HOMEOSTATIC TENDENCIES OF THE EARTH'S ATMOSPHERE

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Abstract. The atmosphere of the earth differs greatly from that of the other terrestrial planets with respect to composition, acidity, redox potential and temperature history predicted from solar luminosity. From the fossil record it can be deduced that stable optimal conditions for the biosphere have prevailed for thousands of millions of years. We believe that these properties of the terrestrial atmosphere are best interpreted as evidence of homeostasis on a planetary scale maintained by life on the surface. Some possible mechanisms of this biological homeostasis have been noted and the implications of this concept for experimental studies pointed out.

The purpose of this paper is to develop the concept that the atmosphere of the Earth flows in a closed system controlled by and for the biosphere. We view the Earth as a planet whose surface physical and chemical state is in homeostasis at an optimum set by the contemporary biota and reexamine in this new context some questions on the past and present condition of the Earth. These questions arise from the observation that the Earth, unlike the other terrestrial planets, has been evading the laws of equilibrium thermodynamics for millions of years. For example, given the temperature and pressure and the amounts of oxygen in the Earth's atmosphere "one can calculate what the thermodynamic equilibrium abundance of methane ought to be.... The answer turns out to be less than one part in 10^{36}. This is then a discrepancy between theory and observation of at least 30 orders of magnitude and cannot be dismissed lightly." (Sagan, 1970)

Surface life on the planet as a whole has certain environmental requirements of temperature, acidity and nutrient elements. The atmosphere of the Earth is anomalous with respect to its predicted temperature, acidity and the presence of certain elements in gaseous form; conditions on the Earth are not those expected for a planet interpolated between Venus and Mars. Conditions, at least at the 'core' (the tropical and temperate regions) are skewed from their predicted values in directions favored by most species of organisms. Such anomalies in the Earth's atmosphere have persisted for times that are very long relative to the residence times of non-noble gases in the atmosphere. We argue that it is unlikely that chance alone accounts for the fact that temperature, pH and the presence of compounds of nutrient elements have been, for immense periods of time, just those optimal for surface life. Rather we present the 'Gaia hypothesis'* the idea that energy is expended by the biota to actively maintain

* 'Gaia' is taken from the Greek for 'Mother Earth', see Lovelock and Lodge (1972) and Margulis and Lovelock (1974).

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these optima. This hypothesis generates numerous experiments in the search for biological mechanisms to maintain homeostasis, as noted.

1. Environmental Factors Delimiting the Biosphere

Ultimately, the organic compounds of life depend on the absorption of visible solar radiation for their production. Life thrives in the temperature range of 20–28 °C, under neutral or slightly alkaline conditions, and only with an assured supply of the elements carbon, nitrogen, oxygen, hydrogen, phosphorus, sulfur, calcium, potassium, sodium, magnesium, chlorine, and about a dozen others required in trace quantities. Active growing replicating organisms always require water. The external environment may vary drastically from optimal conditions of temperature and ionic concentrations in aqueous solution, yet optimal conditions are maintained within the interiors of cells. Desert organisms do not live in the absence of water, they conserve water. Temperate and arctic organisms conserve heat rather than metabolize at subzero temperatures. Aridity and low temperatures are significant limiting variables on earth: no large organisms and only a limited microbiota are associated with the Anarctica desert, an environment still more permissive than that expected on Mars (Horowitz *et al.*, 1972). It is true that some organisms are able to survive and grow in extreme environments such as boiling water (Bott and Brock, 1969), subzero temperatures, pressures exceeding 10^3 atm, or pH 1 (Kushner, 1971). Yet if such conditions became world-wide, almost all life would instantly perish, and presumably the survivors could not persist indefinitely. Furthermore life is a surface phenomenon and most abundant at the interface between water, solid substratum and air.

Although some oxygen respiring organisms require a greater quantity of O_2 in solution than that in equilibrium with 20% in the gas phase, many grow only in the total absence of free oxygen. Nearly 10^3 species of anaerobic organisms, varied with respect to their oxygen tolerances, have been described (Prevot and Fredette, 1966). From the alpine to the ocean abyss, living organisms can be found; life can survive over a total pressure variation from about 0.3 to 10^3 atm. Neither oxygen nor pressure per se limit the distribution of life as a whole. Rather the major physical variables determining the distribution of organisms are: solar radiation, temperature, water abundance, and the concentrations of hydrogen and other ions and elements.

