Environmental Role of Nitrogen-fixing
Blue-green Algae and Asymbiotic Bacteria
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CONTRIBUTION OF NITROGEN FIXATION TO ECOSYSTEM FUNCTIONING AND NITROGEN FLUXES ON A GLOBAL BASIS

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Introduction

The recent proceedings of international meetings on nitrogen fixation (Lie & Mulder, 1971; Stewart, 1975; Nutman, 1975; Newton & Nyman, 1976) have provided a great deal of useful information concerning the amount of nitrogen fixed on specific sites. The general interest in nitrogen fixation and the need to know the contribution that nitrogen fixation makes to the nitrogen required for plant growth have emphasized the requirements for synthesis of data concerning nitrogen fixation on a variety of sites. There is also a great deal of interest in the role that nitrogen fixation plays in global nitrogen flows.

Burns & Hardy (1975) averaged a great deal of data in arriving at the information shown in Table 1. Svensson & Söderlund (1976), in calculating the effects of nitrogen fixation on the global nitrogen cycle, accepted the data of Burns & Hardy for terrestrial systems. They, however, revised Burns & Hardy's figure of 36×10^6 metric tons for the aquatic systems. This was done by averaging values from Goering *et al.* (1966) for a bloom of *Trichodesmium* and taking into account Gundersen's (1974) data for fixation

Table 1. N_2 fixation in the biosphere.

Land Use*	ha $\times 10^{-6}$	kg N fixed ha^{-1} yr^{-1}	Metric tons yr^{-1} ($\times 10^6$)
Legumes	250	140	35
Rice	135	30	4
Other cultivated crops	1015	5	5
Permanent meadows, grasslands	3000	15	45
Forest and woodland	4100	10	40
Unused	4900	2	10
Ice covered	1500	0	0
Total Land	14900		139
Sea	36100	1	36
TOTAL	51000		175

* Adapted from Burns & Hardy (1975). Arable land includes land under crops, land temporarily fallow, temporary meadows for mowing or pasture, land under garden, fruit trees, vines, shrubs and rubber plantations. Land in legumes is estimated at 250×10^6 ha or 18% of the arable land. Permanent meadows and grasslands refers to land under herbaceous forage crops other than rotation grasses and clovers. Forested land includes land under natural or planted stands of trees. Unused land includes some potentially productive land, but primarily consists of wasteland and built-on areas.

by a mixed flora of algae, primarily *Trichodesmium* and diatoms. Svensson & Söderlund calculated the possible range of nitrogen fixation for tropical waters to be $15-80 \times 10^6$ metric tons per year. It was further estimated that the fixation rate in temperate and cold waters would be about one-quarter that in the tropics. As the area is twice as large, another 40×10^6 tons per year could be fixed in temperate cold waters, yielding a total range of $20-120 \times 10^6$ tons per year for oceanic fixation. Fixation for sediment areas, including reefs and algal beds, estuaries and the Continental Shelf, accounted for another 10×10^6 tons per year.

The presence of a large number of scientists at the present symposium interested in the role of nitrogen fixation in nature presented a unique opportunity to:

1) compile the rates of fixation given for different portions of terrestrial and aquatic systems,
2) attempt to integrate the data on a broader basis, and
3) discuss the relative significance and accuracy of the data on a global basis.

Summary reports from the four discussion groups convened during the symposium are included in this paper.

Distribution of nitrogen fixation in the biosphere

Calculations of nitrogen fixation must be based on adequate information concerning the type and extent of different vegetation-soil types for the areas concerned and should relate nitrogen inputs to requirements for plant growth and microbial decomposition of litter. Table 2 shows Leith's (1975a) summary for plant productivity in the various portions of the globe. Tropical rain forest with 17×10^8 ha represents a land mass, third only in size to desert-scrub vegetation and rocks, ice and sand, which together comprise 42×10^8 ha. Cultivated land comprises 10% of the total terrestrial area.

Nitrogen fixation should be compared to the requirements for nitrogen in plant growth and the rate of photosynthesis. The large area of rain forest with its productivity of 22 tons per hectare results in a total primary production of 37×10^9 tons per year, in comparison to only 9 tons of production for cultivated lands. The rain forest is associated with only a three-fold range in production values. Cultivated land, because of the wide diversity of crops and environmental factors, shows a forty-fold range in production. Table 2 also shows that the rain forest does not have a particularly high chlorophyll content for its high production. This is also true for other highly productive areas such as swamps and marshes, indicating that the areas with high productivity have high plant turnover rates and must be able to recycle a great deal of their nitrogen. Thus, they may not have high input requirements.

