In addition to being sensitive to all of the corrections above, our uranium projectiles should be sensitive to the effects of electron capture and loss. Such was not the case for previous studies of higher order corrections. Studies of the charge state in air of uranium ions at 10 to 70 MeV yield a semiempirical expression (*14*) for charge state which, when extrapolated to 147.7 MeV/amu, indicates that about five electrons are captured by uranium projectiles. One can take the effect of charge state into account for calculations of S by replacing Z_1 with Z_{eff}, the root-mean-square charge state of the ion. This is valid since the effective minimum impact parameter for scattering of electrons bound to the absorber material is typically larger than the orbits of electrons captured by the projectiles. To estimate the charge state of the uranium ions in this experiment, we used the expression for Z_{rms} given by Pierce and Blann (*15*), which is more suitable for solid absorbers than that in (*14*).

By including all the effects above except the relativistic Bloch correction (which cannot be calculated reliably for uranium), we calculate a net range for the uranium in this experiment to be 0.654 g/cm^2, 13 percent larger than observed. By neglecting the higher order corrections, we obtain a result only 3 percent larger than observed. The latter result differs from the Barkas and Berger result due to the slightly different manner in which electron capture was taken into account. This indicates the sensitivity of the range calculation to this effect. Nevertheless, unless the energy of the ^{238}U is grossly incorrect (which seems unlikely since it was calculated from known magnetic fields, radio frequency, and flight paths), it seems that for 147.7 MeV/amu and below, all higher order corrections to S for uranium cancel.

Since the nonrelativistic Bloch correction far exceeds the polarization and Mott corrections at the relevant energies for the uranium beam, the relativistic Bloch correction must almost completely cancel the nonrelativistic Bloch correction, as was observed to be the case for the faster neon, argon, and iron beams (*7, 10*). Our calculations indicate that such magnitudes and sign of the relativistic Bloch correction are possible. It will be interesting to see if the cancellation of higher order terms continues to higher uranium energies as such beams become available.

It is apparent that theory does not provide reliable information on the stopping power of relativistic uranium ions and that an experimental approach is a prerequisite to the interpretation of responses of detectors used to identify relativistic ultraheavy nuclei.

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Nitrogen Fixation in the Marine Environment

Abstract. *Cyanobacteria of the genus* Oscillatoria (Trichodesmium) *account for annual inputs of nitrogen to the world's oceans of about 4.8 × 10^{12} grams while benthic environments contribute 15 × 10^{12} grams. The sum of these inputs is one-fifth of current estimates of nitrogen fixation in terrestrial environments and one-half of the present rate of industrial synthesis of ammonia. When the total of all nitrogen inputs to the sea is compared with estimated losses through denitrification, the marine nitrogen cycle approximates a steady state. Oceanic nitrogen fixation can supply less than 0.3 percent of the calculated demand of marine phytoplankton. The minor contribution by nitrogen fixation to the overall nitrogen economy of the sea is not consistent with the supposition that nitrogen is the primary limiting nutrient and suggests that factors other than nitrogen availability limit phytoplankton growth rates.*

Recent accountings of the global nitrogen cycle have uniformly relied on a limited number of studies in deriving their estimates of marine nitrogen fixation (*1, 2*). Relatively large errors and uncertainties are therefore inherent in these calculations. We now provide an estimate for marine nitrogen fixation based on intensive research into this process conducted over the last 15 years, along with existing information on the distribution and abundance of the predominating diazotrophic systems.

In the open ocean, high specific rates of nitrogen fixation have been associated with several species of free-living cyanobacteria in the genus *Oscillatoria* (formerly *Trichodesmium*) (*3–7*), epiphytes on the pelagic phaeophyte *Sargassum* (*8*), and bacteria and a cyanobacterium (*Richelia* sp.) endophytic in the diatom *Rhizosolenia* (*5, 9*). *Rhizosolenia*-associated nitrogen fixation has generally been detected only under bloom conditions (*9*), and available data do not suggest this to be a major source of combined nitrogen. For epiphytes on pelagic *Sargassum* sp., a minor overall input of 0.018 × 10^9 g of nitrogen per year was computed from the seasonal abundances given for the North Atlantic and the Gulf of Mexico (*10*) and an average rate of 18 μg of nitrogen per gram (dry weight) per day derived from (*8*).

Studies on the abundance, productivity, and capacity for nitrogen fixation by pelagic marine *Oscillatoria* are widespread, spanning the major oceanic basins (*3–7*). Total nitrogen fixation computed from available data gave a total annual rate of 4.8 teragrams (Tg) (4.8 × 10^{12} g) of nitrogen per year (Table 1). Highest rates occurred in the Indian Ocean during the northern monsoon, and overall the Indian Ocean had the highest annual rate of nitrogen fixation, followed by the Atlantic, then Pacific, oceans. As with the rhizobia of terrestrial ecosystems, a limited taxonomic group (*Oscillatoria* spp.) is responsible for a substantial fraction of the nitrogen fixation that occurs in the sea.

