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Life span of the biosphere

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There has been life on Earth for at least 3,500 Myr but the assumption that a comparable future lies ahead may not be justified. Main sequence stars appear to increase their burning rate as they age. Thus the Sun, if a typical star, can be predicted to have increased its output by 30% since the Earth's origin 4,500 Myr ago[1]. The maintainance of an equable climate since life began probably required some means of planetary thermostasis. The Gaia hypothesis proposed by Lovelock and Margulis[2] included an unspecified biological means for climate control. Walker et al.[3] suggests an abiological automatic thermostasis in which the atmospheric abundance of CO_2, a greenhouse gas, adjusts to resist the warming tendency of the increased solar flux. Here we discuss possible links between the biological and geological control mechanisms. It is clear that whatever the mechanism, atmospheric CO_2 is now close to its lower limit of partial pressure, so the biosphere may soon, in geological terms, be exposed without protection to the predicted progressive increase of solar luminosity.

In spite of the probability of a 25% increase in solar luminosity it is reasonably certain that the Earth's climate has undergone little change since life began. Both the geological record and the persistence of life indicate that neither global freezing nor boiling conditions have ever prevailed. Indeed, the Earth's mean surface temperature has probably never departed from the range 5–50 °C and, contrary to the predictions of simple physics, may have been warmest at the beginning when the Sun was small and has cooled ever since[4].

Several models have been proposed to account for the Earth's relatively constant temperature. Sagan and Mullen[5] were the first to suggest that the infant biosphere was warmed by an atmospheric gas which exerted a 'greenhouse' effect by transmitting sunlight while hindering the escape of heat to space.

Although water vapour makes the most significant contribution to the greenhouse effect in the contemporary atmosphere, because of its physical properties water is an unlikely candidate for long-term thermostasis. Its relatively high freezing and boiling points render its blanketing effect prone to positive feedback in the face of extreme temperature excursions. For example, a sudden fall in temperature could result in an increase in the size of the polar ice caps and the seasonal snow fields (thus increasing the efficiency with which radiation is reflected from the Earth) and a corresponding fall in the atmospheric humidity. Both effects could contribute to a further drop in temperature. On the other hand, a sudden rise in temperature would increase the water vapour content of the atmosphere, which would in turn push the temperature still higher. In consequence, the complexities of cloud cover feedback effects over

long periods of time have focused attention on simpler atmospheric models involving other greenhouse gases[3–5].

Sagan and Mullen[5] suggested that the early atmosphere was rich in ammonia and other reduced gases and that these provided the blanket which kept the Earth sufficiently warm for life to emerge. Relatively high partial pressures of ammonia were also seen as essential for the chemical evolution of life and, as ammonia is rapidly photolysed in the atmosphere, a significant inorganic source was sought[6]. Recent work, however, suggests that high partial pressures of ammonia are not essential for the abiological production of amino acids[7] and that the primordial atmosphere probably contained little ammonia but relatively high partial pressures of CO_2[8]. The concept of an early Earth warmed by the blanketing effect of its atmosphere is still therefore feasible but with CO_2 the preferred blanket gas[4,7]. According to this hypothesis whatever greenhouse gas or other agency kept the young planet warm, it must have been smoothly and actively reduced from then until now; otherwise the mean temperature would have progressively increased with increasing solar heat flux and might by now have exceeded 50 °C, the critical upper limit for most life[9].

Walker et al.[3] have proposed that the climate could have been controlled solely by abiological negative feedback involving a gradual decline in the atmospheric partial pressure of CO_2 in response to a continuous increase of the Sun's luminosity. Briefly, an increase in temperature accelerates the rate of reaction between CO_2 and calcium silicate rock. The input of CO_2 from tectonic sources is assumed to be constant so that an increased heat flux leads to increased weathering of the rock, a faster removal of CO_2 and hence a lower atmospheric CO_2 partial pressure. This cybernetic process acts to resist the rise in temperature which would otherwise result from the increase in solar luminosity.