The open oceans comprise 70% of the area of the earth. Because of large areas of low productivity, oceanic carbon fixation accounts for only one-third of the global total. The high turnover rate of the biomass of aquatic systems is shown by the low plant biomass relative to that of terrestrial systems.

The ranges of net productivity for the various ecosystem types indicate that an adequate estimate of nitrogen fixation should be based on more detailed subdivisions. Detailed maps such as the FAO soil maps and specific vegetation maps when available should provide a reasonable data base.

The Russian scientists have developed a thermal-bioclimatic classification, consisting of 106 zones with particular soil-vegetation formations and a characteristic biomass

Table 2. Primary production and biomass estimates for the biosphere.*

Ecosystem type	Area (10^6 km^2, 10^{12} m^2, 10^8 ha)	Net primary productivity, metric tons ha^{-1}		Total net primary production, (10^9 tons year^{-1})	Mean plant biomass, (tons ha^{-1})	Chlorophyll (kg ha^{-1})
		Range	Mean			
Tropical rain forest	17.0	10–35	22	37.4	450	30
Tropical seasonal forest	7.5	10–25	16	12.0	350	25
Temperate evergreen forest	5.0	6–25	13	6.5	350	35
Temperate deciduous forest	7.0	6–25	12	8.4	300	20
Boreal forest	12.0	4–20	8	9.6	200	30
Woodland and shrubland	8.5	2.5–12	7	6.0	60	16
Savanna	15.0	2–20	9	13.5	40	15
Temperate grassland	9.0	2–15	6	5.4	16	13
Tundra and alpine meadow	8.0	0.1–4	1.4	1.1	6	5
Desert scrub	18.0	0.1–2.5	0.9	1.6	7	5
Rock, ice and sand	24.0	0–0.1	0.03	0.07	0.2	0.2
Cultivated land	14.0	1–40	6.5	9.1	10	15
Swamp and marsh	2.0	8–60	30	6.0	150	30
Lake and stream	2.0	1–15	4	0.8	0.2	2
Total continental	149		7.8	117.5	122	15
Open ocean	332.0	0.2–4	1.25	41.5	0.03	0.3
Upwelling zones	0.4	4–10	5	0.2	0.2	3
Continental shelf	26.6	2–6	3.6	9.6	0.01	2
Algal bed and reef	0.6	5–40	25	1.6	20	20
Estuaries	1.4	2–40	15	2.1	10	10
Total marine	361		1.55	55.0	0.1	5
Full total	510		3.36	172.5	3.6	4.8

Metric ton = 1000 kg

* Adapted from Leith (1975a).

(Rodin, *et al.*, 1974, 1975). These authors in their calculation assumed all areas of the world to be in a pre-agricultural state. Their value for continental productivity (11.5 million tons ha^{-1} for 150 × 10^8 ha) is equal to 172 × 10^9 tons. This is 1.47 times the value shown in Table 2. Table 3 gives an example of the subdivisions available in the tundra (polar). Estimates of nitrogen fixation for these regions also have been included. Other areas, although subdivided by Rodin *et al.*, are not shown in Table 3.

Nitrogen fixation in agricultural lands

The small percentage of the earth that is cultivated is of special significance for the food and fiber it produces and the extent to which it has been manipulated. Table 4 gives the FAO (1974) production data for cultivated seed crops. Wheat occupies the largest single acreage. Rice, maize, barley and millet also make up very significant areas. The total for the seed crops comprises only 10.9 × 10^8 ha out of a total cultivated area estimated in 1974 to be 14.7 × 10^8 ha. The difference of 3.85 × 10^8 ha is improved pastures, fallow land, or land taken out of production by other factors such as roadways or industrial development.

The area of land in hay and pastures and the proportion of legumes in grass-legume

Table 3. Production and nitrogen fixation based on thermal belts, bioclimatic regions and soil vegetation formation (pre-agricultural).

