INCREASE IN TOTAL GLOBAL BIOMASS OVER TIME

Michael J. Benton, Department of Geology, The University, Newcastle upon Tyne, England, U. K., NE1 7RU.

Received September 27, 1978; March 22, 1979

ABSTRACT. It has been proposed recently that global biomass has not increased significantly in the last 3.3 x 10^9 years. However, several lines of evidence suggest that biomass has increased considerably several times in the evolution of life and an alternative explanation is given for lines of geochemical evidence that apparently contradict this conclusion.

* * *

Van Valen (1976: 190-1) reviews some evidence relating to levels of organic carbon in Precambrian rocks and concludes that any increase in primary productivity in the Precambrian "was negligible even on a time scale of many million years". The amount of primary productivity determines the total biomass of plants and animals present at a particular time, and Van Valen's conclusion is equivalent, therefore, to saying that biomass levels have remained constant throughout and since the middle Precambrian ("an approximate constancy in available worldwide trophic energy since at least the Precambrian"). The evidence apparently in favour of this conclusion derives from studies of $^{13}C:^{12}C$ ratios and carbon cycling rates. However, these geochemical data have been wrongly interpreted, and biological evidence (evolution of aerobes, effects of changes in early earth atmosphere composition, introduction of terrestrial life) seem to contradict this conclusion. In this paper, these lines of evidence for and against Van Valen's conclusion are reviewed. The intuitive assumption that biomass has increased (whether or not the total number of species has increased) appears to be supported by the greater weight of evidence and an explanation is offered for the evidence that seems to oppose this assumption.

EVIDENCE GIVEN FOR CONSTANT BIOMASS OVER TIME

Many studies of carbon isotopes in rocks of all ages have been made (e.g. Oehler et al., 1972; Eichmann and Schidlowski, 1975; Schidlowski et al., 1975; Dimroth and Kimberley, 1976; Goodwin et al., 1976; Veizer and Hoefs, 1976; Galimov, 1977). During photosynthesis, plants select ^{12}C in preference to ^{13}C and the ratio $^{13}C:^{12}C$ ($\delta^{13}C$) is lower in organic carbon than in inorganic carbon (Garrels and Mackenzie, 1971; Faure, 1977). The conclusion from these studies seems to be that $\delta^{13}C$ in limestones and dolomites has remained constant for some 3.3 x 10^9 years and this could be used as evidence for constancy of trophic energy through time (e.g. Van Valen, 1976). However, since they are proportions, they do not indicate the total relative amounts of either organic or inorganic carbon at any one time in the earth's history, and merely suggest that photosynthesis of the present kind has been the dominant mechanism for primary production through time. It should be noted, also, that some authorities find $\delta^{13}C$ values that increase with time in Precambrian to Recent kerogens (Degens, 1969), in Palaeozoic sediments (Welte et al., 1975), and in mudstones (Jackson et al., 1978). But probably none of these apparent time trends is significant since $\delta^{13}C$ values seem to correlate with relative continental area and tectonic state, if anything (Galimov, 1977).

* * * * * *

Evolutionary Theory 4:123-128 (July, 1979)
The editors thank M.E. Baur, R.M. Garrels, and K.J. Towe for their help in evaluating this paper.

Junge *et al.* (1975) present a mathematical model for the operation of the terrestrial carbon cycle that offers an explanation for the approximate constancy of the $\delta^{13}C$ values of marine carbonates in terms of constant phosphate levels (the limiting nutrient for plants). The constancy over time of $\delta^{13}C$ values fits well the dynamic steady state model of the carbon/oxygen cycle proposed by Garrels *et al.* (1976), who also show that, theoretically, a doubling of photosynthesis (or biomass) does not increase the organic carbon buried in the long term.

A second suggested line of evidence for the constancy of trophic energy through time is derived from the conclusion, based on studies of carbon cycling, that the present-day "annual oxidation of fossil organic carbon exposed to weathering must be about equal to the new carbon buried" (Garrels and Perry, 1974). Van Valen (1976) interprets this "to mean that there has been an approximately steady state in the rate of deposition of reduced carbon for at least much of the Phanerozoic" and that net photosynthesis and the efficiency of trophic energy use have remained roughly constant worldwide. This may be true for the Phanerozoic, but Garrels *et al.* (1976) propose that, when atmospheric O_2 levels were low, the organic carbon fraction buried was much higher than its present level of 0.1%. Thus, constant levels of organic carbon in ancient rocks indicate that the rate of photosynthesis (and total biomass) could have been much lower than today since relatively more of the organic carbon produced was buried.