This abiological mechanism could have operated early in the Earth's history but the resulting climatic control would have been easily perturbed by fluctuations in the volcanogenic flux of CO_2. These effects could have been exaggerated by the positive feedback loops introduced by the ocean–atmosphere interaction. As the solubility of CO_2 in water decreases with increasing temperature, an atmospheric (and hence oceanic) warming would result in a release of CO_2 to the atmosphere which would produce a further temperature rise. A corresponding positive feedback would occur on cooling. At present geological input and removal constitute only a few tenths of a per cent of the biologically driven fluxes[10] and so it is instructive to see how the biological and geological mechanisms can be linked.

There is little doubt that current weathering of silicate rocks is biologically, not geochemically, determined. The partial
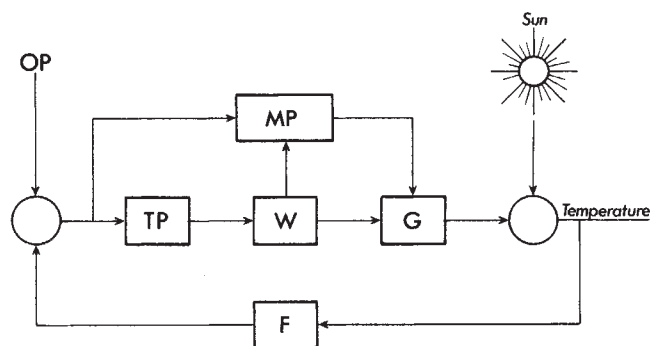

Fig. 1 A feedback process in which the productivity of the terrestrial biosphere (TP) or the marine biosphere (MP) influences the greenhouse effect (G) and hence the global mean temperature via control of the atmospheric partial pressure of carbon dioxide. These biological processes modulate the geological control exerted by the weathering process (W) against a constant input from tectonic sources. The loop is closed by the feedback process (F, see text) which transduces from the mean temperature a productivity that can be compared with the operating productivity (OP) of the biosphere.
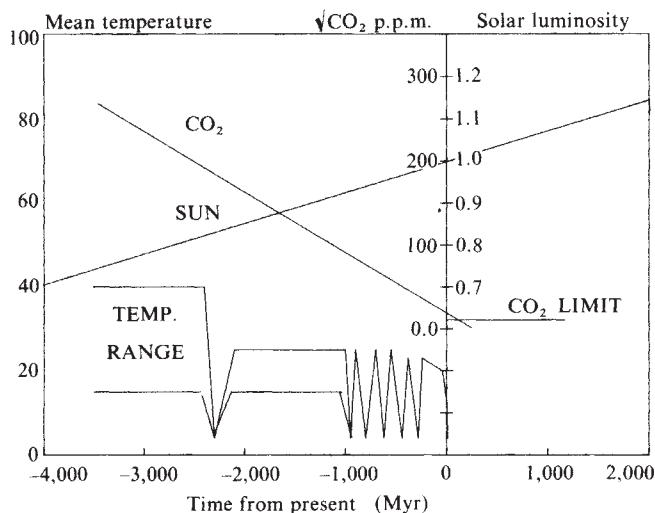
Fig. 2 Evolution of the climate showing the variation of solar luminosity, relative to its present value taken as 1.0. Also illustrated on the same time scale are the proposed decline in carbon dioxide concentration, expressed as the square root of the concentration in parts per million (p.p.m.) by volume and the approximate range of mean surface temperatures in °C (see text).

pressure of CO_2 in the soil where the chemical weathering takes place is 10–40 times higher than the atmospheric level[11]. These high partial pressures are maintained by the biological oxidation of organic detritus and the rate of oxidation approximately doubles for each 10 °C rise in temperature. The biota seem to act as a sensor of temperature change and as an amplifier to magnify the rate of weathering of the silicate rocks and pumping of CO_2 from the air. The present geochemical balance for CO_2 between input from tectonic sources and removal by weathering[10] requires a partial pressure in the soil of nearly 10 mbar.