Thermal belts, bioclimatic regions and soil-vegetation formations*	Area (10^6 km^2)	Production (metric tons ha^{-1})	N_2 fixation (kg N ha^{-1})	References
Polar belt, humid and semihumid regions				
Polar deserts (arctic) on polygonal and other arctic soils	0.71	1.0	0.3	Stutz (1975)
Tundras on tundra gley soils	3.76	2.5	1.7	Alexander (1974), Barsdate & Alexander (1975), Hanssen *et al.* (1973), Billington & Alexander (1978)
Bogs (polar) on bog permafrost soils	0.19	2.2	0.8	Kallio & Kallio (1975), Granhall & Selander (1973)
Floodplain formations	0.01	1.7		
Mountainous polar desert formations on arctic mountain soils	0.44	1.5		
Mountainous tundra formations on mountain-tundra soils	2.94	0.7	1.7	Alexander (1974)
POLAR BELT TOTAL	8.28	1.6	~1	(cf. Table 5)
Boreal belt, humid and semihumid regions				
TOTAL	26.10	6.54	~3.5	(cf. Table 6)

* Adapted from Rodin, *et al.* (1975).

mixtures appears to be extremely difficult to obtain. Values for alfalfa have been published at 0.33 × 10^8 ha (Hanson, 1972). One or two personal communications have indicated that the non-alfalfa leguminous area is at least twice that of the alfalfa; others have said a factor of 3 to 4 should be applied. This would indicate that 10% of the cultivated area is in legumes whereas Burns & Hardy (1975) estimated a total of 18%.

Calculation of nitrogen fixed

The group assembled in Uppsala was presented with the tabulation for the various areas of land and estimates of primary productivity (or yield) in the hope that the combined expertise could be used to compile data for the various systems under investigation. The participants were divided into: 1) agricultural lands, 2) tundra, grassland and desert areas, 3) forests, 4) tropical lands including cultivated rice, and 5) aquatic systems.

The attached reports indicate that most of the individual participants were very reluctant to extrapolate their data to similar systems in other portions of the globe, let alone calculate a global figure for nitrogen fixation. The group discussing tropical fixation could not come to a concensus concerning the impact that fixation has in this very large and important area; therefore, no report is enclosed.

Table 4. Extent and yield of agricultural crops (1974 FAO Production Handbook).

Crop	Area (10^6 km^2, 10^8 ha, 10^{12} m^2)	Yield (tons ha^{-1})	Production (10^8 tons)
Wheat	2.25	1.6	3.60
Rice	1.36	2.4	3.23
Barley	0.89	1.9	1.71
Maize	1.16	2.5	2.92
Rye + oats and others [1)]	0.45	2.0	0.94
Millet	0.68	0.68	0.46
Sorghum	0.42	1.1	0.46
Root and tubers	0.56	10.0	5.6
Pulses [2)]	0.66	0.67	0.44
Soybeans	0.44	1.28	0.56
Groundnuts and castor bean	0.36	0.83	0.30
Other oil seeds [3)]	0.31	0.94	0.29
Fruits and vegetables	0.38		
Sugar	0.15		
Fibre	0.69		
Beverage, rubber and tobacco	0.11		
Total	10.87		
Total arable	14.72		
Difference	3.85		

1) Mixed grain – buckwheat, canary seed, Quinca, popcorn.

2) Dry beans, chick peas, cow peas, lentils, pigeon peas, vetches, lupines.

3) Sunflower, rapeseed, sesame seed, linseed, mustard poppy, safflower.

Conclusions

The discussion pointed out the wide range of estimates that occur for various ecosystems. Most of these estimates have been conducted with the acetylene-ethylene technique with some confirmation by ^{15}N. The large range in estimates within a particular land form-vegetation unit was generally ascribed to site differences rather than to methodology problems.

Nitrogen fixation is known to be dependent on the relative need for fixed nitrogen in comparison to the total nitrogen flow. In open systems with high losses, such as clay desert sites, nitrogen fixation could be expected to contribute a significant proportion of the annual nitrogen flow. In more closed systems such as the grasslands in a steady state, nitrogen fixation should have a smaller impact on the annual flows of nitrogen.

Nitrogen fixation has often been shown to be carbon limited and primary productivity in many parts of the world is often limited by nitrogen availability. Therefore, the attempt to relate nitrogen fixation to primary productivity of different soil-vegetation complexes should be a useful exercise. The fairly representative estimates for tundra, forest and temperate grasslands indicate generally very low fixation rates of $2-5$ kg ha^{-1}. Similar low values occur for dryland crops such as wheat, maize and millet which cover such an extensive area of the world. It must be concluded that a very significant portion of the globe has low fixation rates.

