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The regulation of the air: a hypothesis

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We propose the hypothesis that natural selection, acting on the specificity of rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) for carbon dioxide over oxygen, has controlled the $\text{CO}_2 : \text{O}_2$ ratio of the atmosphere since the evolution of photosynthesis and has also sustained the Earth's greenhouse-set surface temperature. Rubisco works in partnership with the nitrogen-fixing enzyme nitrogenase to control atmospheric pressure. Together, these two enzymes control global surface temperature and indirectly the pH and oxygenation of the ocean. Thus, the co-evolution of these two enzymes may have produced clement conditions on the Earth's surface, allowing life to be sustained.

1 Introduction

The modern air is a biological construction (Fig. 1). Air pressure is largely (78 %) determined by nitrogen. Nitrogen is a product of the biological nitrogen cycle, with N_2 made by denitrification and anammox reactions. It is fixed by nitrifying bacteria, with only small inorganic N fluxes via volcanic gases and lightning. The nitrogen cycle is closely linked to the carbon cycle (Falkowski, 1997). Nearly 21 % of the air is O_2 , which is the product of the extraction of carbon from CO_2 in the air by photosynthesis. CO_2 is now about 390 parts per million, but $\sim 280\text{--}300$ ppm in the pre-industrial Holocene, and as low as 190 ppm in glacial maxima. Respiration, in which cells take up O_2 and release CO_2 , is the inverse side of the photosynthetic coin. On a planetary scale, the fluxes of photosynthesis and respiration are broadly reciprocal (e.g. Keeling and Shertz, 1992). Without photosynthetic oxygen, in a biosphere dominated by anaerobic metabolic processes such as fermentation, only limited cellular respiration could occur. The production of methane (now ~ 1.8 ppm; ~ 0.65 ppm in the Holocene, ~ 0.35 ppm in glacial maxima) by methanogenesis is carried out by archaeobacteria using substrates such as acetate or hydrogen. Methanogenesis is largely dependent on the degradation of

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organic compounds and thus is in essence the recycling of photosynthetic productivity. Even the biota living around hydrothermal vents on mid-ocean ridge volcanoes depend on the supply of sulphate from the oxygen-rich surface ocean (although methanogenesis can also occur using H₂ produced abiotically by the reaction between water and hot newly-erupted basalt).

2 Carbon transfers

The transfer of atmospheric CO₂ from the air to the interior of photosynthetic cells is expedited by a variety of mechanisms including the CO₂ concentrating mechanism (Badger et al., 2005). The delivery of CO₂ to photosynthetic organelles is not a trivial accomplishment. Despite this, carbon entry into the cell is generally efficient, with little fractionation between ¹²C and ¹³C. This high isotopic efficiency implies a high yield and thus nearly all the carbon accessed from the external environment is transferred into the cell.

Once inside the cell the rubisco enzyme, the most abundant protein on Earth, catalyses the fixation of CO₂. There are various forms of rubisco. Rubisco I, the most abundant, facilitates oxygenic photosynthesis. As a carboxylase/oxygenase, rubisco operates with either CO₂ or O₂ as substrate, either selecting CO₂ from the atmosphere to capture C into organic life, or acting in reverse. As the enzyme is highly selective, only a part of the accessible carbon dioxide inventory within the cell is chosen for incorporation into organic product. Thus, rubisco-catalysed carbon fixation causes strong isotopic fractionation.

Rubisco I may have evolved nearly 3 Ga ago (Nisbet et al., 2007), yet rubisco's "specificity" (its preference for CO₂ over O₂) remains paradoxically restricted. In contrast with other enzymes, rubisco seems inefficient, with a sluggish reaction rate (Tcherkez et al., 2006). However, rubisco's 'inefficiency' may be deceptive. On a molecular level, analysis of the kinetics and isotopic fractionation of Rubisco I in oxygenic photosynthetic organisms (Tcherkez et al., 2006) suggests that evolution has led

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showed that the Tolbert et al. (1995) experiments may have been affected by problems such as leakage artefacts.

