the burial of surface ice or snow by eolian or alluvial deposits (*13*). The fretted terrain (Fig. 1) occurs in an area thought to be composed of volatile-rich, blanket deposits, probably having a large eolian component (*14*). Although terrestrial thermokarsts are significantly smaller in scale than the martian fretted terrain the terrestrial fretted terrain may be significantly older and consequently more well developed. This interpretation is in agreement with that of Sharp (*2*).

Analysis of adjacent ERTS-1 scenes suggests that much of the surface topography on the Alaskan Arctic Coastal Plain is an expression of subsurface structural control of the underlying Cretaceous rocks (*15*). The drainage patterns of most of the major rivers (for example, upper courses of the Colville River, Maybe Creek, Price River, and Kay River) probably reflect underlying structural trends. This is remarkable inasmuch as this underlying structure finds expression through as much as 50 m of overburden. In Fig. 2, one notes that the general alignment of the thermokarsts and undegraded upland areas parallels regional structural trends. In fact, initial degradation of the subsurface ice in this area may have initiated along en echelon minor faults where thermal anomalies were transmitted upward. With continued degradation thermokarst depressions probably became enlarged and began to coalesce. The drainage networks present are undeveloped and insignificant in comparison with the thermokarsts which dominate this setting. Fluvial erosion appears to be inconsequential here in comparison with thermal erosion as the agent responsible for the development of the local relief.

The recognition of this terrestrial analog was possible because of the obliteration of the confusing albedo patterns of standing water and vegetation by snow cover, a low sun angle, and the availability of suitable image enhancement techniques. Success in this area leads one to expect that other terrestrial analogs of martian permafrost terrain will be found. We are presently investigating satellite imagery of the arid Yakutian Lowlands of eastern Siberia where ovoid thermokarst depressions up to 40 m in depth and 5 to 10 km in length have been reported.

LAWRENCE W. GATTO
DUWAYNE M. ANDERSON
U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, New Hampshire 03755

References and Notes

1. The 10 July 1973 issue of the *Journal of Geophysical Research* presents the results of the analysis of Mariner 9 data through 15 November 1972; D. M. Anderson, L. W. Gatto, F. Ugolini, paper presented as part of the North American Contribution to the Second International Permafrost Conference, National Academy of Sciences, Washington, D.C., 1973; R. B. Leighton and B. C. Murray, *Science* **153**, 136 (1966); D. J. Milton, *ibid.* **183**, 654 (1974); D. M. Anderson, E. S. Gaffney, P. F. Low, *ibid.* **155**, 319 (1967); R. B. Leighton, N. H. Horowitz, B. C. Murray, R. P. Sharp, A. H. Herriman, A. T. Young, B. A. Smith, M. E. Davies, C. B. Leovy, *ibid.* **166**, 49 (1969); R. P. Sharp, L. A. Soderblom, B. C. Murray, J. A. Cutts, *J. Geophys. Res.* **76**, 331 (1971).
2. R. P. Sharp, *J. Geophys. Res.* **78**, 4073 (1973).
3. As determined by aerial reconnaissance and reference to U.S. Geological Survey topographic maps.
4. Dr. A. Goetz of the Jet Propulsion Laboratory provided computer time and suggested processing techniques to enhance features of interest. P. Paluzzi of the IPL prepared computer programs, described the processing techniques, and acquired the enhanced photographs. A. Gillespie made several useful suggestions for computer processing. Their assistance is greatly appreciated.
5. J. Dylik, in *Encyclopedia of Geomorphology* (Reinhold, New York, 1968), pp. 1149–1151.
6. F. E. Are, paper presented at the Second International Permafrost Conference, Yakutsk, U.S.S.R., 1973.
7. H. M. French, *Can. J. Earth Sci.* **2**, 785 (1974).
8. R. F. Black, *U.S. Geol. Surv. Prof. Pap. 302-C* (1964), p. 59.
9. T. G. Payne, S. W. Dana, W. A. Fischer, S. T. Yuster, P. D. Krynine, G. Gryc, H. Tappen, R. H. Morris, E. H. Lathram, *U.S. Geol. Surv. Oil Gas Invest. Map OM-126* (1952).
10. J. R. Mackay and R. F. Black, paper presented as part of the North American Contribution to the Second International Permafrost Conference, National Academy of Sciences, Washington, D.C., 1973.
11. R. F. Black, *Biul. Peryglacjalny* **19**, 131 (1969).
12. T. Czudek and J. Demek, *Qualt. Res. (N.Y.)* **1**, 103 (1970).
13. The stratified appearance of some of the martian polar terrain may be caused by similar interlayering.
14. D. U. Wise, personal communication.
15. E. H. Lathram, I. L. Tailleur, W. W. Patton, Jr., *2nd ERTS-1 Symp. Significant Results* **1**, 257 (1973); E. H. Lathram, *3rd ERTS-1 Symp. Significant Results* (1973), p. 39 (abstr.); W. A. Fischer and E. H. Lathram, *Oil Gas J.* **71** (No. 21), 97 (1973).
16. We thank R. P. Sharp, J. A. Cutts, and D. U. Wise for helpful suggestions and for critically reviewing this manuscript during its preparation. This report presents the results of research performed with funds provided by the Planetology Program Office, Office of Space Science, National Aeronautics and Space Administration Headquarters, under grant NGR W-13,277, PR:10-9336,R/D 80X0108(71) 384-50-80.