The review by Fogg (1978) estimates oceanic nitrogen fixation at a level of 100×10^6 tons. This value is in general agreement with that of Svensson & Söderlund (1976). One of the major points of discussion at the meeting concerned the role of salt marsh communities. Different environments within the salt marsh communities have vastly different rates of fixation. The average value of 50 kg $ha^{-1} \cdot yr^{-1}$ estimated by Patriquin (Table 8) for salt marsh takes this into account. His calculations for salt marshes account for 2% of the aquatic fixation.

The lack of meaningful data for the tropical forest and seasonal forests which together account for nearly 50% of the plant productivity makes it very difficult to establish global nitrogen fixation rates. The nitrogen of a tropical forest is generally considered to be in a highly cyclic state. This would indicate that the fixation levels in these areas would not be closely related to the carbon fixation.

The first geochemical interpretation of carbon fixation was made in 1862 by Liebig (Pudoc, 1975). He calculated that if the earth was covered with a green meadow yielding 5 metric tons ha^{-1} yr^{-1}, the atmospheric CO_2 would be adequate for 21 years growth. Modern figures by Leith (1975a) show Liebig to have over-estimated by a factor of 1.5. Extrapolation for nitrogen fixation cannot be made as easily as this. The data collected in this discussion indicated that Burns and Hardy's (1975) estimate for grassland, forests and cultivated land is probably too high. With the large unknown tropical areas, fixation for terrestrial systems cannot yet be accurately predicted. It was, therefore, not surprising that the group could not arrive at any global estimates.

Comparison of nitrogenase activity to photosynthesis and possibly to chlorophyll content would be useful in understanding nitrogen flows. Carbon fixation values are now being calculated for computer based productivity maps (Leith, 1975b; Box, 1975). Incorporating nitrogen flow and nitrogen fixation into such maps should prove most useful.

I. Report of Discussion Group on:
N_2 fixation by cultivated crops

Chairperson: R. H. Burris

The concern of the group was for the accumulation of more reliable data on the contribution of N_2 fixation to total crops. Although fertilizer additions and crop yields can be estimated with reasonable accuracy, the data are much less reliable on what percentage of the N in leguminous crops comes from N_2 fixation and what percentage from fixed N in the soil. Data on losses by leaching, erosion and denitrification are also unreliable. These uncertainties have resulted in large discrepancies in published values for various facets of the nitrogen cycle.

It was the opinion of the group that the recently cited average value of 140 kg N fixed annually per hectare of cultivated legumes is probably double a realistic value, and 15 kg N fixed annually per hectare of grasslands may be two or three times the real value. The fact that authorities in the field differ by a factor of 2 or more in their published estimates on specific items of N input and turnover illustrates that the basis for estimates is ''soft''.

In recent years, particular emphasis has been placed on the acetylene reduction assay for evaluating N_2 fixation. Caution must be exercised to ensure that measurements are made during a period of linear reduction of C_2H_2, that diffusion of gas in the exposure vessel is not limiting, that samples are representative and that times of exposure to C_2H_2 are reasonably short. It is useful to employ independent evaluations of N_2 fixation whenever possible, and when new methods are introduced an evaluation of these with soybeans or other vigorous N_2-fixers is advisable. *In situ* incubation is desirable, and investigators should adopt an experimentally determined C_2H_2/N_2 conversion factor if data are to be expressed in terms of N_2 fixed.

Alternative methods for estimating N_2 fixation such as fixation of $^{15}N_2$, isotope dilution of ^{15}N-enriched N compounds in the soil by normal biologically fixed N, or measurement of isotope discrimination of the N isotopes at natural abundances should not be ignored but should be exploited when suitable.

Diurnal fluctuations in the rate of N_2 fixation dictate that samples should be taken at a specific time of day and should be multiplied by a suitable factor to yield realistic estimates of daily fixation. Several samples should be taken during the growing season to incorporate an estimate of changing rates of N_2 fixation at various stages of growth. The influence of incorporation of crop residues on N_2 fixation should be taken into account.

Although the exercise of estimating the N balances of different parts of the nitrogen economy of nature is an interesting process, it is apparent that the data base must be improved greatly before the results of the exercise can be taken seriously.

