrogen [*Crawford and Gosz*, 1982]. For example, in the American southwest *Prosopis glandulosa* fixes 2.3-15.0 kg N ha^{-1} yr^{-1} [*Rundel et al.*, 1982; *Johnson and Mayeux*, 1990]. In Australia, native desert legumes fix between 0.04 and 7.46 kg N ha^{-1} yr^{-1} [*Lawrie*, 1981]. However, unsuitable temperature and moisture often limit nodule development in desert legumes, and little is known on the rates of legume-*Rhizobium* N fixation in other desert ecosystems [*Crawford and Gosz*, 1982].

Associative symbioses in the rhizosphere and nonsymbiotic cyanobacteria are spatially more important sources of N fixation in deserts than symbiotic sources [*Herman et al.*, 1993; *West and Skujins*, 1977]. Surfaces of desert soils are often covered by cryptogamic crusts composed of fungi, lichens, and cyanobacteria, and nitrogen fixation by cyanobacteria-dominated crusts provides a significant input of nitrogen to many desert ecosystems worldwide [*West and Skujins*, 1977]. In the Great Basin desert, estimates of N fixation by cryptogamic crusts range from 10.0 to 100.0 kg N ha^{-1} yr^{-1} depending on environmental conditions [*Rychert and Skujins*, 1974]. On the basis of estimates of both symbiotic (1.5-7.5 kg N ha^{-1} yr^{-1}) and nonsymbiotic N fixation (3.3 kg N ha^{-1} yr^{-1}), we estimate that N fixation contributes between 4.8 and 10.8 kg N ha^{-1} yr^{-1} to desert ecosystems globally (Tables 11a and 11b).

3.11. Temperate Broadleafed Evergreen Forests (21)

The majority of the world's temperate broadleafed evergreen forests are located in Southeast Asia and South America, with smaller tracts in Eastern Australia. Increasing population,

Table 9a. Summary Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation Estimates in Tropical Nonforested Floodplain (16) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}		Method	Source
		Symbiotic (% Cover)	Nonsymbiotic		
Brazil	*Paspalum* spp.	2.850 (NA)	-	unspecified	*Dobereiner*, [1977]
Brazil	Amazon floodplain	-	0.630	C_2H_2	*Doyle and Fisher*, [1994]

Table 9b. Data-Based Estimates of N Fixation in Tropical Nonforested Floodplain (16) Ecosytems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
5% cover	0.950	0.630	1.580	15.80
15% cover	2.850	0.630	3.480	34.80
25% cover	4.750	0.630	5.380	53.80

coupled with an increase in the demand for timber has resulted in a decrease in area of these forests [*Domingo,* 1983]. They are composed mainly of rain forest-like dipterocarp species but are distinguished from evergreen tropical forests, as these more temperate forests experience cooler average temperatures and a more pronounced seasonality, with most of the rain falling during a 4-5 month period [*Domingo,* 1983].

We were unable to locate N fixation rates for temperate broadleafed evergreen forests in the literature; therefore, because of the similarity of climate and overall physiognomy of these forests to other temperate forests, our best estimate suggests that the remaining temperate broadleafed evergreen forests fix a minimum of 6.5 and a maximum of 26.6 kg N ha^{-1} yr^{-1} (i.e., rates equal to rates in other temperate forests; Tables 4a and 4b).

3.12. Mediterranean Shrublands (22)

Mediterranean ecosystems all share similar climates, with cool, moist winters and hot, dry summers [*Schlesinger et al.,* 1982]. The shrubland formations (matorral, chaparral, and maquis), which characterized these ecosystems, are common in central Chile, northern Mexico, and southern California [*Yates et al.,* 1982]. *Ceanothus* shrubs, which are common in Mediterranean shrublands, contribute to the nitrogen balance of these systems via symbiotic associations with the N fixer *Frankia* [*Kummerow et al.,* 1978]. We estimate that this symbiosis contributes 0.5 to 2.5 kg N ha^{-1} yr^{-1} to Mediterranean-type ecosystems (Table 12a). In addition, asymbiotic N fixation may provide an additional 1.0 kg N ha^{-1} yr^{-1} to these ecosystems [*Schlesinger et al.,* 1982]. Therefore we estimate that BNF contributes between 1.5 and 3.5 kg N ha^{-1} yr^{-1} to Mediterranean shrublands (Table 12b). Published rates of N fixation in European Mediterranean shrublands are unavailable, so we assume that this value is typical of these ecosystems worldwide.

