GAIA HYPOTHESIS

T Lenton, Centre for Ecology and Hydrology, Edinburgh, UK

Introduction

The Gaia hypothesis postulates that the Earth's surface is maintained in a habitable state by self-regulating feedback mechanisms involving organisms tightly coupled to their environment. The concept is based on several observations:

- The atmosphere is in an extreme state of thermodynamic disequilibrium owing to the activities of life, yet aspects of its composition are remarkably stable.
- Present conditions at the surface of the Earth are close to optimal for the dominant organisms.
- Life has persisted for over 3.8 billion years despite increasing solar luminosity and variable exchange of matter with the inner Earth.
- The Earth system has repeatedly recovered from massive perturbations.

The Daisyworld model demonstrated that planetary self-regulation can occur without teleology, in a manner consistent with natural selection. Since the origin of life, organisms have had a profound effect on the Earth's atmospheric composition and the climate. The 'faint young Sun' was initially counteracted by a carbon dioxide and methane 'greenhouse' atmosphere. The biological amplification of silicate rock weathering has progressively reduced the carbon dioxide content of the atmosphere and acted as a long-term climate stabilizer. Atmospheric oxygen rose in a stepwise fashion to $\sim$21% of the atmosphere, about which it has been tightly regulated for the past 350 million years. Feedbacks involving terrestrial and marine biota also affect the climate over shorter time scales. The predominance of positive feedback in the recent glacial–interglacial cycles suggests that the Earth system is nearing a transition to an alternative state. Eventually, self-regulation will collapse and the Earth will be sterilized, but this is unlikely to occur for at least another 0.5–1.2 billion years.

Earth's Remarkable Atmosphere

The Gaia hypothesis arose from the involvement in the 1960s space program of the British independent scientist and inventor James Lovelock. Lovelock was employed by NASA, as part of the team that aimed to detect whether there was life on Mars. Lovelock's interest in atmospheric chemistry led him to seek a general, physical basis for detecting the presence of life on a planet. He recognized that most organisms shift their physical environment away from equilibrium. In particular, organisms use the atmosphere to supply resources and as a repository for waste products. In contrast, the atmosphere of a planet without life should be closer to thermodynamic equilibrium, in a state attributable to photochemistry (chemical reactions triggered by solar ultraviolet radiation). Thus, the presence of abundant life on a planet may be detectable by atmospheric analysis.

Such an analysis can be conducted from Earth using an infrared spectrometer (which detects the characteristic absorption due to specific gases) linked to a telescope. Using this technique with ground-based telescopes, it was discovered that the atmospheres of Mars, and Venus are dominated by carbon dioxide and are relatively close to chemical equilibrium, suggesting that they are lifeless (**Figure 1A**). In contrast, the atmosphere of the Earth is in an extreme state of disequilibrium as a result of the activities of life, in which highly reactive gases, such as methane and oxygen, coexist many orders of magnitude from photochemical steady state (**Figure 1A**). Large, biogenic fluxes of gases maintain this disequilibrium (**Figure 1B**). Yet the composition of the Earth's atmosphere is fairly stable over geological periods of time. Lovelock concluded that life must regulate the composition of the Earth's atmosphere.

The dominant atmospheric gases, nitrogen and oxygen, are biological products: atmospheric oxygen is the result of past photosynthesis, and denitrifying organisms maintain atmospheric nitrogen (the thermodynamically stable form of nitrogen in the presence of oxygen should be as nitrate dissolved in the ocean). The proportions of these gases are particularly suited to the dominant organisms. Nitrogen serves to dilute oxygen, which at 21% of the atmosphere is just below the level at which fires would disrupt land life. Yet oxygen is sufficiently abundant to support the metabolism of large respiring animals such as humans.