Oxygen compensation Γ_{O_2} (stated in %) is related to rubisco specificity and CO_2 concentration, C . Crucially, André (2011a) demonstrated that only a single reciprocal function exists linking Γ_{CO_2} and Γ_{O_2} . André (2011a) defined a plant-specificity-factor (Sp) which took into account both the specificity of the rubisco enzyme and also the CO_2 gradient between the atmosphere and the Rubisco site. Where E is the gross Oxygen evolution, a parameter linked to the electron transport rate generated by light in chloroplasts, and R is the rate of respiration, André (2011a) showed that a finite or realistic Γ_{O_2} cannot be reached in a closed biosystem without a high rate of respiration (R).

$$\Gamma_{O_2} = Sp C(E - R)/0.5(E + R) \quad (1)$$

André (2011a) showed that the CO_2 and O_2 exchanges of the green (productive) part of plants can be fitted, in large range of environmental parameters, by a simple model that mimics the Rubisco response to O_2 and CO_2 variations. In a closed biosystem, André (2011a) showed that, dependent on plant specificity Sp , crossing points of oxygenation and carboxylation gas exchanges exist, between net photosynthesis and the opposite net photorespiratory processes, where net photosynthetic uptake of CO_2 equals gross O_2 uptake. Taking O_x as the oxygen concentration (in %) at the crossing point, and C_x as the CO_2 concentration (in ppm), the crossing point is expressed by reciprocal relationships (André, 2011a):

$$O_x = 0.5 C Sp \text{ and } C_x = 2 O / Sp \quad (2)$$

For average C3 plants, with an average plant specificity Sp of $0.132 \% \text{ ppm}^{-1}$, André's (2011a) relationship gives CO_2 of 317 ppm for the modern atmospheric mixing ratio of dioxygen of 20.95%. CO_2 in the pre-industrial air had a mixing ratio of roughly 290 ppm. Tolbert et al. (1995) noted that the atmospheric $CO_2 : O_2$ ratio is very close to the balance determined by the specificity of rubisco. They suggested that the "global

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atmospheric 0.03 % CO₂ and 21 % O₂ equilibria seem to be limits set by the average specificity properties of rubisco from plants and algae”.

This leads to the central hypothesis (Tolbert et al., 1995; Igamberdiev and Lea, 2006; Nisbet et al., 2007; Nisbet and Nisbet, 2008; André, 2011a) that Rubisco controls the balance of CO₂ and O₂ in the air. Assuming a very simplified global system consisting only of C3 land plants (with a specificity of 0.132 % O₂ per ppm CO₂) and atmosphere (omitting oceans and the geological cycling of carbon dioxide in the ocean-atmosphere system), the fit is remarkable. As André (2011a) points out, “the O₂ and CO₂ concentrations of the pre-industrial atmosphere are the compensation points of the global biosystem”.

But is this accidental, or has it evolved over time? If “the present is the key to the past” the specificity of rubisco may have helped sustain planetary habitability over geological time. Nisbet and Nisbet (2008) considered the greenhouse implications of this hypothesis, suggesting that, by setting the O₂ : CO₂ ratio, the evolution of the enzymatic specificity of Rubisco I, as it controlled plant specificity, may have controlled the planetary greenhouse ever since 3Ga ago, and hence also the maximum abundance of CH₄ and water vapour in the air. André (2011a), suggested the O₂ : CO₂ ratio is not merely fortuitous but is a consequence of a dynamic stabilisation of the atmosphere. More generally, André (2011a) strongly supported the hypothesis of co-evolutionary plant-atmosphere-climate feedbacks on the modern planet.

3 The Greenhouse and its geological record

If the atmospheric O₂ : CO₂ ratio is biologically set, the obvious evolutionary hypothesis is that the planetary greenhouse, the Earth’s surface temperature and the acidity of the oceans, has been biologically set by natural selection over the aeons (Nisbet, 2002; Nisbet and Nisbet, 2008). Evolutionary competition, by natural selection of rubisco, has produced a mechanism that inherently has the ability to set the greenhouse warming of

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the air. But did rubisco specificity co-evolve with the global greenhouse? Can natural selection sustain an equable global temperature? Or is the clemency of the planetary climate over the aeons simply an inorganic geochemical consequence of the nature of the planetary surface?