3.13. Tropical Deciduous Forests (23)

Reported rates of N fixation in dry tropical deciduous forests are extremely rare, due to deforestation and conversion to other land uses such as savanna and cropland [*Srivastava and Singh,*

Table 10a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Xeromorphic Forest/Woodland (13) and Tropical Deciduous Forest (23) Ecosystems

Ecosystem Location	Vegetation type	N Fixation Rate, g N m^{-2} yr^{-1}		Method	Source
		Symbiotic (% Cover)	Nonsymbiotic		
Nigeria	mixed deciduous forest	3.000 (NA)	0.331	C_2H_2	*Stewart et al.,* [1978]
India	*Casuarina* plantation	1.760 (NA)	-	N accumulation	*Ambasht and Srivastava,* [1994]
India	*Casuarina* plantation	0.750 (NA)	-	N accumulation	*Ambasht and Srivastava,* [1994]

Table 10b. Data-Based Estimates of N Fixation in Xeromorphic Forest/Woodland (13) and Tropical Deciduous Forest (23) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	1.837	-		
Standard deviation	1.127	-		
Geometric mean	1.582	0.331		
Variance	1.270	-		
5% cover	0.612	0.331	0.943	9.43
15% cover	1.837	0.331	2.168	21.68
25% cover	3.062	0.331	3.393	33.93

Table 11a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation in Desert (15) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, g N m^{-2} yr^{-1}		Method	Source
		Symbiotic (% Cover)	Nonsymbiotic		
North America (Mojave Desert)	cryptogamic crusts		0.050	C_2H_2	*Rychert et al.*, [1978]
North America (Sonoran Desert)	cryptogamic crusts	-	0.900	C_2H_2	*Rychert et al.*, [1978]
North America (Sonoran Desert)	unspecified	2.950 (NA)	-	C_2H_2	*Rundel et al.*, [1982]
North America (Great Basin)	cryptogamic crusts	-	1.300	C_2H_2	*Crawford and Gosz*, [1982]
North America (Great Basin)	cryptogamic crusts	-	1.000	C_2H_2	*Rychert and Skujins*, [1974]
Australia	cryptogamic crusts	-	0.130	C_2H_2	*Metting*, [1991]
Australia	unspecified	0.067 (NA)	-	C_2H_2	*Lawrie*, [1981]
Africa (Kalahari Desert)	crytogamic crusts	-	0.190	C_2H_2	*Sharpe and Hendrickson*, [1987]

1991]. However, tropical and subtropical deciduous forests and woodlands are likely to have high rates of N fixation because high temperatures, moderate moisture, and fertile soils provide conditions conducive to N fixation [*Stewart et al.*, 1978]. Work by *Ambasht and Srivastava* [1994] suggests that actinorrhizal tree species such as *Casuarina* may contribute 7.5-17.6 kg N ha^{-1} yr^{-1} to tropical dry forests (see Tables 10a and 10b). In addition, it has been demonstrated that canopy lichens and epiphytes may be a source of nitrogen fixation in the canopies of tropical dry forests; however, the magnitude of this input is largely unknown [*Lugo and Scatena*, 1995]. Our best estimate is that BNF rates in dry tropical deciduous forests range from 9.4 to 34.0 kg N ha^{-1} yr^{-1} (see Table 10b).

3.14. Global Patterns of Terrestrial BNF

Woodmansee and Wallach [1981] postulated a strong relationship between climatic factors conducive to high productivity (such as high precipitation and air temperature) and the potential for significant N fixation by symbiotic species. In addition, since nitrogen fixation is an energetically "expensive" process [*Vitousek and Field*, 1999; *Vitousek and Howarth*, 1991], it stands to reason that it would be most important in systems where large amounts of energy as carbon are available for fixing organisms. These are likely to be systems with at least seasonally high solar radiation, precipitation, and resultant net primary productivity. ET provides information on both water and energy availability in an integrated fashion [*Rosenzweig*, 1968], and we believe that ET may relate to BNF as a correlate for the resources available to nitrogen fixing organisms. *Schimel et al.* [1996, 1997] argued that N inputs may be correlated with actual evapotranspiration based on the qualitative observation that high rates of N fixation are highest in ecosystems (e.g., temperate and tropical rain forests) and seasons (rainy periods in deserts and grasslands) with high ET.

