KEYNOTE ADDRESS

BIOFIXATION AND NITROGEN IN THE BIOSPHERE AND IN GLOBAL FOOD PRODUCTION

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Meetings such as this one are triumphs of scientific reductionism. In this room, we have dozens of people who know more about some extremely specialized attribute of biofixation or bacterial and plant physiology than does anybody else on this planet of more than six billion people. As a counterweight to this restrictive attention, and following the tradition of keynote addresses (including some given at these biannual meetings) to look further afield, I will offer some broad perspectives on biofixation's peculiar place in the biosphere and on its role in modern food production. I will start with quantifying the remarkable rarity of diazotrophs and end with an appeal for improving efficiencies of existing practices and processes rather than for engaging in a more glamorous search for radically new supplies of reactive N.

I am sure that all of you are aware of the often noted relative scarcity of biofixation among existing species but using the recent reevaluations of global biodiversity makes it even more obvious how rare that capacity is. Of course, we do not know how many species are out there, but the latest consensus points to a much larger total than anticipated just a generation ago. As of the late 1990s, about 1.75 million species were named and described, twice that amount would seem to be a very conservative estimate of actual total biodiversity, and 13.6 million was the most likely total offered by the most comprehensive global assessment (Heywood, Watson 1997). Similarly, we have yet to identify all diazotrophic species. For example, a recent examination of *nifH* gene fragments retrieved from rice roots showed that most of them could not be assigned to any known bacteria (Ladha, Reddy 1999).

Even when assuming that there are no more than 3.5 million species (i.e. twice the known diversity) and that there are 10^2 species of prokaryotes harboring one of the nitrogenases, it means that fewer than 0.0003% of all living organisms can cleave N_2. And when we assume, again, that the eventual grand total of bacteria and archaea will be at least twice the currently identified number of some 5,000 species, 10^2 diazotrophs would still represent only a few percent of all prokaryotes.

What is no less remarkable is the highly conservative evolution of this ability. Although we still cannot reconstruct a satisfactory evolutionary timeline of nitrogenase's emergence and diffusion, it is plausible to speculate that, given the biofixation's undoubted Archaen origins, only a small number of species acquired N-fixing capability during the subsequent 1.5 billion years of late Precambrian evolution and during more than half a billion years of the Phanerozoic eon. The share of diazotrophs among all living organisms peaked, most likely, during the late Archaean era when cyanobacteria ruled the biosphere and when atmospheric oxygen levels were a small fraction of today's concentration. And when the vascular plants conquered the continents some 360 million years ago, fewer than 20,000 of the more than 270,000 species of gymnosperms and angiosperms, that is less than 8% of the total, evolved symbioses or association with N-fixing bacteria.

The single most important reason for this paucity of N-fixing species and N symbioses is the high energy cost of biofixation. Perhaps the best indicator of this high price is the fact that the Haber-Bosch synthesis of NH_3 that takes place in massive steel converters under high pressure (mostly above 10 Mpa) and high temperature (above 350°C) actually requires less energy than the enzymatically-mediated work of N-fixing bacteria operating at ambient conditions. Theoretical calculations indicate

that energy cost for the legume nodule is typically between 3-6 g Cg^{-1} N, and actual whole-plant energy costs of symbiotic N_2 fixation can be easily twice as high (Phillips 1980; Hardarson, Lie 1984). Even the lower range is equivalent to roughly 100-200 kJ g^{-1} N. For comparison, the energy requirements of the earliest coal-based Haber-Bosch plants were just over 100 kJ g^{-1} and today's best single-train Kellogg or Topsøe plants need less than 35 kJ g^{-1}, or 1/6 of the energy cost of biofixation (Smil 2001). Of course, there is the essential difference in requisite energies: nonrenewable fossil fuels (now overwhelmingly CH_4) are needed for the Haber-Bosch synthesis while the photosynthetically renewable glucose energizes biofixation.

High energy cost of biofixation is also the best explanation why most plants have eschewed any association with diazotrophs and rely on less energy expensive uptake of nitrates: energy costs of this reduction range from negligible amounts (when done entirely in shoots) to about 1.5 g C g^{-1} N for complete reduction in roots at the expense of respired assimilate (Hardarson, Lie 1984). Although costly in energy terms, biofixation remains the only major provider of reactive N in natural ecosystems (except in those receiving heavy atmospheric N deposition), and recent reevaluations of the global supply of fixed N have only raised its relative importance for the functioning of the biosphere.

Quantifying the contributions of diazotrophs to the biosphere's supply of reactive N remains an uncertain task but the best recent assessment of terrestrial biofixation offers a significantly higher mean than did most of the often cited previous estimates. Appropriately, it uses a range as wide as 100-290 Mt N $year^{-1}$ but it sets the best mean at about 195 Mt N for the Earth's potential natural ecosystems (Cleveland 1999). With no more than 5 Mt N fixed by lightning (Galloway *et al.* 1995), diazotrophs would have provided about 98% of all reactive N available to preagricultural land ecosystems. Today's biofixation adjusted for land use changes would lower the aggregate by about 15%, to almost 170 Mt N $year^{-1}$.