3 September 1974; revised 24 December 1974 ■

Nitrogen Fixation in a Coral Reef Community

Abstract. *Algal reef flats at Enewetak Atoll, Marshall Islands, fix atmospheric nitrogen at rates comparable to those in managed agriculture. The dominant nitrogen fixer appears to be the blue-green alga* Calothrix crustacea. *Since this nutrient enrichment contributes to the high productivity of adjacent coral reefs and undoubtedly to atoll lagoons, it is recommended that the algal reef flats receive increased conservation priority.*

Coral reef communities are characterized by high rates of biological productivity. The mechanism by which this is accomplished has puzzled marine biologists for years. These communities obtain their nutrients from the overlying waters, and tropical marine waters are generally characterized by low levels of dissolved and particulate nutrients. Fixed nitrogen is in particularly low supply and has been shown to be the major limiting nutrient for phytoplankton production in the tropical Pacific (*1*).

In 1971, during the Symbios expedition to Enewetak Atoll, we observed that the ocean water became markedly enriched with various forms of dissolved and particulate nitrogen as it flowed across a shallow windward interisland reef (*2*). The net rate of nitrogen export was of the order of 3 kg ha^{-1} day^{-0} (*3*). We subsequently found that the source of this localized superabundance of fixed nitrogen was a number of nitrogen-fixing algae, the most abundant and important of which was *Calothrix crustacea* (*4*). Here we describe the role of this species in the nitrogen budget and the biological productivity of Enewetak reef communities.

Calothrix crustacea, a heterocystous blue-green alga, occurs as a thin, yellow-brown, often almost unispecific film covering large portions of the windward intertidal reef flat at Enewetak. At low tide, most of these algae remain moist. During higher stages of the tide, herbivorous reef fish, notably several species of parrotfish and surgeonfish, graze the intertidal reef flat *Calothrix* community. Their tooth marks in the reef rock provide evidence of the thoroughness with which they crop this alga.

Along the upper intertidal bench zone another growth form of the same species occurs as a black, feltlike mat up to 5 mm thick. At low tide, most of this mat dries out. It is not heavily grazed by fish owing to the shallowness of the water in which it grows. In areas of the windward reef flat and outer

Table 1. Nitrogen fixation rates of various communities at Enewetak Atoll, January to February 1974. Values for nitrogen fixed are given for the substrate surface areas as means (10^{-9} mole hr^{-1} cm^{-2}) ± the standard error. Number of replications in parentheses.

Location	Mean rates (10^{-9} mole hr^{-1} cm^{-2})	
	Full daylight intensity	Dark
Intertidal reef flat *Calothrix* community	55 ± 12.1 (11)	1.9 ± 0.14 (3)
Upper intertidal reef bench *Calothrix* community	34 ± 6.0 (7)	
Random interisland coral community and reef rubble community samples	24 ± 6.0 (11)	0.27 ± 0.039 (2)
Outer reef slope	4.5 ± 1.2 (4)	

reef slope dominated by other algae, *C. crustacea* is found ubiquitously as an epiphyte.