Life has been present at interfaces (intertidal, lake edge and riverbank environments) throughout most of the Precambrian and Phanerozoic – that is, over 3 b.y. (Kvenvolden, 1972 and Schopf, 1972). Therefore, these stable temperature, pH and element cycling requirements for life must have been met on this planet consistently for the entire 'recorded' history of the Earth. Organisms found in extreme environments are highly specialized. If the Earth had frozen out for even a few tens of thousands of years, or if hot acid springs had been widely distributed for even a single epoch, these occurrences would have been discerned form the fossil record.

It doesn't seem possible to us that this veneer of living slime, composed of several million species, all within a few thousand feet of the surface of the Earth could possibly affect the solar system; thus the environment of the biosphere should be considered to be outer space. The atmosphere, far from being an inert sink, we regard as a regulated fluid component of the biosphere, a contrived circulatory system to assure the perpetuation of conditions optimal to the whole of the interconnected living organisms. We do not mean to imply any mystical vital force. Our point is that it is not merely a coincidence that the conditions from which the Earth has not deviated are those optimal for life.

Our assumption that the atmosphere-biosphere system is actively controlled clarifies some problems in atmospheric science and generates useful experiments.

2. Were there no Life on Earth

To model the temperature and atmospheric composition of a lifeless Earth has been very difficult; the factors determining the mean surface temperature of the Earth as a physical system are still only poorly understood. For a recent review of this complex and controversial subject see the SMIC report* and (Robinson and Robins, 1971). The responses of the atmosphere-ocean to small changes, for example, in solar output are very non-linear. A comparatively small decrease should lead (assuming the absence of perturbing influences of life) to an accelerating decline in temperature. A lower surface temperature implies more snow cover which in turn reduces the quantity of sunlight retained by the surface, which leads to further cooling, and so on. Similarly, it has been calculated (Rasool and De Bergh, 1970) that if the Earth had formed only 6 million miles closer to the Sun the positive feedback of temperature increase, through the greenhouse properties of water vapor and CO_2, would have led to Venus-like conditions with surface temperatures above the boiling point of water. Thus the atmosphere-hydrosphere temperature seems to be dynamically maintained between the two precarious and stable extremes.

Although the details are obscure there is general agreement that from a physical viewpoint the climate of the Earth is not at a stable equilibrium. That it should have persisted in a state of disequilibrium for billions of years strikes us as highly improbable. Were life obliterated now, the nitrogen and oxygen of the atmosphere would react to form nitric acid which would soon dissolve in the seas and the nitrogen would revert to its stable chemical form, the nitrate ion (Sillen, 1966). The atmosphere would then be a reasonable interpolation between Mars and Venus with a redox potential $pE = 5-7$, rather than $pE = 13$**. Also like Venus, and possibly also Mars, the Earth would then have acidic land surfaces. Because the climate is strongly dependent on the chemical composition of the atmosphere, such chemical changes would profoundly affect the climate.

The sources, sinks, and residence times for the major nonnoble gaseous components

* *Inadvertent climate modification: Report of the Study of Man's Impact on Climate, 1971*, MIT Press, Cambridge, Mass. (multi-authored).

** pE, a concept analogous to pH, measures electron concentration and equals $-\log [e^-]$.

TABLE I

Principal sources and sinks

Gas	Concentration		Production			
	(parts per million)	Inorganic sources[a]	Emissions ($\times 10^9$ tons yr^{-1}) Biological nonanthropogenic		Anthropogenic	
			Quantity	Source	Quantity	Source
Nitrogen, N_2	7.9×10^5	< 0.001	1	denitrifying bacteria, from nitrate and nitrite	0	—
Oxygen, O_2	2.1×10^5	1.6×10^{-4}	110	blue green algal, nucleated algal, green plant photosynthesis	0	—
Carbon dioxide, CO_2	320	0.01	140	waste product of aerobic respiration, bacteria, animals and plants	16	waste product of fuel oxidation
Methane, CH_4	1.5	0	2	product of bacterial fermentation	0	—
Nitrous oxide, N_2O	0.35	0	1	produced from nitrate by denitrifying, heterotrophic; ammonia oxidizing bacteria	0	—