The direct involvement of the biota in weathering would only be possible after the evolution of a land microfauna and flora and the establishment of viable soil communities. Although such communities probably predate the invasion of land as deduced from fossils, it is possible that life was largely confined to the sea during the Archaean. Once communities based on photosynthetic carbon fixation were established in the oceans, however, they could amplify indirectly the geochemical feedback. In the contemporary ocean the biota limit the atmospheric partial pressure of CO_2 by maintaining a continuous flux of particulate organic matter into the deep ocean[12]. This flux results from primary production in the surface layers which is limited by the rate of supply of nutrients, notably nitrogen and phosphorus, from riverine inputs and from the slow recirculation of nutrient- and carbon dioxide-rich deep-ocean water. If, as suggested by the geological model[3], the rate of rock weathering increases due to a rise in global temperature, then the rate of supply of nutrient elements to the oceans will also increase. This will enhance primary productivity and further reduce atmospheric CO_2 levels. If, on the other hand, the temperature falls the nutrient supply will diminish, productivity will decrease and excess CO_2 will be released from the recirculating deep-ocean water into the atmosphere, thus encouraging a temperature rise[12]. Here, too, the biota can use geologically driven processes to provide additional temperature stabilization. If life ceased now, the new geochemical balance would require an increase of atmospheric CO_2 and hence temperature until removal by weathering again equalled the input of CO_2 from volcanoes. The present low atmospheric CO_2 pressure and relatively low temperature are therefore a direct consequence of life. This is consistent with the Gaia hypothesis[2] which suggests that evolutionary pressures ensure that biologically driven processes which influence the chemical composition of the atmosphere and hence the climate so as to keep the environ-

ment optimal for the biosphere will have been preferentially selected.

Figure 1 illustrates a highly simplified model of the combined biological and geological regulation of temperature. As the temperature falls, CO_2 fixation by photosynthesis and chemical weathering declines until at ~0 °C it nearly ceases. CO_2 input from tectonic sources continues and the atmospheric partial pressure of CO_2 will rise. Through the greenhouse effect, this increase resists any further decline in temperature. In a similar way high temperatures and high CO_2 pressures are both conductive to rapid weathering which serves to resist a continuing rise in temperature. Thus the mean surface temperature will tend to a value optimal for the contemporary biota within the other constraints of its planetary environment.

Figure 2 illustrates the probable solar output from 4,000 Myr ago to 2,000 Myr hence and gives on estimate of the corresponding global mean temperature and CO_2 partial pressure. Solar luminosity is predicted to increase, according to Newkirk[1]. An alternative analytical expression for the time variation of solar luminosity[13] might be useful for more detailed calculations.

The range of past temperatures is not accurately known. That shown in Fig. 2 is our estimate of the probable limits of palaeoclimates and it is based on the following assumptions. (1) During the Archaean the biosphere was wholly prokaryotic. As the upper temperature limit for contemporary prokaryotes is 50 °C, the upper limit for the Earth's mean temperature was set lower, at 40 °C, to allow for zonal and other variations. No glaciations are known during this period[14,15] so the lower limit of temperature is set at 15 °C, close to the present value. (2) −2,200 Myr marks the end of the Archaean and the first extensive glaciation[14,15], as well as the appearance of free oxygen. Temperatures might have risen after this glaciation to Archaean levels or they may have been similar to the levels now thought characteristic of the interglacial periods—20–30 °C. We chose the latter estimate as the upper limit from −2.2 Gyr until the present. The lower limit is set by the physical properties of water. There is no indication that total freezing took place, so a mean temperature of 0 °C or below is very unlikely. Glaciations[14,15] are associated with mean temperatures of 5–10°C and interglacials with lower limits perhaps 5–15 °C higher. The time scale of the figure is so compressed that the present interglacial climate cannot be resolved from the low values of the last glaciation 10,000 yr ago.