Nitrogen fixation rates on the algal reef flat and elsewhere in the reef communities at Enewetak were estimated by the acetylene reduction technique (*3*). Rather than use only a starting and terminal determination on an incubation, we analyzed the gas phase for ethylene a number of times during the incubations. We found considerable variation in the length of time required for these communities to reduce acetylene at linear rates under the natural light regime. Similarly there was variation in the time required for reduced rates to become linear when samples were placed in the dark. About 25 percent of the samples immediately reduced acetylene at a linear rate; most of the remainder also started abruptly (the median lag time was about 45 minutes), but a few showed a gradually increasing rate with time. We have no explanation of this observation but caution other workers that using only a starting and terminal ethylene value may underestimate nitrogen fixation rates if their experimental materials exhibit a similar lag phenomenon.

Calothrix crustacea growing on the reef flat appears well adapted to the harsh intertidal environment at Enewetak, where at low tide it is exposed to essentially fresh water during heavy rains and, during clear days, to high salinities due to evaporation, and to temperatures as high as 38°C. Experimental salinities of 45 parts per thousand (ppt) and 3 ppt had no appreciable effect on fixation rates. Fixation rates approximately doubled between temperatures of 27° and 36°C; at 39°C nitrogen fixation rates were higher than at 36°C for 1 to 2 hours, then became erratic and finally dropped to zero. At 24°C, a lower temperature than the algae ever encountered naturally at Enewetak, nitrogen fixation ceased entirely. Stirring of the incubation medium had no effect on fixation rates (*5*). When *Calothrix*-covered rocks were incubated moist in air, fixation rates were the same as in seawater.

Nitrogen fixation rates at the reef surface (Table 1) are equivalent to an average rate of 1.8 kg ha^{-1} day^{-1} (*6*). This is not significantly different from the rate previously mentioned based on the nitrogen budget of the interisland reef (*3*). These rates are among the highest ever reported for terrestrial or marine communities (*7*).

Although the biomass of *C. crustacea* was much higher on the upper intertidal reef bench, largely because of its inaccessibility to grazing fish, fixation rates of moist samples averaged only about 60 percent of the fixation rates on the reef flat (Table 1). This is probably a result of the algae not being in an active growth phase because of reduced grazing. Samples taken from the dry mat at low tide did not fix nitrogen.

Samples of algal communities not dominated by *C. crustacea*, taken at random in shallow interisland coral and coral rubble communities fixed nitrogen at a mean rate of about 40 percent of that on the reef flat per unit area of substrate surface (Table 1). Here the surface area colonized by algae per unit of horizontal area (*8*) is much greater than that on the algal flat. Per unit of horizontal area, nitrogen fixation rates in the coral and reef rubble zones may be as high as on the reef flat.

There are at least three important routes by which nitrogen fixed by *Calothrix* enters the rest of the reef community.

1) As noted above, fish graze upon these algae (*9, 10*). Chartock (*10*) has shown that fish grazing on the reef flat at Enewetak have a low assimilation efficiency. More than half the fixed carbon in the food they consume (and thus presumably a sizable fraction of the nitrogen they consume) is released into the water as feces. The recently fixed nitrogen in the feces once again enters the food chain when ingested by a variety of scatophagous reef invertebrates.

2) There are areas on the reef front where *Calothrix* grows prolifically, but continuous strong turbulence associated with breaking waves prevents herbivorous fish from grazing it efficiently (and prevents us from sampling it). Here large portions of *Calothrix* are broken off by the surge and washed downstream into the reef community where they settle out and are fed upon by various reef herbivores and detritivores. Benthic algal fragments constituted by far the largest portion of the net plankton on the windward interisland reef at Enewetak, and *Calothrix* constituted 20 to 60 percent (by volume) of these fragments (*11*). The input of fixed carbon in the form of benthic algal fragments was shown by Johannes and Gerber (*11*) to be essential to balance the respiratory energy requirements of the coral reef community downstream of the outer reef edge, and amounted to a mean net input of about 0.5 g m^{-2} day^{-1}. Newly fixed nitrogen enters the reef community simultaneously by the same mechanism.

3) Finally, members of the genus *Calothrix* in culture are known to release 40 to 60 percent of their fixed nitrogen into solution, largely in the form of peptides and free amino acids (*12*). The major fraction of the fixed nitrogen exported by the Enewetak reef community is in the form of dissolved organic compounds (*2, 3*), at least some of which are undoubtedly available to benthic as well as planktonic saprophages. Jones and Stewart (*13*), working with *Calothrix* in Scotland, showed that a large fraction of the nitrogen fixed was subsequently transferred to associated plant species, presumably through transfer of organic nitrogen.