II. **Report of Discussion Group on:**
Tundra, desert and grassland nitrogen inputs

Chairperson: Vera Alexander

Before launching into the serious business of evaluating total global input in the three ecosystems, a general discussion of the value of this exercise produced the following general conclusion: since nitrogen fixation in ecosystems appears to relate more to the maturity of the particular system than to other factors, perhaps the emphasis should be elsewhere than on trying to produce averages. Rates in mature, more conservative ecosystems tend to be moderately low, whereas high rates are characteristic of immature, leaky systems, or possibly stressed systems. In tundra and desert, the rates are high with respect to the overall inputs and outputs of nitrogen, even though they are not high on an absolute basis.

A second problem is the inadequacy of some methodology. For example, estimates based on microbial enumeration using standard plate count methods are questionable.

The third problem, which relates directly to the attempted exercise, was the difficulty of obtaining estimates of the areas of the various types of tundra discussed. The group therefore concentrated on what was known about average rates for specific sites.

The results of the distillation of available knowledge are shown in Table 5. True tundras of the dry meadow, wet meadow or polar desert type have rates less than 1 kg N ha^{-1} yr^{-1}. Taiga and subarctic forests range from about 2 to 5 kg N ha^{-1} yr^{-1}, with the exception of the non-typical example of minerotrophic sites within an ombrotrophic mire in Sweden. For the deserts, high rates (coupled with high denitrification occur only in high clay deserts ($10-100$ kg N ha^{-1} yr^{-1}), whereas the average for other desert types appears closer to $2-3$ kg N ha^{-1} yr^{-1}.

Table 5. Nitrogen fixation in tundra, desert and grassland.

Location	Site characteristics	kg N ha^{-1}	References
Tundra			
Devon Island, Canada	arctic, mesic meadow	1.9	Alexander (1974)
Devon Island, Canada	arctic, polar desert	0.3	Stutz & Bliss (1975)
Hardangervidda, Norway	subarctic, snowbed	2.9	Alexander (1974)
Puksalskaidi, Finland	subarctic, ombrotrophic mire	1.0	Kallio & Kallio (1975)
Stordalen, Sweden	subarctic, ombrotrophic mire	1.8	Granhall & Selander (1973)
Raessineva, Finland	subarctic, minerotrophic mire	1.3	Kallio & Kallio (1975)
Stordalen, Sweden	subarctic, minerotrophic mire	94.0*	Granhall & Selander (1973)
Hardangervidda, Norway	subarctic, dry meadow	2.6	Alexander (1974)
Barrow, Alaska, USA	subarctic, wet meadow	0.7	Barsdate & Alexander (1975)
Hardangervidda, Norway	subarctic, wet meadow	1.0	Hanssen *et al.* (1973)
Kevo, Finland	subarctic, birch forest	1.4	Alexander (1974)
Hardangervidda, Norway	subarctic, birch forest	1.7	Hanssen *et al.* (1973)
Alaska	subarctic, black spruce taiga	2.2	Billington & Alexander (1978)
Kevo, Finland	subarctic, Scots pine forest	3.5	Alexander (1974)
Northern Alaska	alpine, dry meadow	0.4	Alexander (1974)
Hardangervidda, Norway	subalpine, heath	0.6	Hanssen *et al.* (1973)
Kevo, Finland	subalpine, heath	1.4	Alexander (1974)
Desert	High clay	10 – 100**	Skujins (1976)
	Other	2 – 3	MacGregor & Johnson (1971)
Grassland			
Sweden	Field with blue-green algae	15 – 50	Henriksson (1971)
Sweden	Lakeside meadow	4 – 44	Henriksson (1971)
Nancy, France	*Dactylis glomerata*	9	Balandreau *et al.* (1974a)
Nancy, France	*Festuca viride*	9 – 24	Balandreau *et al.* (1974a)
Nancy, France	*Lolium perenne*	3	Balandreau *et al.* (1974a)
Montreal, Canada	Pasture	1	Knowles (1975)
Saskatoon, Canada	Revegetating coal mine waste	20	Paul (1975)
Matador, Canada	Native prairie	2	Paul (1975)
Pawnee, USA	Prairie	1	Copley & Reuss (1972)
USSR	*Poa pratensis*	3 – 14	Pankratova & Vaskrushev (1971)
Ivory Coast	*Andropogon*	0.12	Balandreau *et al.* (1974b)
Ivory Coast	*Loudetta*	0.3 – 8	Balandreau *et al.* (1974b)
Ivory Coast	*Hyparrhenia*	3 – 30	Balandreau *et al.* (1974b)
Brazil	*Paspalum*	9	Döbereiner *et al.* (1972)

* Small depressions and pools.
** High denitrification throughout.