The other quantity illustrated in Fig. 2 is the CO_2 pressure needed to compensate for the changing solar luminosity. This estimate is based on a partial pressure 3,500 Myr ago of 7,000 p.p.m. (refs 4, 17). It is linked to the present value of 320 p.p.m. on the assumption of a linear relationship between the square root of the CO_2 pressure and the solar luminosity for a constant mean temperature. The exact relationship may be different, however, and an analysis of the geological mechanism[3] suggests that a 2/3 power relationship might be more appropriate. Nonetheless, such differences are unlikely to affect the qualitative conclusions that can be drawn from Fig. 2.

If the principal agent for temperature regulation is the partial pressure of CO_2 in the atmosphere and even if the solar luminosity is constant, it seems that we are very close to the lower limit of possible adjustment; also there are no other gases in the air which could serve significantly in this way by the reduction of their partial pressures. Other mechanisms such as an increase in albedo by desert cover might sustain an equable climate but as observed by Henderson-Sellers[16], this is generally neutralized by a concomitant change in cloud cover. On the other hand, if we accept the predicted increase in luminosity and assume that the future decline of CO_2 matches the solar output as may have been the case in the past, then 150 p.p.m. pressure will be reached in about 100 Myr. This concentration is the lower limit tolerable for photosynthesis. Some adaptation to lower CO_2 concentrations and to higher temperatures is possible but it would not buy much time. In human terms the crisis is still infinitely distant but in terms of the life span of the biosphere,

rich with familiar metazoans, we might forecast an end to the
long spell of cool and favourable climate.

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LDH-B genotype-specific hatching times of *Fundulus heteroclitus* embryos

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**The evolutionary significance of protein polymorphisms has long
been debated. Exponents of the balanced theory advocate that
selection operates to maintain polymorphisms, while those of
the neoclassical school argue that most genetic variability is
selectively neutral[1]. As the 'neutralist' hypothesis implies that
allelic isozymes are functionally equivalent, some investigators
have examined the biochemistry of protein polymorphisms[2-15],
while others have concentrated on life history correlates[16-23].
Few studies, however, have established that *in vitro* functional
differences are reflected at the whole organism level[5,21-23], yet
this is a critical link in understanding the significance of protein
polymorphisms. We have studied the effects of the kinetically
different lactate dehydrogenase-B (LDH-B) allelic isozymes
on the rate of development and physiological performance of
the fish, *Fundulus heteroclitus*, and report here that hatching
time is highly correlated with LDH-B genotype: *LDH-B^{a}B^a*
individuals hatch before *LDH-B^{b}B^b* fish while heterozygote
(*LDH-B^{a}B^b*) hatching is intermediate. The basis for this
phenomenon may be a differential ability to deliver oxygen to
respiring tissues. As precisely timed hatching is critical to the
survival of *Fundulus*[24], such differences in hatching time
between LDH-B genotypes may be an important component
of the species' evolutionary strategy.**

The LDH-B polymorphism in *F. heteroclitus* is due to two
co-dominant alleles[25,26] which exhibit a cline in gene frequencies
along the Atlantic Coast of the United States[4,27]. We have
shown that there are temperature- and pH-dependent kinetic
differences between the LDH-B allelic isozymes[7]. Moreover,
intra-erythrocyte ATP differences among individuals are corre-
lated with LDH-B phenotype[3]. The role of ATP as an allosteric
modifier of *Fundulus* haemoglobin is similar to that of 2,3-
diphosphoglycerate in human red blood cells, in that it decreases
the affinity of haemoglobin for oxygen[28,29]. Thus, fish with the
highest levels of intra-erythrocyte ATP (that is, LDH-B^{b}B^b)
have the lowest blood oxygen affinity[3]. As respiratory stress
has been shown[30,31] to trigger the hatching mechanism in
Fundulus, we hypothesized that the hatching times of LDH-B
genotypes should differ because of differences in blood oxygen
affinity. Specifically, *LDH-B^{a}B^a* fish should hatch before *LDH-
B^{b}B^b* individuals.