5 Planetary surface temperature is governed by CO_2 , supplemented by CH_4 and minor gases, and indirectly by N_2 and O_2 pressure. The dominant greenhouse gas, water vapour in the air, can be thought of as a “responding” feedback to variations in gases such as CO_2 , CH_4 and N_2O , rather than a “controlling” gas. The modern atmosphere is globally mixed over a period of a year, and equilibrates quickly with the ocean surface and upper waters, a process speeded by planktonic use of carbonic anhydrase. Stability in the ocean/atmosphere system is conferred by the very large (and long-lived) biologically-created reservoirs of atmospheric N_2 and O_2 , and reciprocally by the burial of reduced organic matter, which is recycled via volcanoes by plate tectonics. In the oxygen-rich atmosphere created by photosynthesis, any emitted CH_4 and CO molecules are within a few years converted to CO_2 . Rates of biological processes vary exponentially with temperature. This means that, compared to geological timescales, biological feedback controls can in principle act rapidly, controlling CO_2 and CH_4 , and thereby managing the temperature of the ocean/atmosphere system.

10 Inorganic processes have a longer time-scale. Atmospheric CO_2 , through acid rain, influences the rate of chemical erosion and the supply of alkalinity by rivers to seawater. By equilibrating with ocean water, atmospheric CO_2 helps to set ocean pH. This in turn influences carbonate precipitation and thus the inorganic feedback controls on CO_2 (Walker et al., 1981; see also Fig. 8.2 in Kasting, 2008). Carbonate precipitation, and hence CO_2 in the air, also depends on the alkalinity of the ocean, set by the combined effects of river runoff (which is influenced by atmospheric CO_2) and mid-ocean ridge hydrothermal processes (which are less linked to the atmosphere but do depend in part on the CO_2 content of the seawater). As the Earth has evolved, the continental area may have changed over time (but see discussion in Arndt and Nisbet, 2011). Moreover, as the potential temperature of the mantle has cooled, thickening lithosphere may have

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notable but isolated time periods, the C isotope ratio in sedimentary carbonates has been broadly modern in aspect (Schidlowski, 1988). The implication is that the controls on carbon partition between organic matter and carbonate deposition into sediment, whether inorganic or biologically precipitated, have been broadly unchanged from 2.9 Ga ago to now.

Photosynthesis is today the key biological control on CO₂ (Hahn, 1987, 1991), and also indirectly controls CH₄ production from dead organic matter. Hence on an annual-to millennium-scale, the global temperature (set by the CO₂ and CH₄ greenhouse) must be determined by the primary control on CO₂ partitioning into organic matter, which is rubisco's specificity (Tcherkez et al., 2006; Gutteridge and Pierce, 2006). If rubisco were more effective at drawing down CO₂ from the air (e.g. with a take-over of the biosphere by C₄ plants, so that the overall average plant specificity changed markedly), eventually sequestering organic carbon on the seabed, the water would freeze. If rubisco were less effective, the oceans would become acidic, hot, and deoxygenated.

Rubisco is a biological product and like all biology is subject to natural selection. As the environment changes, evolution will act on rubisco. It is thus a tenable hypothesis that, at least in part, the broad stability of planetary temperature over the aeons occurred because natural selection of competing rubisco molecules favoured those biological processes that, by managing the atmosphere, maximised the likelihood of the survival of microbial consortia.

Consider the plankton, both eukaryotic and prokaryotic. Intrinsically, only a few species would be expected, equal in number to the number of bio-limiting resources – N, P, Fe, Si, inorganic carbon, light energy, trace metals. Yet thousands of plankton species coexist in natural waters. This paradox is resolved by the hypothesis (Huisman and Weissing, 1999) that resource competition creates oscillating and chaotic populations. These oscillations allow many species to coexist, although depending on only a few discrete resource types. Natural selection, presumably including selection for rubisco specificity in photosynthesisers, operates on the oscillating populations, to select for survivability.

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Separately, there is evidence that large variations in key indicators such as the N:P ratio occur in the various microbial “biomes” in the ocean. While the bulk global ocean N:P ratio (16:1) is very highly conserved on a planet-wide basis, the local N:P can vary widely, from 11:1 to 20:1 (Weber and Deutsch, 2010). In the global ocean, reservoirs of N and P may be kept near the Redfield ratio (C:N:P = 106:16:1, the stoichiometric molecular ratio of carbon, nitrogen and phosphorus in oceanic plankton), by competition between species that add N to the ocean through biological N₂ fixation when N is limiting, but when it is not limiting are out-competed by other plankton (Weber and Deutsch, 2010). Collectively in the global ocean circulation, the biomes manage a very efficient global regulation of N:P, yet individual biomes can be very different, each selected to be best adapted for local conditions. If this is so for microbial N and P, could a similar evolutionary mechanism control CO₂?