Carbon monoxide, CO	0.08	< 0.001	1.5	from methane oxidation, marine, soil bacteria	0.15	waste product of fuel oxidation
Ammonia, NH_3	0.01	0	1–2	excretory product of nearly all organisms from amino acids, nucleotides via urea or uric acid	0	—
Hydrocarbons $(CH_2)_n$	0.001	0	0.2	plant emissions; released from organisms buried under anaerobic conditions	0.2	waste product of fuel oxidation
Oxides of *nitrogen*, NO_x	0.001	(total, 0.7)		?	0.16	waste products of fuel oxidation
Hydrogen sulfide, H_2S	$< 10^{-4}$	?	?	produced by sulfate-reducing bacteria; waste product of sulfur-containing amino acids	0.001	waste product of chemical industry
Sulfur dioxide, SO_2	2×10^4	variable	0	—	0.16	waste product of fuel oxidation
Dimethyl-sulfide, CH_3SCH_3	2×10^{-4}	0	0.2	marine algal emissions	0	—

[a] Abiologic sources: includes volcanic, tectonic emissions and upper atmosphere photolysis.

Table I (Continued)

Gas	Removal	Residence time	References
N_2	Nitrogen fixing bacteria and blue green algae	10^6–10^7 yr	See Brock (1966, 1970) for general discussion of all microbial activities in this table and further references
O_2	Respiration: aerobic bacteria, fungi, animals, plants	10^3 yr	Robinson and Robins (1971); Donahue, 1966
CO_2	Fixation by heterotrophic and photosynthetic bacteria, algae, green plants	2–5 yr	Schutz *et al.* (1970)
CH_4	Methane-oxidizing bacteria, oxidation to water and CO_2 in stratosphere	7 yr	See note on p. 95; Donahue (1966)
N_2O	Photolyzed, reacts with ozone in stratosphere to form higher oxides	10 yr	Schutz *et al.* (1970); Yoshida and Alexander (1970)
CO	Utilized by organisms, reacts with OH radicals in troposphere	months	Weinstock and Niki (1972)
NH_3	Oxidized by aerobic marine and soil bacteria; reactions with acids to form ammonium chloride and sulfate: fixation into amino acids by most bacteria; direct incorporation into leaves of plants	$\approx$ 1 week	See note on p. 95; Hutchinson *et al.* (1972)
$(CH_2)_n$	Atmospheric oxidation, source of food for specialized heterotrophic bacteria	$\approx$ 1 day	Robinson and Robins (1971); Brock (1970)
NO_x	Atmospheric reactions to form nitrate and nitrite salts; major N source for green plants, algae, denitrifying bacteria	$<$ 1 year	Robinson and Robins (1971); Alexander (1961)
H_2S	Atmospheric and hydrospheric oxidation to sulfur or surlfate; to organic sulfur by photosynthetic bacteria	$\approx$ 1 day	Schiff and Hodson (1970); Grey and Jensen (1972)
SO_2	Atmospheric oxidation; sulfate ion reduced by organisms to organic sulfur, H_2S and elemental sulfur	days	Lovelock *et al.* (1972)
$(H_3C)_2S$	Atmospheric oxidation to dimethyl sulfoxide	days	Lovelock *et al.* (1972)

of the atmosphere are shown in Table I. The residence times of these gases are very small fractions of the total history of the Earth, which again suggest an ongoing dynamic process maintains atmospheric stability. This stability is even more impressive if the concept is correct that the Sun's luminosity has increased by several tens of per cent as the Sun proceeds up the main sequence (Sagan and Mullen, 1972; Dilke and Gough, 1972). If the Earth's temperature merely reflected the solar luminosity, a change in luminosity in either direction of more than ten per cent might be all that would be required to freeze the oceans or to set off a runaway to extremes of heat (see note on p. 95; Rasool and De Bergh, 1970). But the fossil evidence very eloquently shows us that throughout periods of billions of years the oceans have neither frozen nor boiled (Schopf, 1972).