Grasslands vary from moist blue-green algal rich meadows through leguminous pastures to dry semi deserts. Most grasslands are characterized by a high internal rate of N cycling with low losses and low requirements for fixed nitrogen for maintainance. Although native legumes occur in most natural grasslands, their percentage is usually low. An annual average fixation of 5 kg N ha^{-1} yr^{-1} would probably be somewhat high on a global basis for a mature system. Areas that are re-establishing a vegetation often have higher fixation rates showing the higher potential if required.

III. Report of Discussion Group on:

Nitrogen fixation in forested ecosystems

Chairperson: R. L. Todd

Data are available for only a limited number of countries. These tend to be restricted to dominant vegetation types. The absence of data for tropical systems was very obvious. In all but one case, natural systems were studied.

Data sets on nitrogen fixation in forest systems are not exhaustive, making an assessment on the significance of such processes difficult. The group encouraged continued research of the role of nitrogen fixation in forest systems with measurements including managed systems as well as natural environments. Table 6 summarizes some of the available data. This table shows that over a range of fixation rates representing 0.4 – 12 kg N ha^{-1} yr^{-1}, nitrogen fixation represented approximately 5 – 10% of the annual nitrogen cycled by the vegetation. Nitrogen fixation in most systems was equal to or greater than the input of nitrogen by precipitation.

The group had a fairly detailed discussion on techniques with the following comments:

1) There is a need to distinguish between field and laboratory values with the recommendation that *in situ* incubation procedures in the field be carried out.
2) Consideration should be given to the lag required for C_2H_2 reduction.
3) When determining a ratio for N_2 to C_2H_2, solubility of N_2, NH_4^+, C_2H_2 and C_2H_4 should be determined for the system under study.
4) The length of incubation and the atmosphere of incubation should be taken into account.

Table 6. Nitrogen fixation rates in forests.

		Location	Nitrogen fixation (kg N ha^{-1} yr^{-1})	Period of assay	Nitrogen input precipitation (kg N ha^{-1} yr^{-1})	Nitrogen fixed / N cycling in vegetation
Northern Boreal	Black Spruce	U.S.A.[1]	2.2	May–Sept.	1–2	n.d.
Middle Boreal	Birch	Finland[2]	1.4	May–Oct.	1.4	n.d.
Middle Boreal	Birch	Norway[2]	1.7	May–Sept.	2.0	n.d.
Middle Boreal	Scots Pine*	N. Sweden[3]	1	May–Dec.	1.5	n.d.
Middle Boreal	Scots Pine	Finland[2]	3.5	May–Oct.	1.0	n.d.
Southern Boreal	Scots Pine Norway Spruce	Sweden[4]	3.2	Apr.–Nov.	2–3	3/30–50
Southern Boreal	Scots Pine	Sweden[4]	0.4	Apr.–Nov.	2.0	0.4/20–30
Cold Deciduous	Planted Douglas Fir*	England[5]	3–5	Jan.–Dec.	n.d.	3–5/17–38
Cold Deciduous	Oak-Hickory	U.S.A.[6]	12	Jan.–Dec.	3.4	12/140

* Only phyllosphere and lichens.

References: [1] Billington & Alexander (1978).
[2] Alexander (1974).
[3] Huss-Danell (1978).
[4] Granhall & Lindberg (1978).
[5] Jones (1974).
[6] Todd *et al.* (1978).

5) The group recommends the publication of acetylene reduction values instead of nitrogen fixed.

6) Fixation rates are generally regulated by carbon (energy available). When possible, data for available carbon should be provided coincident with data for nitrogen fixation.

7) The impact of denitrification rates on fixation rates should be considered in further investigations of nitrogen fluxes in natural and manipulated systems.

8) It is imperative to assess all components of the system (i.e. phyllosphere, lichens, soil) over a complete annual cycle to provide a realistic evaluation of the nitrogen fixation.