We performed a regression analysis of our data-based estimates of N fixation on ecosystem ET, as computed by Century (Figure 1). We found significant relationships between ET and our data-based estimates of N fixation (conservative estimate: R^2=0.60, P<0.001; central estimate: R^2=0.63; P<0.001; upper-bound estimate: R^2=0.62; P<0.001). Just as ET may relate to N fixation (as a correlate for the resources available to nitrogen fixing organisms), NPP could also relate to N fixation; NPP may be a proxy for carbon potentially available to fixers. The relationships between N fixation and modeled NPP are depicted in Figure 2. Although the relationships between the data-based N fixation and NPP are not as strong as with ET (conservative estimate: R^2=0.22; P=0.02; central estimate: R^2=0.34; P=0.004; upper-bound

Table 11b. Data-Based Estimates of N Fixation in Desert (15) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	1.509	0.595		
Standard deviation	2.039	0.535		
Geometric mean	0.445	0.336		
Variance	4.156	0.286		
5% cover	0.148	0.336	0.484	4.84
15% cover	0.445	0.336	0.781	7.81
25% cover	0.742	0.336	1.078	10.78

Table 12a. Summary of Literature-Derived Estimates of Symbiotic and Nonsymbiotic N Fixation Estimates in Mediterranean Shrubland (22) Ecosystems

Ecosystem Location	Vegetation Type	N Fixation Rate, N m^{-2} yr^{-1}		Method	Source
		Symbiotic (% Cover)	Nonsymbiotic		
Coastal California, U. S.	chaparral	0.010 (32)	-	C_2H_2	*Kummerow et al.*, [1978]
Coastal California, U. S.	chaparral	-	0.100	C_2H_2	*Schlesinger et al.*, [1982]
Australia	shrubland	0.075 (NA)	-	C_2H_2	*Groves*, [1981]
Coastal California, U. S.	chaparral	0.690 (NA)	-	C_2H_2	*Lepper and Fleschner*, [1977]
Unspecified	chaparral	1.000 (NA)	-	C_2H_2	*Rundel and Neel*, [1978]

estimate: R^2=0.38; P=0.002), the general trend suggests that higher nitrogen fixation corresponds with higher NPP. However, we believe that higher rates of NPP may be, in part, a consequence of a given level of BNF as the cause.

We utilized the observed relationship between our central, data-based N fixation estimate and ET to map global N fixation rates using the ET values in Century (Plate 2). The fact that ET accounts for >60% of the variability in our whole range of estimates of N fixation suggests that it may be a useful predictor for annual nitrogen fixation at the ecosystem scale. However, this procedure is certainly not appropriate for estimating instantaneous nitrogen fixation rates (e.g., in units of mol cm^{-2} d^{-1}) which can be transiently high even in very arid ecosystems under appropriate conditions. Nevertheless, as demonstrated in Plate 2, the highest rates of N fixation occur in tropical latitudes and decrease with increasing latitude. On the basis of our calculations, greater than 20% of global terrestrial BNF occurs in tropical rain forests (Table 13). This may help explain why these systems are frequently N-rich, with primary productivity apparently limited by some combination of P, base cation and/or light availability rather than by N [*Vitousek and Howarth*, 1991; *Martinelli et al*, 1999]. Combined, tropical rain forests, arid shrublands and tropical savannas account for > 60% of the total global BNF, where as all the temperate forests combined account for <10% of global BNF (Table 13). However, the paucity of available estimates of N fixation in tropical rain forests, arid shrublands, and tropical savannas and the large variability in the estimates that are available (Table 13) decreases the reliability of these estimates relative to estimates of N fixation in temperate forests (where reported rates are much more abundant) and emphasizes the need for more data-based estimates in such ecosystems, where N fixation appears to be extremely important.