The Earth's climate is close to optimal for the dominant organisms, and has always been habitable despite major changes in the input of energy and matter to the Earth's surface. Notably, stars on the

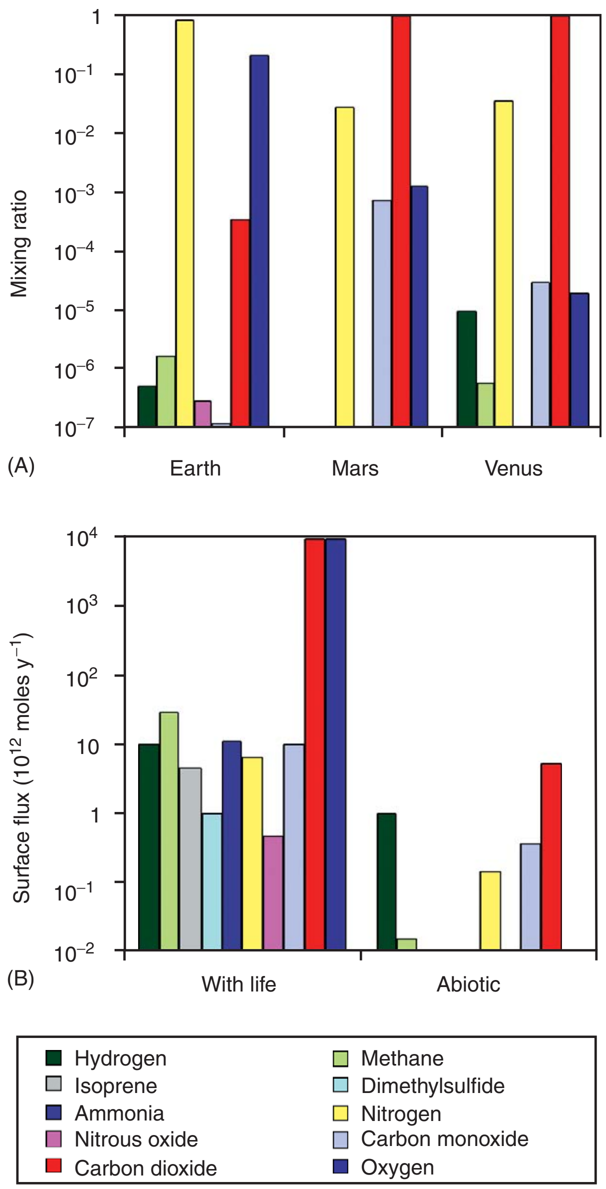

Figure 1 The effect of life on the Earth's atmosphere. (A) Atmospheric compositions of Earth, Mars and Venus (excluding water vapor and noble gases). (B) Fluxes of gases at the Earth's surface with life (preindustry) and without life. (Reprinted with permission from Lenton (1998). Copyright 1998 Macmillan Magazines Ltd.)

main sequence, such as the Sun, gradually become more luminous with time as the hydrogen in their core is converted to helium (increasing their density and accelerating the fusion reaction). The Sun was about 25% less luminous when life originated on Earth, over 3.8 billion years ago. This increase in solar output alone should raise the Earth's surface temperature by $\sim 20^{\circ}C$, but the current average temperature is only $15^{\circ}C$. This posed the 'faint young Sun' puzzle of why the early Earth was not frozen. The atmosphere was probably richer in greenhouse gases, so that the early Earth's surface was actually warmer then than it is now, in which case cooling of the Earth in the face of warming from the Sun demands an explanation. Lovelock suggested that life has been regulating the Earth's climate together with its atmospheric composition.

The idea was named 'Gaia' after the Greek goddess of the Earth, by the novelist William Golding. The first scientific paper presenting 'Gaia as seen through the atmosphere' was published in 1972. Lovelock then sought an understanding of the organisms that might be involved in regulating their planetary environment. Lynn Margulis contributed her intimate knowledge of microorganisms, and the diversity of chemical transformations that they mediate, to the development of what became the Gaia hypothesis that 'the environment at the surface of the Earth is homeostated by and for the benefit of, the biota'. The Gaia hypothesis was used to make predictions – for example, that marine organisms would make volatile compounds that can transfer essential elements from the ocean back to the land. Lovelock and colleagues tested this ancillary hypothesis on a scientific cruise between England and Antarctica. They discovered that the biogenic gases dimethylsulfide and methyliodide are the major atmospheric carriers of the sulfur and iodine cycles.