In benthic environments, studies have been carried out in deep sea (*11*), coastal (*11–13*), and estuarine (*13, 14*) sediments, as well as in sea grass (*15*), coral reef (*16*), salt marsh (*17*), and mangrove (*18*) communities (Table 2). Values have been scaled up with the use of current estimates of the extent of these areas (*19–21*). Overall, annual benthic nitrogen fixation is estimated to account for 15 Tg of nitrogen or about three times that catalyzed by the predominant diazotrophs of the pelagic zone (*22*).

The quality of these estimates depends on both the accuracy of measurement of nitrogen fixation and the areal estimate for that ecosystem. Advantages and limitations of means presently used to assess nitrogenase activity have been discussed in detail (*3, 22, 23*). The areal extent of the shelf and deep sea are generally agreed upon (*19*). However, Woodwell *et al.* (*20*) suggest that their approximation of intertidal marshes and estuaries may be accurate only within 50 percent. Given this constraint and the reported variances in average nitrogen fixation (see Tables 1 and 2), it is tentatively concluded that salt marshes may be the most important sites of nitrogen fixation in the marine environment, possibly exceeding the total input by pelagic *Oscillatoria* spp. Coral reefs, which have an areal specific rate similar to that of salt marshes, but cover an overall area less than half that of the marshes, may account for an input similar in magnitude to all shelf (< 200 m) sediments.

We therefore estimate total oceanic nitrogen fixation to be 20 Tg of nitrogen per year; in comparison, previous estimates ranged from 10 to 130 Tg of nitrogen per year (*1, 2*). Our estimate is conservative, since data on nitrogen fixation by pelagic bacteria and cyanobacteria are limited and do not yet permit extrapolation. Also, other benthic environments may prove to be active sites of nitrogen fixation; for instance, the recently discovered hydrothermal vent areas of the deep sea have been suggested by Fogg (*2*) and Capone (*22*) as likely sites. Nevertheless, we consider our present estimate to be far more substantive than previous estimates, since it draws on the studies of marine nitrogen fixation over the last 15 years, as well as extensive data on *Oscillatoria* distributions and biomass. Considerable nitrogen fixation occurs in the sea—amounting to about one-fifth of present estimates of biological nitrogen fixation in the terrestrial environment and about one-half of that annually synthesized industrially (*1*)—and should therefore be taken into account in global nitrogen budgets.

Oceanic nitrogen fixation is roughly equivalent to the estimates of riverine input of 13 to 35 Tg of nitrogen per year (*1, 2, 24*). Atmospheric washout of NH_4^+ and NO_3^- is thought to account for 15 to 83 Tg of nitrogen per year (*1, 2*). Major losses of nitrogen from the sea occur through either sedimentation and burial or denitrification. The first process, although thought to be of minor significance, is only vaguely characterized on an oceanic scale (*1, 2*) and does not lend itself to any quantitative comparisons. Denitrification in the oceans, a much more active area of study, was recently summarized by Hattori (*25*). In the pelagic zone, this process may account for losses of combined nitrogen of upward of 30 to 50 Tg of nitrogen per year. Hattori (*25*) has also estimated that sediment-associated denitrification amounts to about 44 Tg of nitrogen per year. Oceanic denitrification appears to exceed our estimate of input through nitrogen fixation by a factor of 4 to 5. While there is no a priori reason to expect a steady state for nitrogen in the seas, it is noteworthy that total inputs (48 to 133 Tg of nitrogen per year) approach estimates for the total dissimilatory capacity of the oceans (77 to 94 Tg per year), thereby suggesting a nearly steady-state condition.

Annual utilization of nitrogen by phytoplankton, based on current approximations of primary productivity (*21*), would indicate that slightly less than 0.3 percent of this demand is met by endogenous nitrogen fixation and, in fact, only about 1 percent by the sum of de novo nitrogen input through endogenous nitrogen fixation, atmospheric washout, and terrigenous runoff. The bulk of this requirement (about 7000 Tg of nitrogen, under the assumption of a 6:1 ratio of carbon to nitrogen assimilation) is furnished from rapid recycling of combined nitrogen within the euphotic zone and from the large pool of nitrate in deeper waters (*24, 26*).

Since there is a clear disparity be-

Table 1. Estimate of nitrogen fixation by *Oscillatoria (Trichodesmium)* spp. in the world's oceans on a seasonal basis. Units are grams of nitrogen × 10^9. Data from five major oceanographic expeditions in the late 1800's, early 1900's, and 85 recent reports were used to map the global distribution and population density of *Oscillatoria* (*3*). Areas of different trichome concentrations were plotted and summed with a planimeter for each season in each of the major ocean basins. Field observations of nitrogen fixation from several investigations encompassing 45 stations (*3–7*) allowed the computation of a mean (± standard error) euphotic zone rate of 3.7 ± 0.8 pg of nitrogen per trichome per hour. Only trichomes in the upper 50 m of the water column and in water 20°C or warmer were assumed to be fixing nitrogen (*30*).