The fact that areas with high ET have correspondingly high rates of N fixation suggests that at the ecosystem level, ET is a reasonable predictor of N fixation. However, the variability in the data-based regressions with ET suggests that contrary to the model, in which ET "drives" N fixation, N fixation is likely influenced by many other factors beyond ET and NPP [*Vitousek and Field*, 1999]. Also, it is possible that the strength of this relationship would be further diminished at smaller scales, where variation in factors such as light availability, soil type, and hydrology may lead to significant ranges in N fixation at the community to ecosystem scale. Finally, the relationship between ET and N fixation may be more applicable to asymbiotic nitrogen fixation, as symbiotic nitrogen fixation may be controlled more by ecosystem successional status, species composition and species abundance.

4. Conclusions

Estimates of potential biological nitrogen fixation by vegetation type are shown in Table 13. From our data-based estimates, we believe that BNF contributes a maximum of 289 Tg N yr^{-1} (1 Tg = 10^{12} g) to terrestrial ecosystems. However, we believe that this estimate is absolutely an upper limit, as this estimate is based on at least 25% coverages of symbiotic N fixers over all ecosystems. Although legumes may be quite

Table 12b. Data-Based Estimates of N Fixation in Mediterranean Shrubland (22) Ecosystems

	N Fixation Rate, g N m^{-2} yr^{-1}		N Fixed,	N Fixed,
	Symbiotic	Nonsymbiotic	g N m^{-2} yr^{-1}	kg N ha^{-1} yr^{-1}
Arithmetic mean	0.444	0.100		
Standard deviation	0.481	-		
Geometric mean	0.151	-		
Variance	0.231	-		
11% cover	0.052	0.100	0.152	1.52
32% cover	0.151	0.100	0.251	2.51
53% cover	0.250	0.100	0.350	3.50

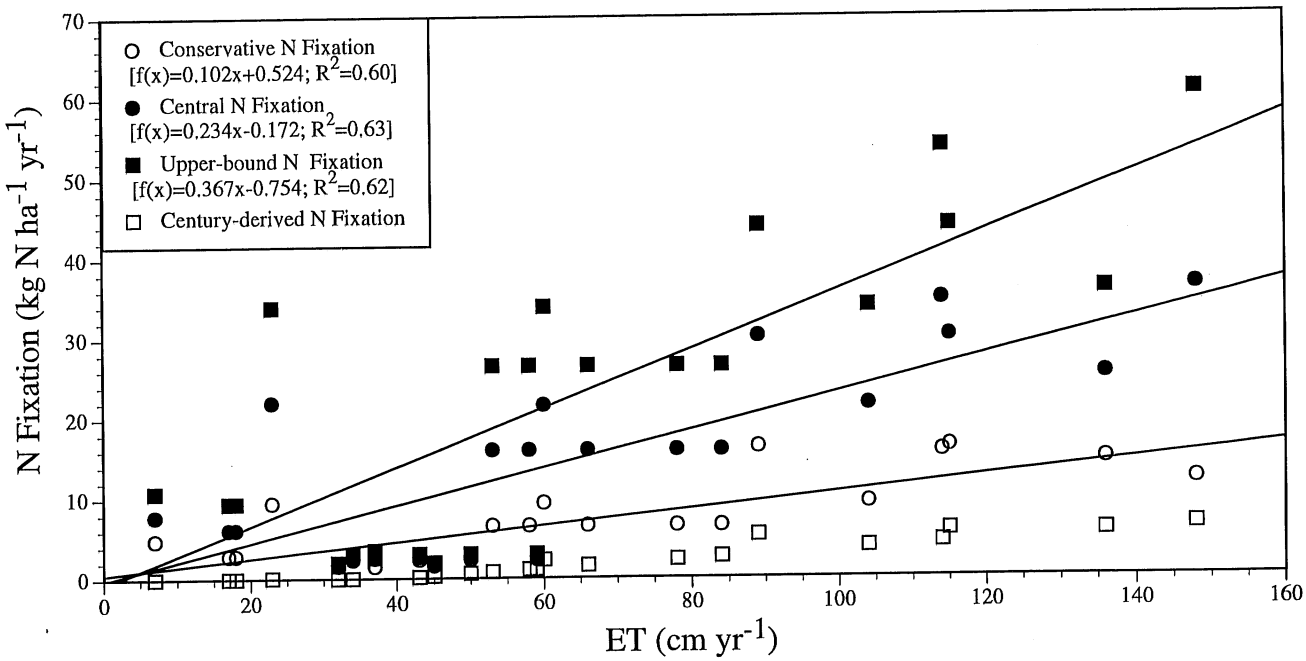

Figure 1. Conservative, central, and upper-bound data-based and modeled estimates of terrestrial biological nitrogen fixation by ecosystem plotted versus modeled ecosystem ET.