3. Questions Generated by the Homeostasis Hypothesis

We assume that the quantities actively modified by the biota are the gas composition, acidity and temperature of the atmosphere. Because the dominant species on the present Earth are obligate aerobes, we assume that oxygen, too, is maintained at its current high level by organisms. What are the mechanisms by which life homeostats the Earth's surface? At this stage in our knowledge we can only list (in Table II) some samples of the many possibilities biology offers. Detailed discussion of these may be found elsewhere (Lovelock and Margulis, 1974). Although the environmental control mechanisms are likely to be subtle and complex, we believe their evolution can be comprehended broadly in terms of Neodarwinian thought (Mayr, 1972). All organisms at any given time are, if circuitously, connected to all others. People are misled by the ease with which 'individuals' can be identified in human and animal populations. (Ambiguity seems to arise only in exceptional cases, such as pregnant women or Siamese twins). However, when considered from the point of view of the survival of the individuals to reproduce and leave offspring to the next generation, the 'individual' is very difficult to delineate from the 'group' or 'population'. Among organisms more distantly related to man the concept of the individual is extremely elusive. Club mosses can be counted as separate plants but when pulled out of the ground it is obvious that hundreds of feet of rhizoid underground connect the countable individuals. Fairy ring mushrooms, social insect and coral colonies are other examples. Passage through the guts of Galapagos tortoises is a requirement for germination of Galapagos solanaceous seeds, thus the tortoise may be considered part of the plant life cycle. Examples like this abound; all species are dependent upon other species for nutrients, the delivery of gases, shelter, support and so forth; none could survive in the total absence of the others.

Presumably the same mechanisms of natural selection that have led to local environmental control have led to near planetarywide control. (For example, humidity and thermoregulation in honeybee hives: the extent of local biological temperature control by these social insects is amazing. Typical hive temperatures of 31 °C have been maintained in −28 °C weather (Wilson, 1971). Analogous with the evolution of local environmental or internal control, in the evolution of atmospheric homeostasis those species of organisms that retain or alter conditions optimizing their fitness (i.e., proportion of offspring left to the subsequent generation) leave more of the same. In this way conditions are retained or altered to their benefit. If the atmosphere is a function-

TABLE II

Possible biological mechanisms to achieve homeostasis of the present terrestrial atmosphere

Quantity controlled	Property changed to achieve control	Biological mechanisms available
Temperature	Surface albedo	Darkening by direct uptake of water: lichen, algal and moss rock cover to retain moisture.
		Physiological control of pigments (carotenoids, xanthophylls, melanins, phycocyanin, phycoerythrin, chlorophylls, hemes, anthocyanins, etc.).
		Shadow casting, soil formation, alteration of surface textures.
		Trapping and precipitation of sediments such as $CaCO_3$, carbon black, iron sulfides.
	Surface IR emissivity	Surface structures and textures, comparable with IR wavelengths (8–14 μm).
	Atmospheric albedo	Emission of dust and aerosol precursors, e.g., terpenes (Rasmussen, 1970), sulfur gases, ammonia Acid and base excretions that react to form precipitating salt particles.
		Plant transpiration, excretion of lipid and detergent surfactants on water surfaces, bacterial and algal scums and slimes, i.e., control of H_2O evaporation and hence of cloud cover (Margulis and Lovelock, 1974).
	Atmospheric emissivity	Emission and removal of IR active gases, e.g., NH_3, CO_2, H_2O (via fermentation, photosynthesis, excretion, etc., see Table I).
	Circulation and heat transfer	Emission of N_2O which could modify ozone layer and hence circulation (Lovelock, 1971) by alteration of the N_2O/N_2 ratio by denitrifying bacteria (Alexander, 1961); evaporation control as above.
pH	Ammonia gas concentration	Control of NH_3 sources so that emission just titrates atmospheric production of H_2SO_4 and HNO_3.
	Removal of carbonic acid	CO_2 removal by blue green algae catalyzes $CaCO_3$ deposition and leads to local alkalinities up to pH 12 (Golubic, 1973).
		Some organisms directly excrete acids and bases (lactic, acetic, uric, nitric, etc.)
pE (See note on p. 95)	Oxygen concentration	O_2 is major excretory product of photosynthesis of algae and green plants.
		Bacterial CH_4 production and transport may be involved in maintaining redox potential, see Lovelock and Lodge (1972).