In the ocean, microbial biomes based on photosynthetic plankton have climate impact. Selection over time will favour biomes that are best fitted to survive by producing favourable responses from the environment, even if those benefits are only marginal. Over millions of years, selection would favour phytoplankton species which contained rubisco with specificities that maximised climate favourability. Ecological consortia that act adversely to climate will be selected against. In extreme cases, global over-heating or rare catastrophic glaciations would eliminate organisms whose blooms destabilised global climate. Over time, by maximising survival, repeated selective evolutionary feed-backs would fine-tune microbial rubisco specificities as the rubiscos in turn controlled the greenhouse impact of the atmosphere.

On land, similar selective pressures must apply. Rainforests substantially manage local and regional climates, controlling albedo via leaf colour and also by trapping and transpiring water and emitting aerosols to nucleate cloud cover. On a large scale, major forest biomes strongly influence global weather, for instance by influencing the location of major convergence zones and the jet streams. Similarly, in the boreal and tropical forests, carbon sequestration by peat bogs has global impact by drawing down CO₂, a global cooling impact that is countered by methane emission.

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In the relatively recent geological past C4 plants have evolved (Sage, 2004). These plants, which through convergent evolution have appeared in many plant groups, pre-concentrate CO₂ around the rubisco, and thus can thrive at lower levels of ambient CO₂ than C3 plants. Globally, they are common at times of ice ages, when atmospheric CO₂ may be below 200 ppm. In these circumstances, the pre-concentration stage clearly gives them advantage over C3 plants. Contrarily, higher CO₂ in interglacial periods gives advantage to C3 plants (André, 2011b). Interestingly, C4 plants (especially grasses) often form fire ecologies: though fires immediately return C to the air, their long-term impact is to remove C by sequestering it as charcoal, which is stable over millions of years. The Holocene global CO₂ level (roughly 290 ppm) may have been set (André, 2011b) by competition between the dominant C3 plants (favouring ~320 ppm CO₂ at ~21 % O₂) and the specialist C4 plants (favouring lower CO₂ values).

More generally, in the oxygen-rich atmosphere, on a warm planet at a time of increased atmospheric CO₂ (say from a volcanic injection), carbon fixation by photosynthesis will increase. In these circumstances, with CO₂ abundantly accessible, it is possible that natural selection will favour photosynthetic organisms that use a catalytically faster variant of rubisco. Eventually photosynthesis will use up the excess CO₂, reducing greenhouse warming by drawing down CO₂ towards Γ_{CO_2} . In the cooler low-CO₂ environment that results, there will be a greater requirement for rubisco variants that have greater specificity for CO₂ over O₂ (Tcherkez et al., 2006), but this adaptation means draw-down rates will be reduced. Eventually, as organic matter is recycled, the ratio of CO₂:O₂ will rebalance temperature again. The very large O₂ reservoir, which changes only slowly as it is much larger than the annual flux, serves as a stabiliser on the system, drawing CO₂ back to long-term average levels.

Figure 3, modelled on industrial PID (proportional-integral-derivative) controllers, illustrates the way natural selection, acting on rubisco specificity, can manage the surface temperature. The “optimum” temperature is the temperature at which the contemporaneous global biosphere has maximum productivity. If an external perturbation

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occurs, such as a volcanic eruption or solar warming, then there will be a proportional response as photosynthesis and respiration increase/decrease or decrease/increase, taking up or releasing CO₂. Methane too will change, especially as temperature change affects water precipitation in rain and snow. Secondly, there will also be an integrated response, as carbon is sequestered or released, for example by precipitation or dissolution of calcite, or by the deposition or release of organic matter, for example in sea bed organic deposits, or in peat bogs or fires. Moreover, there will be a strong integrated response from methane recycling organic matter. Thirdly, in addition to this, there will be a derivative response, as organisms are favoured or selected against, according to their balance between rubisco specificity and the rate of catalytic turnover and productivity. Over the longer term via this natural selection for specificity, especially if the external perturbation is prolonged (e.g. solar warming), the control will be adaptive, iteratively ramping up so that evolution will change the contemporaneous optimum temperature at which the biosphere has maximum productivity. For example, in future as the aging Sun brightens, dynamically adaptive evolution will favour C4 plants, capable of thriving in low-CO₂ air over C3. This will stabilise global temperature by reducing the atmospheric greenhouse as the solar input increases.

Thus there is circumstantial but permissive evidence to support the hypothesis that rubisco manages the atmosphere and has done so for the past three billion years.