abundant in some parts and/or successional stages of all ecosystems, we believe that it is extremely unlikely that this value represents a realistic average spatial and temporal coverage. The contribution suggested by the conservative and central data-based estimates (100 Tg N yr^{-1} and 195 Tg N yr^{-1}, respectively) are much more reasonable values, and since our central value is based on an average of explicitly reported coverages of N fixers, our best estimate of potential N fixation in natural ecosystems globally is 195 Tg N yr^{-1}, or an average of ~15 kg N yr^{-1} for each hectare of the Earth's land surface. Our failure to include an error term on this central value reflects the fact that we are unaware of an appropriate statistical

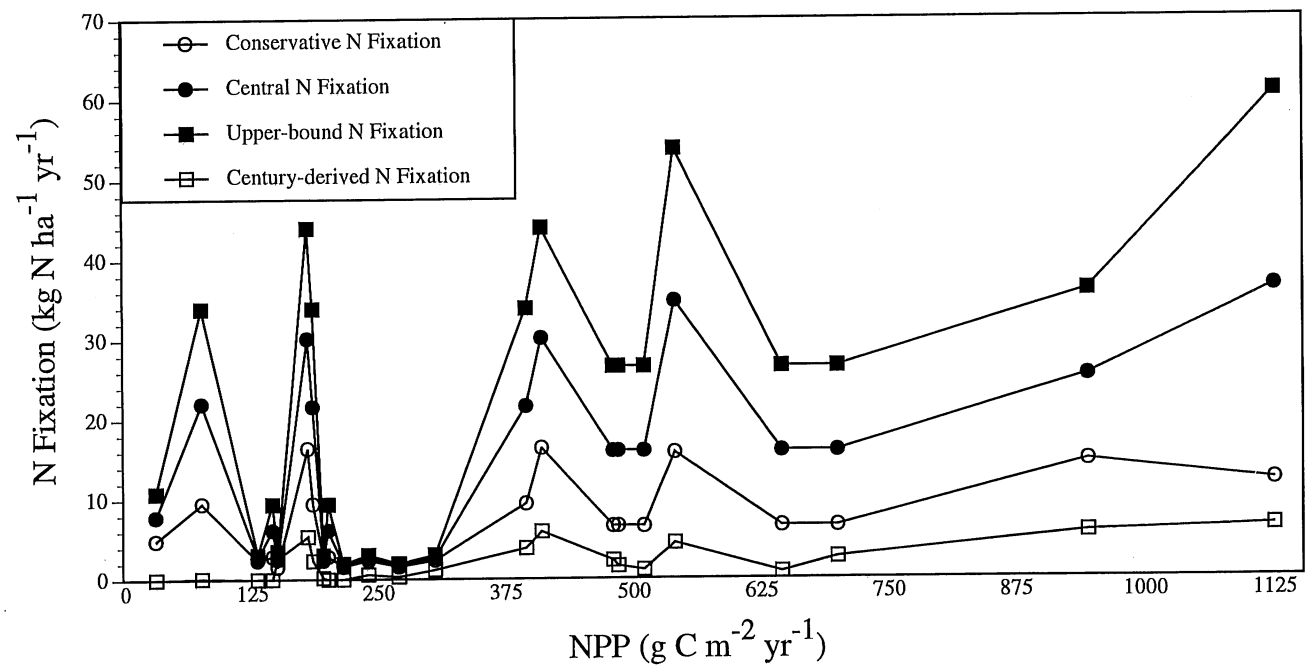

Figure 2. Conservative, central, and upper-bound data-based and modeled estimates of terrestrial biological nitrogen fixation by ecosystem plotted versus modeled ecosystem NPP.