Oceanic basin	Nitrogen fixation (g × 10^9)				
	Spring	Summer	Autumn	Winter	Total
Pacific	11	163	162	0.9	337
Atlantic	101	474	133	614	1322
Indian	1890	0.5	267	966	3124
South China and Arafuru Seas	7	0.9	0.1	10.2	18
Total	2009	638	562	1591	4801

Table 2. Estimate of the total annual contribution of combined nitrogen to the global nitrogen cycle by nitrogen fixation in the benthic environments of the oceans. Areas for the coastal and deep sea were taken from (*19*). The estimates (*20*) for subtidal estuaries worldwide were divided into an unvegetated (80 percent) and sea-grass vegetated (20 percent) component, while the estimates for intertidal marsh were fractionated into temperate salt marsh (67 percent) and mangrove (33 percent) components. The areal estimate of the extent of coral reefs worldwide was taken from (*21*). Values for nitrogen fixation are annual averages ± the standard error, as calculated in (*22*) from the indicated studies. For temperate shallow-water environments, only investigations spanning a seasonal cycle were considered. For the 200- to 1000-m depth interval, a rate tenfold less than the average calculated for 0 to 200 m was used while for the 2000- to 3000-m interval a 100-fold decrease was assumed.

Environment	Area (km² × 10^6)	N_2 Fixation		Reference
		(g/m²-year)	(Tg/year)	
Depth				
> 3000 m	272	0	0	(*11*)
2000 to 3000 m	31	0.0007	0.022	(*11*)
1000 to 2000 m	16	0.001	0.016	
200 to 1000 m	16	0.01	0.16	
0 to 200 m	27	0.1 ± 0.04	2.7	(*11–13*)
Bare estuary	1.08	0.4 ± 0.07	0.43	(*14*)
Sea grass	0.28	5.5	1.5	(*15*)
Coral reefs	0.11	25 ± 8.4	2.8	(*16*)
Salt marsh	0.26	24 ± 10.5	6.3	(*17*)
Mangroves	0.13	11	1.5	(*18*)
Total	363		15.4	

tween phytoplankton nitrogen demand and de novo input through nitrogen fixation in a supposedly nitrogen-limited system (*24, 27*), it is enigmatic that diazotrophic phytoplankton (that is, nitrogen-fixing cyanobacteria) are not more prevalent. In whole-lake experiments, Schindler (*28*) reported that nitrogen limitation (low nitrogen-to-phosphorus ratio) regularly results in nuisance blooms of nitrogen-fixing cyanobacteria, whereas phosphorus limitation (high nitrogen-to-phosphorus ratio) yields phytoplankton populations dominated by eukaryotic algae (*28*). He also found that, for nitrogen-limited lakes, nitrogen fixation contributed substantially (19 to 38 percent) to the total nitrogen economy. Further circumstantial evidence indicative of a nonnutrient limited growth status for oceanic phytoplankton is found in the work of Goldman *et al.* (*26*), who suggest that phytoplankton in the marine environment are growing at near maximum rates, despite apparent nutrient impoverishment. In the sea, diazotrophic bacteria (including the cyanobacteria) may themselves be limited by either availability of other trace nutrient requirements (for example, molybdenum, iron, or phosphorus) reducing power, or oxygen inactivation (*29*). An alternative explanation is that growth or productivity of phytoplankton, or both, is in general not nitrogen-limited but is controlled instead by some other biological (for example, grazing), chemical (macro- or micronutrient), or physical (for example, light or temperature) factor.

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Late Quaternary Zonation of Vegetation in the Eastern Grand Canyon

Abstract. *Fossil assemblages from 53 packrat middens indicate which plant species were dominant during the last 24,000 years in the eastern Grand Canyon. Past vegetational patterns show associations that cannot be attributed to simple elevational displacement of the modern zones. A model emphasizing a latitudinal shift of climatic values is proposed.*

In an early life zone study of the San Francisco Peaks and adjacent parts of the Grand Canyon in northern Arizona, Merriam (*1*) concluded that modern vegetation is distributed along topographic gradients in elevational zones that resemble latitudinal zones. The similarity of elevational and latitudinal zonation of vegetation in the western United States has made the interpretation of past climates through the fossil record difficult. Patterns of climate in elevational zones may be different from those in latitudinal zones, but paleoecological records often lack the detail necessary to distinguish between elevational and latitudinal analogs of vegetation and hence the nature of past climate.

Analysis of fossil plant remains from packrat (*Neotoma* spp.) middens (*2–4*), unlike pollen analysis, often allows specific identification in difficult genera such as *Pinus* and *Quercus*. The local nature of fossil assemblages from middens—material from within 100 m of the site (*4*)—allows reconstruction of vegetational distributions along the elevational gradient as well as along the moisture gradient from insolated (xeric) to shaded (mesic) slopes. Radiocarbon dates for 48 of 53 packrat middens collected along an 1800-m elevational gradient in the eastern Grand Canyon (*5*) ranged from 34,300 to 1170 years old. The present vegetation, as described from 131 vegetational relevés (*6*) or plots, was compared with the fossil assemblages.

The elevational zonation of vegetation