6 Testable implications of the hypothesis of co-evolution between rubisco and climate

This hypothesis implies testable propositions:

1. That inorganic controls on carbonate precipitation are not the primary controls on atmospheric CO₂ and O₂, but rather that atmospheric abundances of CO₂, O₂ and CH₄ are primarily set by biological control. This biological control determines the wider environment (pressure, temperature, acidity, redox) in which inorganic

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reactions occur. The proposition predicts that atmospheric mixing ratios of CO₂, O₂ and CH₄, and their variability, are fully explicable by biological processes.

2. That, in addition to management of carbon dioxide, biological sequestration of nitrogen into the atmosphere (which creates atmospheric air pressure) has overwhelmed the inorganic (geological) processes that otherwise would be in control. This predicts that nitrogenase, often thought of as inefficient, must be as well tuned to its task as Rubisco I.

3. That for any planet, chance trajectories of surface temperature which sustain clement conditions over geological aeons are very improbable, given the complex parameters of solar brightening, geological partitioning of C, O, N and S species between the planetary interior and the surface, exchange between ocean and air; and time. In the Earth's early history, inorganic processes may have produced clement conditions for a relatively brief period (10⁵–10⁷ yr) (Sleep et al., 2001), but this could not have been sustained over aeons. The implication is that it will be very difficult to create an inorganic feedback model that successfully sustains clement temperatures over the aeons. In contrast, the continually selective nature of biological evolution has inbuilt adaptation.

Perhaps only biological processes (Lovelock and Whitfield, 1982), driven by natural selection, could have allowed Earth to remain clement, with surface temperatures following a very improbable trajectory through time. By mutually tuning rubisco and the environment to each other, the action of natural selection on the kinetics of carbon acquisition by the plants of the planetary estate, may have directed the temperature, ocean pH and wider setting in which equilibrium sea chemistry has acted and new life forms have evolved. Gutteridge and Pierce (2006) cite the allusion by Dr. Pangloss to the Great Chain of Being “*There is a concatenation of events in the best of possible worlds*”. Pangloss may be right. Given our present intervention to change atmospheric CO₂ and oceanic pH, and to deoxygenate the oceans, it is also worth considering Candide's reply “*let us cultivate our garden*”.

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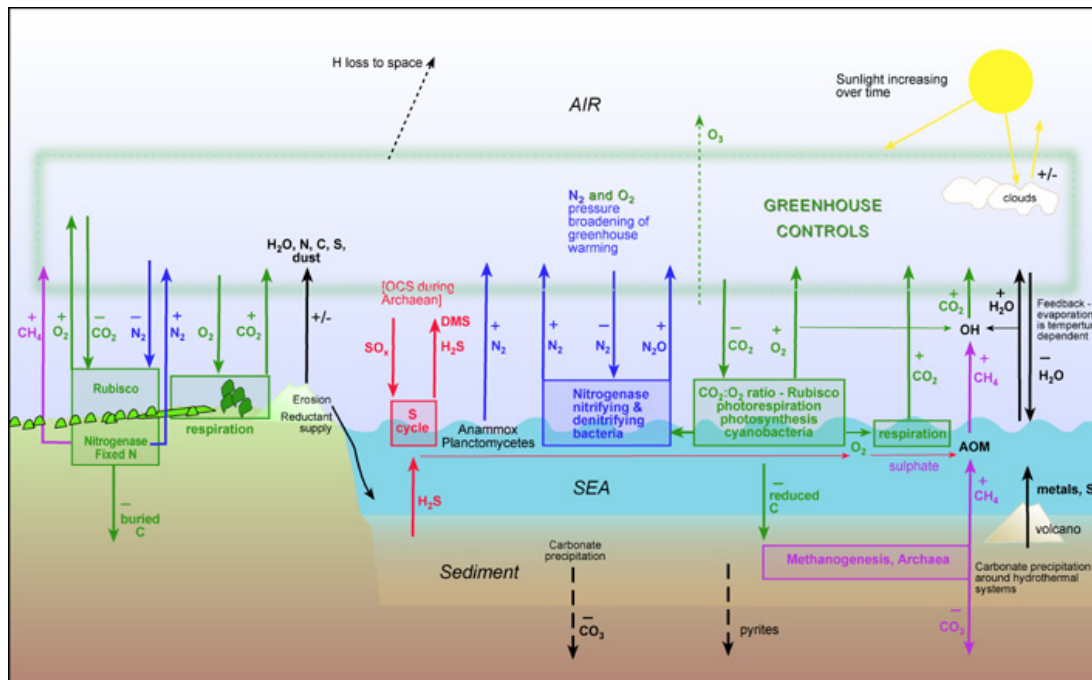


Fig. 1. Biological controls on atmospheric composition, pressure and temperature. Positive and negative temperature forcing is shown by + and – symbols. Green shading on land represents photosynthetic life. Abbreviations: (AOM) Anaerobic methane oxidation. AIR – natural mix, now mainly N₂ and O₂ but previously with CO₂ and CH₄. Other letters are chemical species.