Later, the Gaia hypothesis was extended to include regulation of much of the chemical composition of the ocean. Then evidence began to accumulate indicating that the Earth has remained habitable despite major, periodic disruptions, including the impact of planetesimals (massive meteorites) and volcanic outbursts. These events appear to have caused mass extinctions and climate change and yet, in all cases, diverse, widespread life and a tolerable climate returned within a short period of geological time. This supports the notion that the Earth is a self-regulating system.

Daisyworld

The Gaia hypothesis was greeted with hostility from many scientists and leading scientific journals, partly because of its mythological name. The first scientific criticism of the hypothesis was that it implies teleology, some conscious foresight or planning by the biota. Most subsequent criticisms have focused on the need for evolutionary mechanisms by which regulatory feedback loops could have arisen or be maintained. The Earth is not a unit of natural selection, and hence planetary self-regulation cannot have been refined in the same way as an organism's physiology. This poses the challenge of explaining how planetary self-regulation could arise.

The Daisyworld model (**Figure 2**) was formulated to demonstrate that planetary self-regulation does not necessarily imply teleology. It provides a hypothetical example of climate regulation emerging from competition and natural selection at the individual level. Daisyworld is an imaginary gray world orbiting a star like our Sun that gets more luminous with time. The world is seeded with two types of life, black and white daisies. These share the same optimum temperature for growth of 22.5°C and limits to growth of 5°C and 40°C. When the temperature reaches 5°C, the first seeds germinate. The paleness of the white daisies makes them cooler than their surroundings, hindering their growth. The black daisies, in contrast, warm their surroundings, enhancing their growth and reproduction. As they spread, the black daisies warm the planet. This further amplifies their growth and they soon fill the world. At this point, the average temperature has risen close to the optimum for daisy growth.

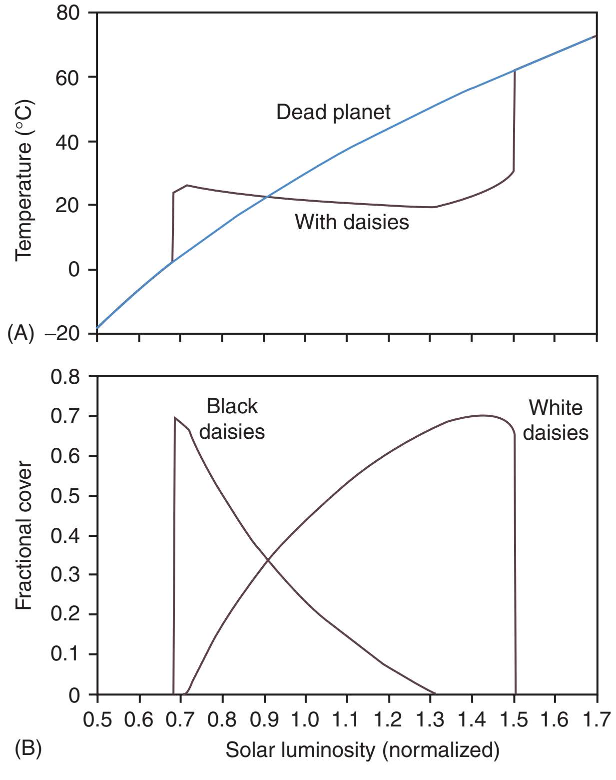

Figure 2 The Daisyworld model (Watson and Lovelock (1983)). A thought experiment to demonstrate that planetary self-regulation can emerge from natural selection at the individual level between types of life with different environment-altering traits. The traits are 'darkness' (albedo = 0.25) and 'paleness' (albedo = 0.75) of black and white daisies on a gray planet (albedo = 0.5). (A) Planetary temperature as solar luminosity increases, with daisies and without ('dead planet'). (B) Areal cover of black and white daisies.