Traditional agricultures expanded their N supply by cultivating leguminous species and this practice became eventually an essential part of intensive cropping particularly in Europe and East and South Asia. My accounts of N inputs in traditional farming show as much as 50% of all available N originating from biofixation by leguminous food, forage and green manure crops in China of the early 1950s (Smil 2001). While the rotations with legumes retain their importance in modern cropping the traditional practice of cultivating leguminous green manure crops has been steadily declining.

I have also prepared the first disaggregated account of N flows in the current global food production (Smil 1999). By far the most accurate part of this exercise, whose results refer to the mid-1990s, is the calculation of N removed by the world's crop harvest: about 60 Mt N in harvested parts and 25 Mt N in crop residues. This total of 85 Mt N includes the nutrient incorporated in all fields crops, be they staple cereals, vegetables or nonfood plants, as well as N in forages grown on arable land and in fruits and plantation species. The only highly accurately known input is the amount of N applied in synthetic fertilizers, close to 80 Mt N during the 1990s (IFA 2001; FAO 2001). Seeds (2 Mt N) and irrigation water (4 Mt N) are minor contributors. Recycling of crop residues and animal manures added more than 30 Mt N (14 and 18, respectively) and atmospheric deposition (all reactive N in precipitation and dry deposition) amounted to some 20 Mt N.

Several factors are responsible for uncertainties in quantifying contributions made by free-living and symbiotic fixers. Fixation rates of all diazotrophs vary widely. Almost all published values for rhizobial fixation in widely cultivated legumes have at least three-fold ranges, much larger spreads are common for some species, and too few fixation rates have been published for many less common legumes (Smil 1997, 1999). Consequently, it is difficult to choose averages needed for national or global calculations. Moreover, unlike for virtually all food and industrial crops, there are no worldwide statistics for the amount of land under leguminous forages and green manures. Previously published totals for the annual global biofixation in agroecosystems were mostly around 40 Mt N (Galloway *et al.* 1995). My best calculation for N fixed by bacteria is about

33 Mt N during the mid-1990s, with the range between 25 to just over 40 Mt N (Smil 1999). Taking the most likely value would mean that diazotrophs now contribute about 20% of all N available to the world's crops.

Their qualitative contribution is even more significant. Bacterially-fixed N is generally much less susceptible to volatilization than are manures and urea, now the world's most important synthetic fertilizer. Biofixed N is also less leaching-prone than the high rates of the nutrient applied in highly soluble nitrates. As a result, more of the biofixed N stays within the soil-plant system to be eventually used by crops. In contrast, losses following applications of N fertilizers have now become the single largest cause of human interference in the global N cycle. They contribute to a variety of undesirable local, regional and even global environmental changes (Galloway et al. 1995; Mosier et al. 2001; Smil 1995, 2001a). These impacts range from N enrichment of coastal waters of all inhabited continents to high levels of atmospheric nitrate and ammonia deposition on forests and grasslands.

Scientific emphases and goals change with time. A quarter century ago it was widely believed that endowing the nonleguminous staple cereals with the ability to secure their own N is the most important long-term challenge for the biofixation research. At that time optimistic forecasts anticipated that this goal would be accomplished by the century's end (Smil 2001). I believe that the failure to do so is not to be regretted, as there would have been almost certainly a substantial yield cost paid by the new grain- or oil-yielding symbionts. Moreover, with the exception of the sub-Saharan Africa, N currently available to crops worldwide is not in short supply. My global balance shows that crops receive roughly twice as much N as they eventually incorporate in their tissues and hence it is the huge loss (50% global average, close to 70% in rice cropping) of the nutrient that should be, rationally, addressed first (Smil 1999, 2000b, 2001).

Affluent nations have no need for increased food production as their food availability is already 50-70% above the actual average per capita consumption (Smil 2000b). Consequently, they should be actually reducing their overall N needs, and some of them, most notably the Netherlands and Japan, have been doing so for about two decades (Smil 2000b, 2001). In contrast, populous low-income nations will need significantly increased food output in order to accommodate at least another 2-3 billion people during the next two generations and also to improve the overall quantity and quality of average food supply. A key challenge for modern intensive cropping in these countries will be to combine higher food production with minimized throughput of reactive N. Biofixation research could thus make the greatest difference to the world's food production and to the biosphere's integrity by helping to raise the productivity of bacterial diazotrophs in Asia, Africa and Latin America and by improving the efficiency with which the biofixed N is used everywhere by both leguminous symbionts and by nonleguminous crops.

The most rewarding way is to raise the prevailing shares of N derived by leguminous crops from biofixation. Such gains could range from relatively marginal improvements (e.g. from 60% to 70%) that would make a major aggregate difference on the global scale to large increments (e.g. from 20 to 40%) that would be of a great local and regional importance. Soybeans are the best candidates in the first category; many bean cultivars that remain an important source of protein in many poor countries exemplify the second case. Another vigorously pursued strategy should come from a wider use of suitable endosymbionts as their introduction and diffusion does not require drastic genetic modification entailed in transferring symbiotic N fixation to nonleguminous species (Ladha, Reddy 1999). Genetic engineering will eventually produce some N-fixing non-legumes but future adequate food supply that is compatible with sound agroecosystemic management can be maintained without such unprecedented advances.