IV. Report of Discussion Group on:

Aquatic fixation; Significance of salt marsh N_2 fixation

Data supplied by D. Patriquin

Table 7. Salt marsh areas.

	10^8 ha
America	0.172
Africa	0.048
Europe	0.109
Asia	0.065
Australia and others	0.050
TOTAL	0.384

Table 8. N_2 fixation rates in salt marshes.

	kg N ha^{-1} yr^{-1}
England salt marsh	
– lowest value	4.3
– highest value	462
USA (New Jersey)	4.1
Canada, Nova Scotia*	
– low marsh	153
– high marsh	9.64
– representative value	56

Global estimates = 19.2×10^5 metric tons N yr^{-1}.
* Patriquin, own calculations.

References

Alexander, V. 1974. A synthesis of the international biological programme tundra biome circumpolar study of nitrogen fixation. – In: Holding, A.J., Heal, O.W., MacLean, S.F. & Flanagan, P.S. (eds.) Soil Organisms and Decomposition in Tundra, pp. 109 – 122. Stockholm: IBP Tundra Biome Steering Committee.

Balandreau, J.P., Millier, C.R. & Dommergues, Y. 1974a. Diurnal variations of nitrogenase activity in the field. – Appl. Microbiol. 27: 662 – 665.

Balandreau, J.P., Rinaudo, G., Oumarov, M.M. & Dommergues, Y. 1974b. Asymbiotic N_2 fixation in paddy soils. – In: Proceedings of the International Symposium on N_2 Fixation, Pullman, Wash.
Barsdate, R.J. & Alexander, V. 1975. The nitrogen balance of Arctic tundra: pathways, rates and environmental implications. – J. Environ. Qual. 4: 111–117.
Billington, M. & Alexander, V. 1978. Nitrogen fixation in a black spruce (*Picea mariana* (Mill) B.S.P.) forest in Alaska. – In: Granhall, U. (ed.) Environmental Role of Nitrogen-fixing Blue-green Algae and Asymbiotic Bacteria. Ecol. Bull. (Stockholm) 26: 209–215.
Box, E. 1975. Quantitative evaluation of global primary productivity models generated by computers. – In: Leith, H. & Whittaker, R.H. (eds.) Primary Productivity of the Biosphere, pp. 265–283.
Burns, R.C. & Hardy, R.W.F. 1975. Nitrogen Fixation in Bacteria and Higher Plants. Berlin–Heidelberg–New York: Springer Verlag, 189 pp.
Copley, P.W. & Reuss, J.O. 1972. Evaluation of biological N_2 fixation in a grassland ecosystem. – IBP US Grassland Biome Technical Report No. 152, Fort Collins, Colo.
Döbereiner, J., Day, J.M. & Dart, P.J. 1972. Nitrogenase activity and oxygen sensitivity of the *Paspalum notatum-Azotobacter paspali* association. – J. Gen. Microbiol. 71: 103–116.
Fogg, G.E. 1978. Nitrogen fixation in the oceans. – In: Granhall, U. (ed.) Environmental Role of Nitrogen-fixing Blue-green Algae and Asymbiotic Bacteria. Ecol. Bull. (Stockholm) 26: 11–19.
Goering, J.J., Dugdale, R.C. & Menzel, D.W. 1966. Estimates of *in situ* rates of nitrogen uptake by *Trichodesmium* sp. in the tropical Atlantic Ocean. – Limnol. Oceanogr. 11: 614–520.
Granhall, U. & Selander, H. 1973. Nitrogen fixation in a subarctic mire. – Oikos 24: 8–15.
Granhall, U. & Lindberg, T. 1978. Nitrogen fixation in some coniferous forests. – In: Granhall, U. (ed.) Environmental Role of Nitrogen-fixing Blue-green Algae and Asymbiotic Bacteria. Ecol. Bull. (Stockholm) 26: 178–192.
Gundersen, K. 1974. A Study of Biological Nitrogen Transformations in the Water Masses of the North Central Pacific Ocean. – Technical Report HIG 74–12. Honolulu: Hawaii Institute of Geophysics, University of Hawaii. 33 pp.
Hanson, C.H. 1972. Alfalfa Science and Technology. Agronomy No. 15. Madison: American Society of Agronomy. 812 pp.
Hanssen, J.F., Lid-Torsvik, V. & Torsvik, T. 1973. Mikrobiologi. – In: IBP i Norge. Årsrapport 1972, pp. 75–93. Oslo: Norsk IBP, (In Norwegian).
Henriksson, E. 1971. Algal nitrogen fixation in temperate regions. – Plant and Soil (Special Volume), pp. 415–419.
Huss-Danell, K. 1977. Nitrogen fixation by *Stereocaulon paschale* under field conditions. – Can. J. Bot. 55: 585–592.
Jones, K., King, E. & Eastlick, M. 1974. Nitrogen fixation by free-living bacteria in the soil and in the canopy of Douglas fir. – Ann. Bot. 38: 765–772.
Kallio, S. & Kallio, P. 1975. Nitrogen fixation in lichen at Kevo, North Finland. – In: Wielgolaski, F.E. Fennoscandian Tundra Ecosystems (ed.), Vol. 1, pp. 292–304. Berlin–Heidelberg–New York: Springer Verlag.
Lie, T.A. & Mulder, E.G. 1971. Biological Nitrogen Fixation in Natural and Agriculture Habitats. – Plant and Soil, Special Volume. 590 pp.
Lieth, H. 1975a. Primary production of the major vegetation units of the world. – In: Lieth, H. & Whittaker, R.H. (eds.) Primary Productivity of the Biosphere, pp. 210–215. Berlin–Heidelberg–New York: Springer Verlag.
Lieth, H. 1975b. Modelling the primary productivity of the world. – In: Lieth, H. & Whittaker, R.H. (eds.) Primary Productivity of the Biosphere, pp. 237–263. Berlin–Heidelberg–New York: Springer Verlag.
MacGregor, A.N. & Johnson, D.E. 1971. Capacity of desert algal crusts to fix atmospheric nitrogen. – Soil Sci. Soc. Amer. Proc. 35: 843–844.
Newman, W.E. & Nyman, C.J. 1976. Proceedings of the International Meeting on Nitrogen Fixation. Pullman, Wash.
Nutman, P.F. (ed.) 1975. Symbiotic Nitrogen Fixation in Plants. IBP Synthesis Series Vol. 7. Cambridge: Cambridge University Press.
Paul, E.A. 1975. Recent studies using the acetylene reduction technique as an assay for field nitrogen fixation levels. – In: Stewart, W.D.P. (ed.) Nitrogen Fixation by Free Living Microorganisms, pp. 259–269. Cambridge: Cambridge University Press.