As the Sun warms, the temperature rises to the point where white daisies begin to appear in the daisy community. As it warms further, the white daisies gain the selective advantage over the black daisies and gradually take over. Eventually, only white daisies are left. When the solar forcing gets too much, the white daisies die off and regulation collapses. While life is present, the system is a very effective temperature regulator. Solar input changes over a range that should heat the planet's surface by 55°C, yet it is maintained within a few degrees of the optimum temperature for daisy growth.

Daisyworld illustrates the importance of feedback mechanisms for planetary self-regulation. Feedback occurs when a change in a variable triggers a response that affects the forcing variable. Feedback is said to be 'negative' when it tends to damp the initial change and 'positive' when it tends to amplify it. The initial spread of life is amplified by an environmental positive feedback – the warming due to the spread of black daisies enhances their growth rate. The long period of stable, regulated temperature represents a predominance of negative feedback. However, if the temperature of the planet is greatly perturbed by the removal of a large fraction of the daisy population, then positive feedback acts to rapidly restore comfortable conditions and widespread life. The end of regulation is characterized by a positive feedback decline in white daisies – solar warming triggers a reduction in their population that amplifies the rise in temperature.

The modeling approach pioneered in Daisyworld provided the beginnings of a theoretical basis for understanding planetary self-regulation. Subsequently, Lovelock began to refer to Gaia as a theory, in which self-regulation is understood as a property of the whole system of life tightly coupled to its environment. This replaced the original hypothesis that regulation is 'by and for the biota'. The term 'homeostasis', which refers to regulation around a fixed set point, was also revised, with Margulis' more appropriate suggestion of 'homeorrhesis', which describes regulation around an evolving point.

Regulation of Atmospheric Composition over Earth History

The Daisyworld modeling approach was adapted to study the regulation of climate and atmospheric composition on the early Earth, through the Archean Eon (4.0–2.5 billion years ago) and the first half of the Proterozoic Eon (2.5–1.5 billion years ago). The Archean was characterized by chemically reducing conditions at the Earth's surface and the Proterozoic by oxidizing conditions. Lovelock proposed that methane was the chemically dominant gas in the Archean atmosphere (whereas oxygen dominated subsequently). The model comprised a bacterial ecosystem of oxygen-liberating photosynthesizers (cyanobacteria), methanogens, and aerobic consumers, together with atmospheric carbon dioxide, methane, and oxygen, and global temperature. The carbon fixed in photosynthesis was returned either by aerobic respiration, as carbon dioxide, or by methanogenesis, as a mixture of methane and carbon dioxide. An atmosphere dominated by carbon dioxide and methane with only traces of oxygen was predicted. This could have provided sufficient 'greenhouse effect' to counteract the faint young Sun.

Although oxygen-liberating photosynthesis originated early in the history of life, oxygen remained scarce (<0.0008 atm; 0.8 hPa) in the Archean atmosphere, because it was consumed in the oxidation of an abundant supply of reduced matter that was continually being replenished by geological activity. The weathering profiles of ancient soils indicate that oxygen rose to >2 hPa and probably >30 hPa in a global oxidation event 2.2–2.0 billion years ago. Lovelock's model predicted this rise of oxygen as the supply of reduced matter began to be exhausted. Once there were two molecules of oxygen for each molecule of methane, oxygen became the chemically dominant gas. Methane rapidly disappeared from the atmosphere, reducing the greenhouse effect and cooling the planet, perhaps causing the Huronian glaciation which occurred roughly 2.3 billion years ago. However, climate regulation soon recovered in the model, with carbon dioxide as the dominant greenhouse gas.