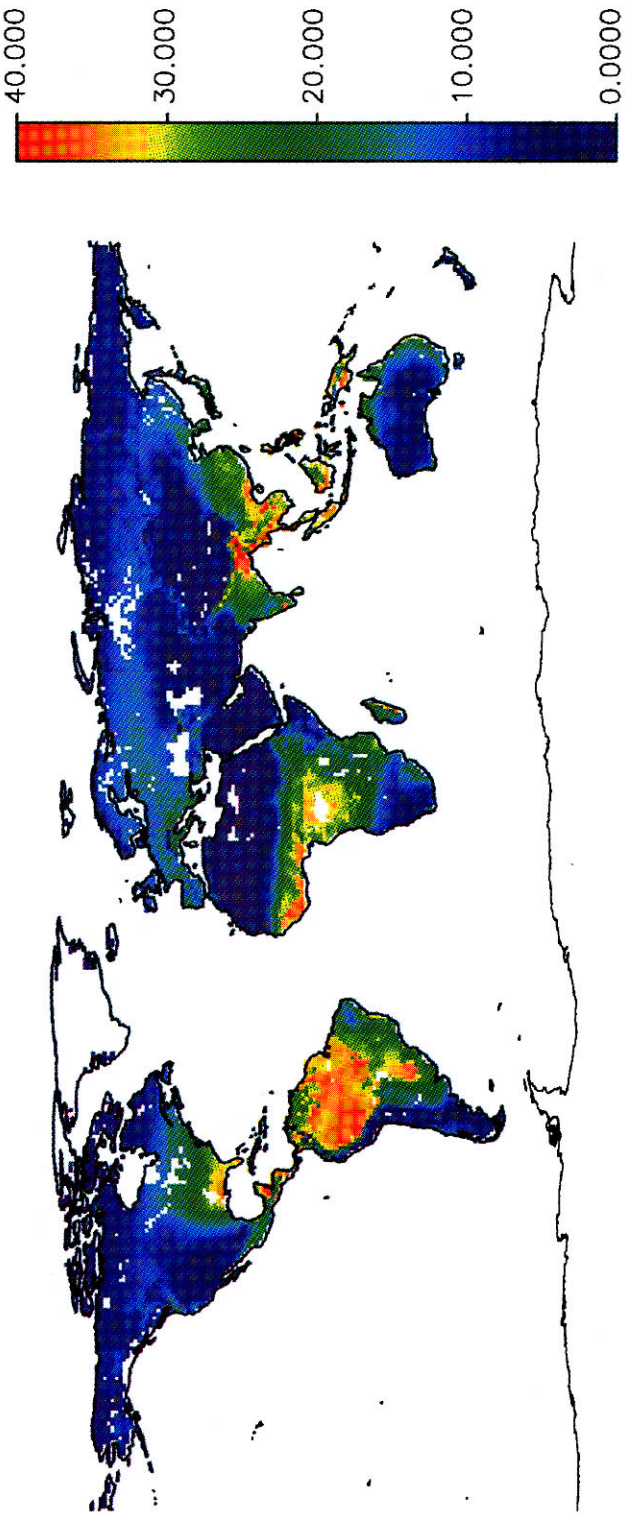

Plate 2. Mapped potential annual BNF by natural ecosystems based on the relationship between the central estimates of BNF (N fixation = 0.234(ET) - 0.172) and ecosystem ET. Values are kg N ha^{-1} yr^{-1}. White areas represent regions where modeled ET values are unavailable.

procedure for doing so. Thus we caution the treatment of this value as an absolute and emphasize that we are much more comfortable that our range of possible global N fixation estimates includes the true value of global N fixation, than we are that our central estimate is the true value of global N fixation. Our data-based estimates compare to a modeled total N fixation input of 25 Tg N yr^{-1} (data not shown), suggesting that while Century does seem to capture broad-scale patterns in N fixation (Figure 2) it also appears to significantly underestimate total inputs.