EVIDENCE FOR INCREASING GLOBAL BIOMASS OVER TIME

On the other hand, several lines of evidence suggest a real increase in available trophic energy with time. Certain authors have drawn this conclusion, probably without justification, from measurements of amounts of organic carbon over time. For example, Ronov and Migdisov (1970) and Ronov (1971) found a rise in the average content of organic matter in sedimentary rocks from 0.3 wt.% in the later Precambrian to about 0.8 or 0.9 wt.% today. The organic matter in sedimentary rocks is composed of kerogen (95%), whose heterogeneity and complexity may mask trends in $C_{org.}$ content (Jackson *et al.*, 1978), producing irregular variations with time in $\delta^{13}C$ for kerogen (Leventhal *et al.*, 1975), and an extractable fraction that gives more standardised values. Jackson (1973, 1975) has shown that the concentration of this benzene/ethanol extractable "humic matter" (diagenetically altered algal pigments and lipids) in sedimentary rocks has tended to increase with geological time.

However, it should be noted that these authors have based their conclusions on relatively small numbers of samples. In a study of 800 shale samples from the Canadian shield, Cameron and Jonasson (1972) obtained values for average "organic" carbon content ranging from 0.10 - 7.6% (means: 0.74 for 2.5 x 10^9 y.a. and 1.61 for 1.8 x 10^9 y.a. - a marked increase in 7 x 10^8 years, of what significance?). Amounts of organic carbon vary enormously in rocks of the same age, and thus ratios of organic carbon, unless averaged worldwide, or measured in rocks deposited in identical conditions (impossible to establish), cannot offer information on biomass. Also, amounts of organic carbon may vary owing to diagenetic effects (Nagy *et al.*, 1974).

The apparent temporal increase in organic carbon was provisionally ascribed to a possible increase in biological productivity (Jackson, 1975; Jackson and Moore, 1976; McKirdy, 1974). Other suggested explanations include increase in rates of accumulation of organic matter in sediments

(Jackson and Moore, 1976; McKirdy, 1974), the evolution of marine metazoans that produced fecal pellets that were rapidly buried and preserved organic carbon (Bordovskiy, 1965), and post-depositional loss of humic matter in more recent sediments. However, Jackson (1977) suggests that post-depositional alteration of "humic" matter at least is minimal and that variations in the chemical properties of the organic matter depend on evolutionary changes in the nature of the biological source material. This geochemical evidence may indicate increased productivity with time and the early history of life tends to support this conclusion.

The first life probably consisted of anaerobes and Cloud (1974, 1976) suggests that the development of photosynthesis and the consequent production of excess oxygen caused problems for them. Since they probably did not have oxidising enzymes, oxygen had to be disposed of in some way, possibly by external combination with ferrous iron. Thus, iron in solution may have imposed a limitation on biomass increase, although some doubts have been expressed regarding Cloud's model (Garrels et al., 1973; Baur, 1978). When oxidising enzymes evolved (approx. 2 x 10^9 y.a.), oxygen could be released freely and, freed from their dependence on external oxygen depressors, the biomass of life could increase rapidly. Aerobic respiration also permitted the development of Metazoa, possibly 6.8 x 10^8 years ago (Cloud, 1974, 1976), which coincides with a rise in organic carbon recorded by several authors (Bordovskiy, 1965; Ronov and Migdisov, 1970; Jackson, 1973, 1975; Eichmann and Schidlowski, 1975; Veizer and Hoefs, 1976). Margulis et al. (1976) suggest that Metazoa developed late because of the complexity of the mitotic-meiotic system and the length of time it took to evolve. Aerobic respiration is more efficient than anaerobic, the complete aerobic cycle producing about 20 times as much energy as the anaerobic from an identical starting mass of glucose (Nason and Dehaan, 1973). The first aerobes could develop a considerably greater biomass than anaerobes and this had profound effects on the atmosphere.

The early earth atmosphere was rich in CO_2 and poor in O_2 (Cloud, 1974, 1976; Margulis et al., 1976; Smith, 1976). CO_2 decreased and free O_2 probably began to accumulate in the atmosphere 2 x 10^9 years ago (Cloud, 1974, 1976). The O_2 was released and carbon may have been passed to carbonate sediments and taken up by the increased biomass of aerobes. Degens (1969) postulates a higher molecular CO_2 content of Precambrian and early Palaeozoic seas than at later periods, and this is also consistent with an increase in global productivity since then.