Since the Archean, long-term climate regulation is thought to have hinged on changes in the carbon dioxide content of the atmosphere, and the resultant 'greenhouse effect' on Earth's temperature. Over million-year time scales, the carbon dioxide reservoir in the atmosphere and ocean is primarily determined by the balance of input from volcanic and metamorphic degassing and removal in the process of weathering of silicate rocks on land and subsequent formation of carbonate rocks in the ocean. A chemical negative feedback mechanism exists whereby increases in planetary temperature are counteracted by increases in the rate of silicate rock weathering and the uptake of carbon dioxide. However, the rate of rock weathering is greatly enhanced by the activities of soil microbes, lichens, mosses, and vascular plants. This biological amplification offers the potential for more responsive stabilization of the Earth's temperature. For example, rising carbon dioxide and temperature trigger increased plant growth, microbial respiration, and weathering that reduces the carbon dioxide content of the atmosphere. Over Earth's history, progressively stronger biological amplification of rock weathering has evolved, culminating in the rise of vascular plants over the last 420 million years. Biologically amplified weathering has made carbon dioxide relatively scarce in the Earth's atmosphere (**Figure 1A**), and cooled the Earth by 20–40°C, thus counteracting the effect of increasing solar luminosity.

Over the last ~ 350 million years the oxygen content of the atmosphere has been remarkably stable. Continuous records of charcoal and vegetation indicate that there has been sufficient oxygen to sustain natural fires throughout this time, but fires have never been so frequent as to prevent forests regenerating. This sets bounds of roughly 15–25% on the oxygen content of the atmosphere. The average amount of time an oxygen atom spends being recycled between organisms, atmosphere, and ocean before being removed in oxidation of rocks is about 3 million years. Hence, the whole oxygen reservoir has been replaced over 100 times, while its size has remained close to constant. This demands that some self-regulating feedback mechanisms exist. The removal process for oxygen is saturated: virtually all the reduced matter exposed gets oxidized. Hence regulation of atmospheric oxygen is thought to involve negative feedback on the source of oxygen. Over geological time, the burial flux of organic carbon in new sediments corresponds to the small excess of oxygen liberated in photosynthesis over that consumed in respiration, which provides a net source of oxygen to the atmosphere. This is balanced by a net sink due to the oxidation of organic matter in sedimentary rocks exposed on the continents.

The burial of organic carbon can be somewhat enhanced under anoxic conditions in sediments, probably because anaerobic consumers are less efficient than their aerobic counterparts. Hence declining oxygen may be counteracted by more efficient organic carbon burial, but the effect appears to be too weak to stabilize atmospheric oxygen. Marine productivity has a more dominant effect on organic carbon burial, and it in turn depends on the supply of nutrients, especially phosphorus, over long time scales. The burial of phosphorus in organic matter and bound to iron minerals is less efficient under anoxic conditions. Hence, declining oxygen should cause more phosphorus to be recycled to the water column, fuelling more productivity and increased organic carbon burial. However, such mechanisms are ineffective against rising oxygen, because it tends to remove anoxia from the ocean, thus switching off the feedback.

Weathering of phosphorus-bearing rocks is the ultimate source of all phosphorus supplied to the land and ocean. Vascular plants amplify the rate of rock weathering by about an order of magnitude relative to primitive land biota (e.g., lichen and moss cover) and the effect is greatest for trees with their deep rooting systems. Increasing atmospheric oxygen tends to suppress vegetation by inhibiting photosynthetic carbon fixation and increasing fire frequency. Fires tend to trigger ecological shifts from forest to faster-regenerating ecosystems such as grassland. By these mechanisms, rising oxygen should suppress rock weathering and hence reduce the supply of phosphorus to the land and ocean, in turn suppressing productivity and organic carbon burial. This mechanism is extremely effective at regulating against rising oxygen because of the high sensitivity of fire frequency to rising oxygen. Furthermore, declining oxygen is counteracted by increases in plant productivity, rock weathering, phosphorus supply, and organic carbon burial.