Pudoc, V.H. 1975. Historical survey of primary productivity research. – In: Lieth, H. & Whittaker, R.H. (eds.) Primary Productivity of the Biosphere, pp. 7–16. Berlin–Heidelberg–New York: Springer Verlag.

Rodin, L.E., Bazilevich, N.I. & Rozov, N.N. 1974. Primary production of the main world ecosystems. – In: Cave, A.J. (ed.) Proceedings of the First International Congress of Ecology. Structure Functioning and Management of Ecosystems, pp. 176–181. Wageningen: Pudoc.

Rodin, L.E., Bazilevich, N.I. & Rozov, N.N. 1975. Productivity of the world's main ecosystems. – In: Reichle, D.E., Franklin, J.F. & Goodall, D.W. (eds.) Productivity of World Ecosystems. Proceedings of a Symposium at the V. General Assembly of the Special Committee for the International Biological Program, Seattle, Washington, pp. 13–26. Washington: National Academy of Sciences.

Skujins, J.J. & Klubek, B. 1978. Nitrogen fixation and cycling by blue-green algae lichen-crusts in arid rangeland soils. – In: Granhall, U. (ed.) Environmental Role of Nitrogen-fixing Blue-green Algae and Asymbiotic Bacteria. Ecol. Bull. (Stockholm) 26: 164–171.

Stewart, W.D.P. (ed.) 1975. Nitrogen Fixation by Free Living Micro-organisms. IBP Synthesis Series Vol. 6. Cambridge: Cambridge University Press. 471.

Stutz, R.C. & Bliss, L.C. 1975. Nitrogen fixation in soils of Truelove Lowland, Devon Island, Northwest Territories. – Can. J. Bot. 53: 1387–1399.

Svensson, B.H. & Söderlund, R. (eds.) 1976. Nitrogen, Phosphorus and Sulphur – Global Cycles. Ecological Bulletins (Stockholm) Vol. 22. 192 pp.