The development of a protective ozone screen (possibly well before 7 x 10^8 years ago (Margulis et al., 1976)), consequent on the release of free O_2, and the evolution of life that could cope with free O_2, and had other adaptations for protection and support, may have enabled an expansion of life into shallow waters and on to land in the Precambrian. Jackson (1973, 1975) and Jackson et al. (1978), working from differences in the isotopic mass of land-derived and marine organic carbon, suggest that algae colonised the land between 1.05 and 1.3 x 10^9 years ago. The development of terrestrial life both in this early form and, more extensively, also in the early Palaeozoic, must have produced increases in global biomass.

EXPLANATION OF THE APPARENT EVIDENCE FOR CONSTANT BIOMASS

Various lines of evidence suggest that global biomass has increased, several times at least, with decreasing geological age. However, certain geochemical data could be interpreted as indicating that levels of organic carbon have remained constant for 3 x 10^9 years. Assuming that the rate of incorporation of organic carbon into sediments has remained approximately constant, it should, however, be noted that by far the largest volume of sedimentary rocks has been formed in seawater (Garrels and Mackenzie, 1971). It has been estimated (Bolin, 1970) that land plants fix ½ to 2/3 of the carbon fixed annually in the sea. Some carbon fixed by land plants is lost to the oceans via streams and groundwater runoff and some is buried on land (less than 1% (Garrels and Perry, 1974)), but most is recycled through terrestrial decomposers and oxidised into atmospheric CO_2. Thus the biomass on land has less chance of being detected in a future sedimentary rock. Although respiratory CO_2 from land life would be available to marine algae for photosynthesis, the amount of atmospheric CO_2 that dissolves approximately equals the amount emitted from seawater (Bolin, 1970). Thus, available trophic energy *in the sea* may have remained constant for any given surface area for 3 x 10^9 years, or rates of biological carbon cycling may have accelerated with an increased biomass, but worldwide trophic energy must have increased because of the additional land life. The amount of carbon stored in sediments does not depend solely on biomass, but also on its distribution over different environments.

It seems most likely that total global biomass has increased over time, although presumably fluctuating widely. Biomass increase is limited by rates of geochemical cycling and by the efficiency of energy uptake. Today, only a very small percentage of solar energy reaching the earth is harnessed by green plants (about 1% (Pianka, 1974)). An even smaller percentage may have been utilised 3 x 10^9 years ago because of the less efficient energy conversion by a smaller biomass of anaerobes and because of the absence of terrestrial life.

ACKNOWLEDGEMENTS

I sincerely thank Dr Togwell A. Jackson (Winnipeg), Dr Michael Pearson and Mr John A. H. Benzie (Aberdeen) for many valuable comments, and the referees, Dr R. M. Garrels, Dr M. Baur, and Dr K. M. Towe, for useful criticism.

REFERENCES

Baur, M. E., 1978. Thermodynamics of heterogeneous iron-carbon systems: implications for the terrestrial primitive reducing atmosphere. Chem. Geol., 22: 189-206.

Bolin, B., 1970. The carbon cycle. Scient. Am., 223(3): 124-132.

Bordovskiy, O. K., 1965. Accumulation and transformation of organic substances in marine sediments. Marine Geol., 3: 1-114.

Cameron, E. M. and Jonasson, I. R., 1972. Mercury in Precambrian shales of the Canadian shield. Geochim. Cosmochim. Acta, 36: 985-1005.

Cloud, P., 1974. Evolution of ecosystems. Am. Scient., 62: 54-66.

________, 1976. Beginnings of biospheric evolution and their biogeochemical consequences. Paleobiology, 2: 351-387.

Degens, E. T., 1969. Biogeochemistry of stable carbon isotopes. *In*: G. Eglinton and M. T. J. Murphy (eds.), Organic geochemistry. Springer, New York, p. 3¼4-329.

Dimroth, E. and Kimberley, M. M., 1976. Precambrian atmospheric oxygen: evidence in the sedimentary distribution of carbon, sulfur, uranium, and iron. Can. J. Earth Sci., 13: 1161-1185.

Eichmann, R. and Schidlowski, M., 1975. Isotopic fractionation between coexisting organic carbon-carbonate pairs in Precambrian sediments. Geochim. Cosmochim. Acta, 39: 585-595.

Faure, G., 1977. Principles of isotope geology. Wiley, New York.

Galimov, E. M., 1977. Variations of the carbon cycle at present and in the geological past. In J. O. Nriagu (ed.), Environmental biogeochemistry. Ann Arbor Science, Ann Arbor, Michigan, p. 3-12.

Garrels, R. M., Lerman, A., and Mackenzie, F. T., 1976. Controls of atmospheric O_2 and CO_2: past, present and future. Am. Scient., 64: 306-315.