Contemporary Climate Feedbacks

As well as its role in regulating oxygen and carbon dioxide over long time scales, vegetation also has self-sustaining short-term feedback effects on climate. Globally, plants increase land surface evapotranspiration and continental precipitation and reduce temperature variability. These climatic effects increase net primary productivity and biomass, and without them it has been predicted that the boreal, Amazonian, and South East Asian forests would disappear. Such hysteresis of the vegetation–climate system may also exist in the south-western Sahara, where models predict that vegetation could sustain itself, by maintaining a wetter climate. Vegetation tends to cool the Tropics and temperate regions but warm the high northern latitudes.

The trees of the boreal forests possess traits of shedding snow and darkness that give them a low albedo (reflectivity) and make them warmer than their surroundings. In this respect they can be likened to the dark daisies of Daisyworld. The presence of forest warms the region, and the Northern Hemisphere, by $\sim 4^{\circ}C$ in winter. The system shows constrained positive feedback that amplifies regional temperature changes. Six thousand years ago, orbital forcing warmed the high-latitudes and triggered the boreal forest to spread northward and amplify the initial warming. One hundred and fifteen thousand years ago the opposite occurred; orbital forcing cooled the high-latitude summer, triggering a southward spread of the tundra, replacing the boreal forest. The resulting increase in albedo because of unmasked snow cover would have added to regional and planetary cooling and may have been critical for the inception of ice sheets.

Marine phytoplankton cool the climate by pumping down atmospheric CO_2 and producing dimethylsulfide (DMS), which ultimately increases cloud albedo. DMSP (dimethylsulfoniopropionate), the precursor of DMS is produced in widely varying amounts by different species of marine phytoplankton. Its conversion to DMS is catalyzed by the enzyme DMSP lyase and is enhanced by virus infection and zooplankton grazing. The main reservoir of DMS is in the ocean, where it is consumed by bacteria and oxidized to dimethylsulfoxide (DMSO). Air–sea exchange results in a net flux of DMS to the atmosphere (**Figure 1B**). In the atmosphere, DMS is oxidized in a range of reactions. The main pathway generates sulfur dioxide, which is further oxidized to sulfate, and can ultimately contribute to sulfate aerosol formation. The aerosol particles grow, often in combination with another biogenic gas, ammonia (**Figure 1B**), to become cloud condensation nuclei (CCN). Increases in the number density of CCN make clouds more reflective, increasing the scattering of solar radiation back to space and thus causing cooling.

Temperature both directly affects phytoplankton growth and determines the degree of stratification in the ocean water column, and hence the supply of nutrients to the surface layers. Therefore, there is the potential for feedback on climate involving the growth of DMS-emitting phytoplankton. Originally, a negative feedback was proposed whereby a reduction in temperature and light beneath clouds reduces photosynthesis and restricts the spread of DMS producers. Subsequent modeling elaborated this proposal with the observation that the formation of a thermocline at $\sim 10^{\circ}C$ limits the supply of nutrients to the surface ocean, thus setting an effective optimum for plankton growth. Beneath this temperature lies the originally proposed regime of negative feedback. Above it, however, an increase in temperature may be amplified by a decrease in photosynthetic production, DMS production, and cloud reflectivity, generating positive feedback. Evidence that DMS production in the Southern Hemisphere was enhanced during the last Ice Age indicated that the feedback may then have been negative but switched to become positive as temperatures rose at glacial termination.