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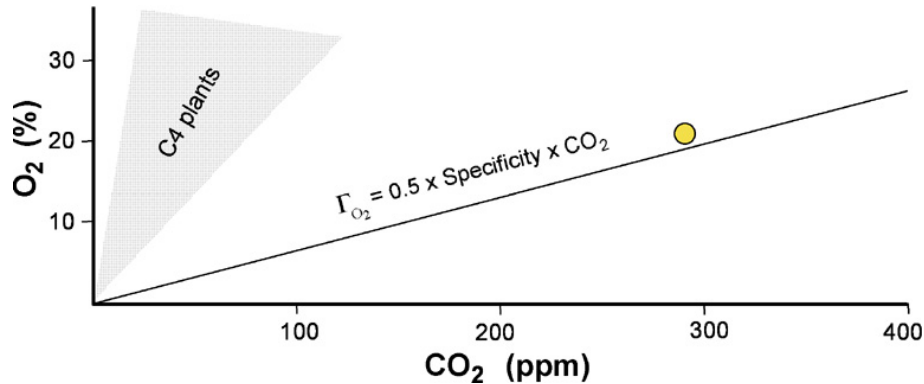


Fig. 2. Plot of $\Gamma_{\text{O}_2} = 0.5 Sp C$, assuming Sp of 0.132, as for average C3 plants (André, 2011a), showing also the field of C4 plants (André, personal communication, 2011) Do not shows the approximate composition of the Earth's atmosphere before the industrial revolution, with about 290 ppm CO_2 and nearly 21 % O_2 .

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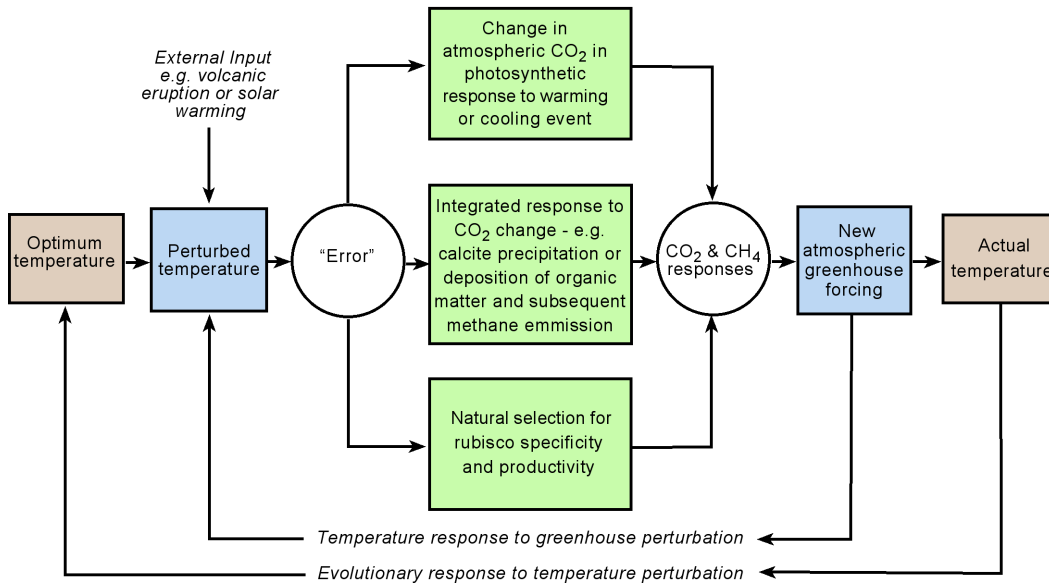


Fig. 3. Possible controls on temperature of the ocean/atmosphere system, modelled on a PID controller, illustrating the way natural selection, acting on rubisco specificity, can manage the surface temperature.

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