Table II (Continued)

Quantity controlled	Property changed to achieve control	Biological mechanisms available
		H_2, CH_4, H_2S are produced by photosynthetic bacteria, desulfovibrios, and methane bacteria in anaerobic environments to locally lower redox potentials.
		O_2 is removed by respiration, e.g., nitrogen fixers (*Azotobacter*), animals, chemoautotrophs. Redox potential control via O_2 removal must be good for small increase in per cent O_2 greatly increases the probability of direct combustion by forest fires, see note on p. 95.
pCx (where x is some essential element, see Frieden (1972) for entire list)	Concentration of gas vapor bearing element x	Emissions of gases such as N_2, N_2O, NH_3, CO_2, H_2S, $(CH_3)_2S$, CH_3I, etc. and where necessary control also of sinks so that pCx is kept within acceptable limits. Volatile methylated derivatives of certain essential elements required in trace quantities such as I, Se, and Br produced by marine algae and bacteria.

ing part of the biological cybernetic system which sustains homeostasis, it is appropriate to question the purpose of its various components. Just as it is reasonable to ask of honeybees: By what mechanisms is hive temperature controlled, or of mammals: What is the function of bicarbonate ion in the blood, it becomes reasonable to ask: What is the function of nitrous oxide or methane? Why are these gases released into the atmosphere in quantities of 10^9 tons yr^{-1}? Such questions would be rightfully considered illogical if the atmosphere were an open system, a product of steady state chemistry only; but if we consider the atmosphere to be in homeostasis we raise as critical questions at least the following: 1. Are the limiting elements essential to life (such as nitrogen, phosphorus, sulfur, iodine, bromine and others (Frieden, 1972)) returned through the atmosphere as volatile biological products in quantities that compensate the losses from the land surfaces in the run-off of rivers? 2. Does the large biological production of ammonia, 2×10^9 tons yr^{-1}, act to maintain the pH of the land surfaces close to neutral? 3. Does the comparably large production of methane keep the atmosphere oxidizing by transporting hydrogen to the stratosphere where it ultimately escapes by photolysis? (The maintenance of oxygen in the atmosphere by hydrogen loss via methane, is an example of an explanation generated by the Gaia hypothesis; it solves the issue raised by Gregor (1971) and Van Valen (1971); if O_2 is maintained by H escape from H_2O, the water originates from the oxidation of methane above the cold trap, the paucity of buried carbon from photosynthesis can be explained. See Lovelock and Lodge (1972) for details. 4. What are the sensors, amplifiers and control mechanisms operating to maintain constant the steady state chemical composition of the gases of the atmosphere? What mechanisms are involved in the maintenance of the physical steady state of atmospheric temperature? 5. What are the limits on these control mechanisms? How did they evolve? How did they cope with the two presumed transitions of the atmosphere in the Earth's history (from primordial hydrogen-methane-ammonia to N_2; from N_2 to the present N_2–O_2 mixture (Cloud, 1968))?

Asking these questions has already led to the discovery of the probable balancing factor in the sulfur cycle of the biosphere. Dimethylsulfide, a product of marine biological activity, was sought as an emission from the oceans on the grounds of the Gaia hypothesis. It was found in quantities sufficient to balance the input of inorganic sulfates washed from the land surfaces (Lovelock *et al.*, 1972). Similarly, iodine is emitted in substantial quantities as methyl iodide from the oceans. We expect to find analogous volatile bromine, phosphorus and selenium compounds that should be emitted by marine organisms.

The temperature of both the hives of honeybees and the blood of mammals is maintained constant by means of highly complex systems. These involve several different control loops to facilitate heat generation and heat loss (Wilson, 1971 and Myers, 1969). Similarly, if the biospheric thermostat is responsible for the constancy of the Earth's surface temperature over the last 3 thousand million years, then it is probable that it also requires a number of different control systems. The concentration of carbon dioxide in the atmosphere has increased during the past 25 yr*. Given this information on a physical model (because of its role as a greenhouse gas), one would expect an increase in the mean temperature over the same period. However, contrary to expectations, there has been a significant decrease in Northern Latitude mean temperatures during the past 25 yr*. On the basis of the Gaia hypothesis it may be worth seeking biological regulatory mechanisms that could overcompensate for the CO_2 increase. In general we are beginning to investigate our prediction that the annual biological production and removal of vast quantities of reactive gases (Table I) will be understood in the context of complex atmospheric control mechanisms involving many species of organisms (Table II). One corollary of 'Gaia' is that air pollution has an ancient history: oxygen itself was one of the first major pollutants. Life, although not necessarily man, has a remarkable ability to adapt to the 'pollutants' produced by the biosphere itself. Life as a whole has survived through the mechanism of the evolution and persistence of new species (and eventually higher taxa) better able to survive and reproduce under changed atmospheric conditions. There is no reason to believe this mechanism will change in the near future, on a geological time scale.

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* See note on p. 95.

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