The cycles of ice ages and interglacial warm periods that have characterized the last ~ 2.5 million years of Earth history appear, at first glance, to conflict with the view that the Earth is self-regulating. The trace gas composition of the atmosphere, including CO_2, CH_4, and N_2O, has varied. However, the recently extended Vostok ice core record reveals that for the last four glacial cycles the frequency, bounds, and amplitude of the oscillations have been remarkably constant, despite highly variable forcing (solar insolation). This is indicative of a regulatory system, but one that is near the limits of its operation, with positive feedback coming to dominate over negative feedback. The long-term climate regulator involving biological amplification of silicate rock weathering is near the lower bound of its operation, having reduced atmospheric CO_2 near to the lower limit for the growth of most plants (which lack a CO_2-concentrating mechanism). Positive feedback is apparent in the onset and termination of ice ages, including the aforementioned changes in boreal forest cover and DMS emissions. Hence, humans may be perturbing the Earth system when it is unusually vulnerable and has the potential to switch to a different state.

At present, members of both the marine and terrestrial biota are involved in processes that are removing more than half of the excess carbon dioxide released to the atmosphere each year by human activities. This negative feedback is not sufficient to prevent the carbon dioxide content of the atmosphere from rising, but it is damping the rate of rise. Atmospheric CO_2 and global warming are expected to peak some time in the present millennium, the precise time depending on how fast the fossil fuel reserve is burned. Over the following $\sim 10\,000$ years, the acidic CO_2 added to the atmosphere by human activities should be neutralized by the dissolution of carbonate sediments in the ocean and the weathering of carbonate rocks on land, processes that increase the alkalinity of the ocean. However, major reorganizations of the climate system could occur in the meantime. Boreal forests are already amplifying winter warming in the northern high latitudes. Global warming and resultant stratification of the ocean may trigger a decline in phytoplankton and their cooling effect via DMS emissions, providing a further positive feedback.

Although human perturbation may shift the Earth system to a state that is uncomfortable for us as a species, it is highly unlikely to destroy all life on Earth. The mechanism of long-term climate regulation involving the biological amplification of silicate rock weathering appears to be extremely robust to short-term perturbation. It should continue to gradually reduce the CO_2 content of the atmosphere as solar luminosity increases, and this will encourage plants with CO_2-concentrating mechanisms to become dominant. Life may eventually perish as a result of lack of CO_2, overheating by the Sun, or catastrophic perturbation. However, models based on the current biota and feedback mechanisms predict that complex life will last at least another 0.5–1.2 billion years.

See also

Biogeochemical Cycles: Carbon Cycle; Nitrogen Cycle; Sulfur Cycle. **Carbon Dioxide**. **Climate Prediction (Empirical and Numerical)**. **Evolution of Atmospheric Oxygen**. **Evolution of Earth's Atmosphere**. **Methane**. **Planetary Atmospheres:** Mars; Venus. **Reflectance and Albedo, Surface**. **Teleconnections**. **Tropospheric Chemistry and Composition:** Ammonia and Ammonium; Biogenic Hydrocarbons (inc. isoprene); Sulfur Chemistry, Organic.

Further Reading

Charlson RJ, Lovelock JE, Andreae MO and Warren SG (1987) Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326: 655–661.

Lenton TM (1998) Gaia and natural selection. *Nature* 394: 439–447.

Lenton TM and Watson AJ (2000) Redfield revisited. 2. What regulates the oxygen content of the atmosphere? *Global Biogeochemical Cycles* 14: 249–268.

Lovelock JE (1979) *Gaia: A New Look at Life on Earth*. Oxford: Oxford University Press.

Lovelock JE (1988) *The Ages of Gaia: A Biography of Our Living Earth*. Oxford: Oxford University Press.

Lovelock JE (1991) *Gaia: The Practical Science of Planetary Medicine*. London: Gaia Books.

Lovelock JE and Margulis LM (1974) Atmospheric homeostasis by and for the biosphere: The gaia hypothesis. *Tellus* 26: 2–10.

Schneider SH and Boston PJ (1991) *Scientists on Gaia*. Boston: MIT Press.

Watson AJ and Lovelock JE (1983) Biological homeostasis of the global environment: The parable of Daisyworld. *Tellus* 35B: 284–289.