These estimates represent potential nitrogen fixation (i.e., ecosystem areas do not account for land-use changes), but accounting for the decrease in natural N fixation due to cultivation would not dramatically alter our estimate, as the greatest reductions in area have occurred in systems characterized by relatively low rates of N fixation (e.g. temperate forests and temperate grasslands; [*Matthews*, 1983]). Matthews [1983] suggests that ~18 × 10^6 km^2 (13.6%) of all lands have been converted for cultivation. This value includes a contribution of ~3 × 10^6 km^2 from extensive subsistence agriculture and ~15 × 10^6 km^2 for global crop acreage [*Matthews*, 1983]. Therefore we believe that decreasing our value by this value (i.e., 13.6%) may provide a conservative estimate of actual present-day terrestrial BNF in natural ecosystems.

Our central value of 195 Tg N fixed per year in terrestrial ecosystems is higher than the values of 90-140 Tg N yr^{-1} previously reported by *Stedman and Shetter* [1983], *Soderland and Rosswall* [1982], and *Galloway et al.*, [1995]. Thus we believe that these authors may have underestimated terrestrial BNF. However, both our conservative and central estimates do fall within the range of 44-200 Tg N yr^{-1} reported by *Schlesinger* [1991]. Despite the similarity, we believe that our rigorous literature review provides a more documented, constrained estimate. Nonetheless, it is noteworthy that our independently derived estimate of terrestrial BNF is remarkably similar overall to this latter estimate.

Although we believe this study provides a much improved estimate of biological nitrogen fixation in terrestrial ecosystems, perhaps the most valuable aspect of this work is that it points out critical gaps in our understanding of N fixation at the local, regional, and global scale. In order to improve our understanding, key research needs include continued and expanded research investigating N fixation rates in natural and managed ecosystems, particularly in parts of Asia, Africa, and South America, where nitrogen fixation is likely to be important, but where data are scarce. For example, several of our ecosystem-scale estimates are based on only one-to-several published estimates, and data often vary widely (Table 13). A more rigorous evaluation of ecosystem-scale estimates will require more studies of BNF at the local scale within individual ecosystems. In addition, a greater emphasis should be placed on estimating the aerial coverage of N-fixing microsites and species, in order to improve estimates of N fixation budgets from the watershed-to-ecosystem scale. Finally, we would suggest that whenever possible, studies estimate BNF inputs within the context of other N inputs (e.g., wet and dry deposition), as well as the full suite of N loss vectors (e.g., trace gas fluxes, organic and inorganic N leaching). However, a recent global inventory of nitric oxide

Table 13. Global Inventory of Terrestrial Biological N Fixation in Natural Ecosystems