The island effect, that is, the observed enhanced productivity adjacent to tropical islands in oligotrophic waters, has been ascribed to land drainage, upwelling, or nutrient accumulation and recycling by the biota (*14*). Observed concentrations of zooplankton have also been higher in atoll lagoons than in the adajacent ocean (*15*). Increased concentrations of particulate and dissolved combined nitrogen resulting from biological nitrogen fixation on adjacent reef algal flats undoubtedly contributed to the increased productivity in both of these situtations (*16*).

Calothrix is distributed abundantly and ubiquitously in Pacific coral reef communities and in other shallow tropical marine environments (*17*). Other nitrogen-fixing blue-green algae such as *Hormothamnion* (*5*) are also abundant in some reef communities. These often drab-looking communities have been accorded a much lower conservation priority than the adjacent colorful coral communities. The research described here indicates that these algal reef flats are indeed of considerable importance as a source of fixed nitrogen for adjacent communities and consequently should be accorded a higher priority for conservation where siting of dredging, construction, and industrial outfalls are concerned.

W. J. WIEBE
Department of Microbiology, University of Georgia, Athens 30602

R. E. JOHANNES
Department of Zoology, University of Georgia

K. L. WEBB
Virginia Institute of Marine Science, Gloucester Point 23062

References and Notes

1. W. H. Thomas, *Limnol. Oceanogr.* **15**, 31 (1970).
2. R. E. Johannes and Symbios Team, *BioScience* **22**, 541 (1972).
3. K. L. Webb, W. D. DuPaul, W. Wiebe, W. Sottile, R. E. Johannes, *Limnol. Oceanogr.* **20**, 198 (1975).
4. The algae were identified at Enewetak by Dr. Roy Tsuda, University of Guam.
5. In contrast, we found that vigorous stirring resulted in an increase of about 50 percent in fixation rates for *Hormothamnion enteromorphoides*, another Enewetak blue-green alga (R. E. Johannes and W. J. Wiebe, in preparation).
6. Our estimate for the daily nitrogen fixation rate on the reef flat was based on an average of the day and night rates, and on the estimate that the ratio of algal-covered surface per horizontal square meter of algal pavement zone is 1.9 for a similar type of reef f [A. L. Dahl, *Mar. Biol. (Berl.)* **23**, 239 (1973)].
7. The highest measured terrestrial rates of nitrogen fixation appear to be from 130 to 330 kg ha^{-1} $year^{-1}$ for alfalfa fields [M. Alexander, *Microbial Ecology* (Wiley, New York, 1971)]. Highest recorded marine rates of about 3 kg ha^{-1} day^{-1} are for shallow tropical seagrass communities [J. J. Goering and P. L. Parker, *Limnol. Oceanogr.* **17**, 320 (1972)].
8. Because the surface contours of these communities are quite variable and complex, we did not attempt to calculate fixation rates per unit horizontal area; however, there is undoubtedly at least 4 m^2 of algal-covered surface per horizontal square meter of reef, and thus it is reasonable to assume at least equal rates.
9. R. Tsuda (personal communication) found that about 60 percent of the gut contents of five specimens of the surgeonfish *Acanthurus guttatus*, which he examined at Enewetak, consisted of *Calothrix crustacea*. Although *Acanthurus triostegus* and *Scarus jonsi* profusely graze the *Calothrix* turf on the reef flat at high tide, the bulk of the tooth marks probably result from *Acanthurus guttatus*; G. J. Bakus, *Micronesia* **3**, 135 (1967).
10. M. Chartock, thesis, University of Southern California (1971).
11. R. E. Johannes and R. Gerber, in *Proceedings of the 2nd International Conference on Corals and Coral Reefs*, Great Barrier Reef Committee, Eds. (1974), vol. 1, p. 97.
12. K. Jones and W. D. P. Stewart, *J. Mar. Biol. Assoc. U.K.* **49**, 475 (196 A. Watanabe, *Arch. Biochem. Biophys.* **34**, 50 (1951).
13. K. Jones and W. D. P. Stewart, *J. Mar. Biol. Assoc. U.K.* **49**, 701 (1969).
14. M. S. Doty and M. Oguri, *J. Cons. Cons. Int. Explor. Mer* **22**, 33 (1956); E. C. J. Jones, *ibid.* **27**, 223 (1962); F. Sander, *Carib. J. Sci.* **13**, 179 (1973).
15. M. W. Johnson, *Trans. Am. Geophys. Union* **30**, 238 (1949); M. W. Johnson, *U.S. Geol. Surv. Prof. Pap.* **260-F**, 301 (1954).
16. Fixed nitrogen levels are generally even lower in the Caribbean than in the tropical Pacific. Nitrogen fixation might thus provide even greater stimulus for marine productivity in the Caribbean. Bunt *et al.* were unable to find much nitrogen fixation in Florida, the Bahamas, or the Virgin Islan [J. S. Bunt, K. E. Cooksey, M. A. Heeb, C. C. Lee, B. F. Taylor, *Nature (Lond.)* **227**, 1163 (1970); ———, in *Scientists-in-the-Sea*, J. W. Miller, J. G. Van Derwalker, R. A. Waller, Eds. (U.S. Department of the Interior, Washington, D.C., 1969), p. VI-247]. Their observations were at depths of 20 m or more. At Enewetak, we also found much lower nitrogen fixation rates at depths of 3 to 6 m on the outer reef slope (Table 1) than in shallower water. This possibly is a result of the spectral distribution of light at these depths. There is an indication that blue light does not support nitrogen fixation in some blue-green algae [W. M. Pulich, Jr., and C. Van Baalen, *Arch. Microbiol.* **97**, 303 (1974)].
17. Species of the genus *Calothrix* also appear to be important in marine environments of the temperate zone. Nitrogn fixation, mainly by *Calothrix contarenii*, could account for the nitrogen biomass of the marsh grasses in a New England salt mar [C. Van Raalte, I. Valliela, E. K. Carpenter, J. M. Teal, *Estuarine Coastal Mar. Sci.* **2**, 301 (1974)]. Nitrogen fixation by *C. scopulorum* has been reported to be significant in the supralittoral zone in Norway [P. Wärmling, *Bot. Mar.* **16**, 237 (1973)].
18. Contribution 666 from the Virginia Institute of Marine Science. Contribution from the Mid-Pacific Marine Laboratory. Supported in part by the Oceanography Section, National Science Foundation (grants GA 35866 and 35806), and by the Atomic Energy Commission [grant AT-(20-2)-226] for the operation of the Mid-Pacific Marine Laboratory. We thank M. Gresham, J. Olmon, P. Postal, and A. Thompson for technical assistance.