As an initial test of this hypothesis, fertilized eggs were
obtained by stripping gametes from males and females that
were randomly paired. Each of the resulting clutches was incu-
bated in a separate Petri dish at 20 °C, pH 7.0 and 15‰
salinity (Instant Ocean). The incubation medium was changed
daily and the fry were collected as they hatched. The LDH-B
genotypes of each parental pair and their offspring were deter-
mined by gel electrophoresis[26,27] (see Fig. 1). Clearly, hatching
of *LDH-B^{a}B^a* eggs was predominant in the first 3 days, while
LDH-B^{b}B^b eggs predominated in the last 3 days. The overall
mean hatching times were 11.9, 12.4 and 12.8 days for the
LDH-B^{a}B^a, *LDH-B^{a}B^b* and *LDH-B^{b}B^b* genotypes, respec-
tively. Individual crosses in which there were more than one
genotype also showed that *LDH-B^{a}B^a* eggs hatched before
LDH-B^{a}B^b, which in turn hatched before *LDH-B^{b}B^b* (Fig. 1).

In addition to establishing an ordered hatching of LDH-B
genotypes, our analysis (Fig. 1) also indicated variations
between crosses that were not due to the *LDH-B* locus. If these
variations were due to other loci, then pooling gametes from
many individuals before fertilization should dramatically reduce
the variation between crosses. To test this hypothesis, we per-
formed experiments in which adult fish were segregated by
LDH-B genotype into breeding stocks[26]. Specific LDH-B
crosses were made by pooling gametes before fertilization.
Consistent with our expectation, these experiments (Tables 1
and 2) almost eliminated variation between similar crosses.
Thus, some of the variation among the 20 random crosses in
Fig. 1 must have been due to contributions from other loci. On
the other hand, Tables 1 and 2 indicate that there are still highly
significant differences (P < 0.01) in hatching time between
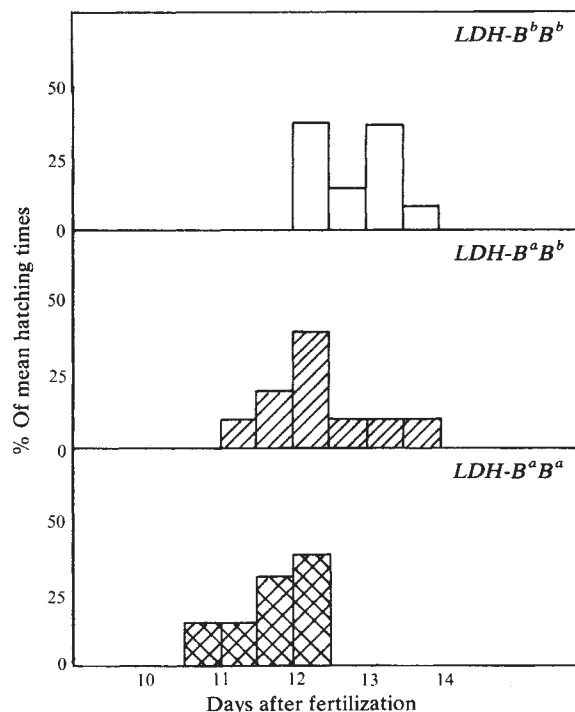LDH-B genotypes. These data (Tables 1 and 2), together with

Fig. 1 Distribution of mean hatching times for three LDH-B
genotypes from 20 random crosses. Analysis of variance[36] indi-
cated significant differences between the crosses (P < 0.05); Dun-
can's multiple range test[36] showed that some of this variation was
due to LDH-B genotype (for example, all the *LDH-B^{a}B^a* ×
LDHB^{a}B^a crosses hatched before all the *LDH-B^{b}B^b* ×
LDH-B^{b}B^b crosses; P < 0.05). There were also significant
differences, however, between similar crosses (for example, two
of the *LDH-B^{a}B^a* × *LDH-B^{a}B^a* crosses hatched sooner than
three other crosses of the same type; P < 0.05). The histogram
shows the distribution of mean hatching times among genotypes
irrespective of parental cross. Separate analyses of each cross in
which there were offspring of more than one genotype, showed
significant differences (P < 0.05) in hatching time between
genotypes in each case.