Potsdam Vegetation Type	Area,	Mean Estimate,	Range of Estimates, kg N ha^{-1} yr^{-1}		Number of	Total N Fixation, Tg yr^{-1}			Total N
	$\times 10^8$ ha	kg N ha^{-1} yr^{-1}	Symbiotic	Non-symbiotic	Estimates*	Conservative	Central	Upper-bound	Fixation, %†
Polar desert/alpine tundra	5.37	6.13	4.90	0.42 - 3.00	8[a]	1.54	3.29	5.05	1.69
Moist tundra	5.36	6.13	4.90	0.42 - 3.00	8[a]	1.53	3.29	5.04	1.69
Boreal forest	12.70	1.77	0.30	0.50 - 2.80	6[b]	2.00	2.24	2.48	1.15
Boreal woodland	6.60	1.77	0.30	0.50 - 2.80	6[b]	1.04	1.17	1.29	0.60
Temperate mixed forest	5.30	16.04	1.00 - 160.00	0.00 - 2.80	31[c]	3.49	8.50	14.10	4.36
Temperate coniferous forest	2.51	16.04	1.00 - 160.00	0.00 - 2.80	31[c]	1.66	4.03	6.68	2.07
Temperate deciduous forest	3.69	16.04	1.00 - 160.00	0.00 - 2.80	31[c]	2.43	5.92	9.81	3.03
Tall/medium grassland	3.65	2.70	0.10 - 10.00	0.10 - 21.00	11[d]	0.86	0.99	1.11	0.51
Short grassland	4.75	2.70	0.10 - 10.00	0.10 - 21.00	11[d]	1.12	1.28	1.45	0.66
Tropical savanna	13.90	30.20	3.00 - 90.00	3.00 - 30.00	7[e]	22.70	41.90	61.10	21.48
Arid shrubland	14.80	22.04	30.00 - 97.50	0.50 - 13.00‡	3	13.99	32.56	50.12	16.69
Tropical evergreen forest (rain forest)	17.80	25.40	16.00	0.50 - 60.00	10	26.20	45.20	64.20	23.17
Xeromorphic forest	6.86	21.68	7.50 - 30.00	3.31	3[f]	6.47	14.90	23.30	7.64
Tropical forested floodplain	0.18	36.45	243.00	NA	2	0.56	0.93	0.93	0.48
Desert	11.70	7.81	0.67 - 29.50	0.50 - 13.00	8	5.65	9.12	12.60	4.68
Tropical non-forested floodplain	0.36	34.80	28.50	6.30	2	0.57	1.25	1.93	0.64
Temperate forested floodplain	0.11	16.04	1.00 - 160.00	0.00 - 2.80	31[c]	0.07	0.17	0.28	0.09
Temperate non-forested floodplain	0.10	2.70	0.10 - 10.00	0.10 - 21.00	11[d]	0.02	0.03	0.03	0.02
Wet savanna	0.16	30.20	3.00 - 90.00	3.00 - 30.00	7[e]	0.27	0.49	0.72	0.25
Temperate savanna	6.89	2.70	0.10 - 10.00	0.10 - 21.00	11[d]	1.62	1.86	2.10	0.95
Temperate broadleafed evergreen forest	3.35	16.04	1.00 - 160.00	0.00 - 2.80	31[c]	2.20	5.37	8.89	2.75
Mediterranean shrubland	1.47	2.51	0.10 - 6.90	1.00	5	0.22	0.37	0.52	0.19
Tropical deciduous forest	4.70	21.68	7.50 - 30.00	3.31	3[f]	4.43	10.20	16.00	5.23
Global Total	132.28	-	-	-	106	100.64	195.06	289.63	100.00

*Like letters indicate estimates derived from the same set of literature values.
†Percentages based on central estimate of global N fixation.
‡Owing to a lack of published estimates, nonsymbiotic N fixation in arid shrublands was assumed to be equal to nonsymbiotic N fixation rates observed in desert ecosystems.

(NO) emissions from soil suggests some possible correlations between N fixation inputs and trace gas outputs [*Davidson and Kingerlee,* 1997]. For example, both NO fluxes and N fixation are relatively low in grassland ecosystems, while both fluxes are relatively high in tropical savannas [*Davidson and Kingerlee*, 1997]. Although these two studies utilize different vegetation classifications (which prohibits a direct comparison), these trends suggest a possible positive relationship between N fixation and N trace gas losses.

It is clear that human activity is dramatically increasing the amount of reactive N in many terrestrial systems and that such increases have a variety of environmental consequences [*Galloway et al.,* 1995; *Howarth et al.,* 1996; *Vitousek et al.,* 1997]. It is worth noting that our estimates of BNF support prior claims that human activity has roughly doubled N fixation [*Vitousek et al.,* 1997; *Vitousek,* 1994a; *Galloway et al.,* 1995]. In addition, our ecosystem specific values show that in much of the temperate zone, the human effect is far greater; in some regions, anthropogenic N fixation is probably at least an order of magnitude greater than BNF. However, both the extent and the consequences of a changing N cycle are difficult to determine without a much improved understanding of biological N fixation. In particular, our ability to predict future changes in terrestrial N cycling is constrained by a lack of mechanistic knowledge about the primary controls over BNF. The simple relationships between ET and BNF shown here may have some predictive power, but a much more mechanistic understanding is necessary to predict how BNF will respond to simultaneous changes in climate, N deposition, and atmospheric CO_2.

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C. C. Cleveland and A. R. Townsend, Institute for Arctic and Alpine Research, Campus Box 450, University of Colorado, Boulder, CO 80309. (cory.cleveland@colorado.edu)

A. Elseroad, L. O. Hedin, R. W. Howarth, E. F. Latty, S. S. Perakis, J. C. Von Fischer, and M. Wasson, Department of Ecology and Systematics, Cornell University, Ithaca, NY, 14853.

H. Fisher and D. S. Schimel, National Center for Atmospheric Research, P. O. Box 3000, Boulder, CO 80307-3000.

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