9 December 1974; revised 31 January 1975

Thyroid Allograft Immunogenicity Is Reduced after a Period in Organ Culture

Abstract. *The survival time of mouse thyroid, transplanted under the kidney capsule of an H-2 incompatible recipient, is extended by holding the thyroid in organ culture for 12 days prior to transplantation.*

The generally accepted view of allograft rejection postulates that histocompatibility antigen (H antigens) are strong immunogens which can elicit a vigorous response to T (thymus derived) cells in the allogeneic host, and that this response is responsible for the initiation of graft rejection. Because H antigens form an integral part of the cell membrane and are widely distributed throughout the tissues of the body (*1*), there would appear to be little point in attempting to reduce the immunogenicity of a tissue transplant by treatments other than those directed at suppressing the host's immune system.

However, our studies of allograft reactions (*2–4*) indicate that the conventional view is inadequate. In our opinion, H antigens by themselves are not strongly immunogenic, and the generation of a vigorous T cell response specific for H antigens requires the simultaneous presentation of both H antigen and an allogeneic stimulus to the potentially responsive T cell population (*4*). The allogeneic stimulus is an inductive stimulus provided by metabolically active lymphoid cells (*5*) (the term lymphoid includes both phagocytic and nonphagocytic lymph-borne cells). According to this view of allograft rejection the fate of an allotransplant might sometimes be enhanced by treatments that remove from the graft those lymphoid cells which provide the postulated allogeneic stimulus. These latter cells play a major role in the sensitization of the host to foreign antigens (*3, 4*).

The reports of Jacobs and Huseby (*6*) and those of Summerlin (*7*) and Summerlin *et al.* (*8*), that allograft survival could be enhanced by the cultivation of tissue in organ culture prior to transplantation, are consistent with our view of graft rejection. The period in organ culture might deplete the tissue of viable hematogenous elements and lymphoid cells that could take part in allogeneic interactions with host lymphoid cells. We were unable to repeat the experiments of Summerlin *et al.* (*8*) with mouse skin allografts. In our experience, both isografts and allografts failed to take on recipient mice after being held in organ culture. We attributed this result to a failure of the cultured skin (either isogeneic or allogeneic) to revascularize before