____________ and Mackenzie, F. T., 1971. Evolution of sedimentary rocks. Norton, New York.

____________ and Perry, E. A., Jr., 1974. Cycling of carbon, sulfur and oxygen through geologic time. In E. D. Goldberg (ed.), The Sea, vol. 5: 303-336.

____________, Perry, E. A. Jr., and Mackenzie, F. T., 1973. Genesis of Precambrian iron-formations and the development of atmospheric oxygen. Econ. Geol., 68: 1173-1179.

Goodwin, A. M., Monster, T., and Thode, H. G., 1976. Carbon and sulfur isotope abundances in Archaean iron formations and early Precambrian life. Econ. Geol., 71: 870-891.

Jackson, T. A., 1973. "Humic" matter in the bitumen of ancient sediments: variations through geologic time. Geology, 1: 163-166.

____________, 1975. "Humic" matterin the bitumen of pre-Phanerozoic and Phanerozoic sediments and its paleobiological significance. Am. J. Sci., 275: 906-953.

____________, 1977. A relationship between crystallographic properties of illite and chemical properties of extractable organic matter in pre-Phanerozoic and Phanerozoic sediments. Clays Clay Miner., 25: 187-195.

____________, Fritz, P. and Drimmie, R., 1978. Stable carbon isotope ratios and chemical properties of kerogen and extractable organic matter in pre-Phanerozoic and Phanerozoic sediments: their interrelationships and possible paleobiological significance. Chem. Geol., 21: 335-350.

____________, and Moore, C. B., 1976. Secular variations in kerogen structure and carbon, nitrogen, and phosphorus concentrations in pre-Phanerozoic and Phanerozoic sedimentary rocks. Chem. Geol., 18: 107-136.

Junge, C. E., Schidlowski, M., Eichmann, R., and Pietrek, H., 1975. Model calculations for the terrestrial carbon cycle: carbon isotope geochemistry and evolution of photosynthetic oxygen. J. geophys. Res., 80: 4542-4552.

Leventhal, J., Suess, S. E., and Cloud, P., 1975. Nonprevalence of biochemical fossils in kerogen from pre-Phanerozoic sediments. Proc. natn. Acad. Sci. USA, 72: 4706-4710.

McKirdy, D. M., 1974. Organic geochemistry in Precambrian research. Precamb. Res., 1: 75-137.

Margulis, L., Walker, J. C. G., and Rambler, M., 1976. Reassessment of roles of oxygen and ultraviolet light in Precambrian evolution. Nature, Lond., 264: 620-624.

Nagy, B., Kunen, S. M., Zumberge, J. E., Long, A., Moore, C. B., Lewis, C. F., Anhaeusser, C. R., Pretorius, D. A., 1974. Carbon content and carbonate ^{13}C abundances in the early Precambrian Swaziland sediments of South Africa. Precamb. Res., 1: 43-48.

Nason, A. and Dehaan, R. L., 1973. The biological world. Wiley, New York.

Oehler, D. Z., Schopf, J. W., and Kvenvolden, K. A., 1972. Carbon isotopic studies of organic matter in Precambrian rocks. Science, N.Y., 175: 1246-1248.

Pianka, E. R., 1974. Evolutionary ecology. Harper & Row, New York.

Ronov, A. B., 1971. Allgemeine entwicklungstendenzen in der Zusammensetzung der ausseren Erdhulle. Ber. deutsch. Ges. geol. Wiss., A. Geol. Paläont., 16: 331-350.

__________ and Migdisov, A. A., 1970. Evolution of the chemical composition of rocks of the shields and the sedimentary cover of the Russian and North American platforms. Geokhimiya (1976): 403-438 (translated, Geochim. Int., 7: 294-325.

Schidlowski, M., Eichmann, R., and Junge, C. E., 1975. Precambrian sedimentary carbonates: carbon and oxygen isotope geochemistry and implications for the terrestrial oxygen budget. Precamb. Res., 2: 1-69.

Smith, B. N., 1976. Evolution of C_4 photosynthesis in response to changes in carbon and oxygen concentrations in the atmosphere through time. BioSystems, 8: 24-32.

Van Valen, L., 1976. Energy and evolution. Evolut. Theory, 1: 179-229.

Veizer, J. and Hoefs, J., 1976. The nature of O^{18}/O^{16} and C^{13}/C^{12} secular trends in sedimentary carbonate rocks. Geochim. Cosmochim. Acta, 40: 1387-1395.

Welte, D. H., Kalkreuth, W., and Hoefs, J., 1975. Age-trend in carbon isotopic composition in Palaeozoic sediments. Naturwissenschaften, 62: 482-483.