

Self-sustained temperature oscillations on Daisyworld

By C. NEVISON^{1*}, V. GUPTA² and L. KLINGER¹, ¹*National Center for Atmospheric Research, PO Box 3000, Boulder, CO 80307-3000, USA;* ²*University of Colorado, Boulder, CO 80303, USA*

(Manuscript received 16 June 1998; in final form 9 March 1999)

ABSTRACT

The daisyworld model of Watson and Lovelock demonstrated that a simple biological feedback system involving coupling between black and white daisies and their physical environment can stabilize planetary temperature over a wide range of solar luminosity. Here, we show that the addition of a differential equation for temperature to the original daisyworld model leads to periodic oscillations in temperature about a homeostatic mean. These oscillations, in which the model alternates between dominance by either black or white daisies, arise from the internal dynamics of the system rather than from external forcing. An important criterion for the oscillations to occur is that solar luminosity be within the range in which both daisy species are viable. A second important criterion is that the ratio of the timescales for daisy population turnover and climate system thermal response be bounded. While internally driven oscillations are well known in predator–prey biological models and in coupled ocean energy balance–cryosphere models, the present study shows that such oscillations also can arise in a model of the biosphere coupled to its physical environment. The potential significance of this result to planet Earth and the science of geophysics is discussed.

1. Introduction

The fundamental rôle of the biota in planetary climate has been articulated by the emerging new science of geophysics (Lovelock, 1995). Geophysics is predicated on the idea that the dynamics of life on Earth is tightly coupled to the dynamics of the soil, rocks, ocean, and atmosphere, and that this coupling results in the self-regulation of the planetary climate. To mathematically illustrate this idea, Watson and Lovelock (1983) developed the famous daisyworld model. Daisyworld is a fictitious planet inhabited by “black” and “white” daisies whose albedos are lower and higher, respectively than the albedo of bare ground. The relative populations of the two daisy types regulate the mean planetary albedo, which plays a key rôle in the radiation balance that determines planetary temperature. Tem-

perature in turn controls the growth rate of the daisies, which completes the feedback loop between the daisies and their environment. Self-regulation of planetary temperature emerges naturally from this coupled biological–physical system, without planning or foresight on the part of the daisies. In this sense, the daisyworld model offers insight potentially relevant to Earth into the nature of coupling between life and climate (Watson and Lovelock, 1983; Lovelock, 1995).

Simple nonlinear mathematical models have long been used for understanding the qualitative features of complex natural systems like Earth’s climate (Budyko, 1969; Sellers, 1969). Some well-known examples are the simple coupled energy balance–cryosphere models developed to study Earth’s paleoclimatic variability (Ghil and Childress, 1987). Qualitative understanding obtained through analyzing simple models provides guidance for interpreting results of much more complex models such as general circulation

* Corresponding author.

models (GCMs) (Gal-Chen and Schneider, 1976), and for identifying observational needs and new research directions.

The simple nonlinear Earth models described above often include an ordinary differential equation (ODE) for temperature which describes the planetary radiative energy balance. Earth is well known to be in imperfect balance, both spatially and temporally, between incoming solar and outgoing longwave radiation (Peixoto and Oort, 1992). In contrast, planetary temperature in the original daisyworld model is calculated by constraining incoming and outgoing radiation to be in exact balance. As a first step toward modifying daisyworld to more realistically resemble Earth, a simple ODE for temperature can be introduced into the original model. This modification adds one new parameter, a climatic heat capacity or thermal response time. In this paper, we examine the results of the daisyworld model when it is modified such that the planet is no longer constrained to be in perfect radiative equilibrium. We discuss the significance of our results to geophysiology in much the same spirit as Watson and Lovelock (1983), who presented the original daisyworld model as a parable with possible implications for Earth.

2. Model description

The model presented here is similar to the original daisyworld model of Watson and Lovelock (1983), with one fundamental modification to the equation describing the balance between incoming solar radiation and outgoing longwave radiation. Whereas Watson and Lovelock assumed an exact balance between these two fluxes,

$$SL(1 - A) = \sigma T_e^4, \quad (1)$$

we have replaced eq. (1) with an ODE for the effective planetary temperature T_e , which allows that T_e is not necessarily at steady state. The ODE can be written as,

$$c_p(dT_e/dt) = SL(1 - A) - \sigma T_e^4, \quad (2)$$

where A (unitless) is the average planetary albedo, c_p ($\text{erg cm}^{-2} \text{K}^{-1}$) is a measure of the mean heat capacity or thermal inertia of the planet, L (unitless) is a dimensionless measure of the luminosity of the sun relative to the present day,

S ($\text{erg cm}^{-2} \text{yr}^{-1}$) is the present-day constant flux of solar radiation reaching the planet $= 2.89 \times 10^{13}$, σ ($\text{erg cm}^{-2} \text{yr}^{-1} \text{K}^{-4}$) is Stefan's constant for blackbody radiation $= 1789$, T_e (K) is the effective temperature at which the planet radiates like a black body.

The greenhouse effect can be easily introduced into eq. (2) through a term expressing deviation from the blackbody radiation (Ghil and Childress, 1987, p. 303). For the present, we will ignore this type of refinement.

The remaining equations describing the growth of the black and white daisies are identical to those used in the original model, as summarized below.

$$da_b/dt = a_b(x\beta - \gamma), \quad (3)$$

$$da_w/dt = a_w(x\beta - \gamma), \quad (4)$$

$$x = p - a_b - a_w, \quad (5)$$

$$A = xA_{gf} + (1 - p)A_s + a_bA_b + a_wA_w, \quad (6)$$

$$\beta = 1 - 0.003265(T_{opt} - T_{l,i})^2, \quad (7)$$

$$T_{l,i} = q'(A - A_i) + T_e, \quad (8)$$

where a_b (unitless) is the fraction of total planetary area covered by black daisies, a_w (unitless) is the fraction of total planetary area covered by white daisies, A_b (unitless) is the albedo of black daisies $= 0.25$, A_{gf} (unitless) is the albedo of fertile bare ground $= 0.5$, A_s (unitless) is the albedo of nonfertile areas $= 0.5$, A_w (unitless) is the albedo of white daisies $= 0.75$, β (yr^{-1}) is the growth rate of the daisies, γ (yr^{-1}) is the death rate of the daisies (generally set to 0.3 in the original model), p (unitless) is the fraction of total planetary area that is potentially fertile $= 1$, q' (K) is the conduction coefficient of solar energy among different surface types $= 20$, $T_{l,i}$ (K) is the local temperature which determines the growth rate of each species i of daisy, T_{opt} (K) is the optimal growth temperature $T_{l,i}$, assumed to be 295.5 K (22.5°C) for both daisies, x (unitless) is the fraction of total planetary area that is potentially fertile but not covered by daisies.

Eq. (7) assumes that the daisy growth rate β is maximum when the local daisy temperature $T_{l,i}$ is equal to T_{opt} and that β is 0 when $T_{l,i} \leq 278$ K (5°C) or $T_{l,i} \geq 313$ K (40°C). Eq. (8) assumes that the local temperature for black daisies $T_{l,b}$ is somewhat warmer than the effective planetary temperature T_e , while the local temperature for white daisies $T_{l,w}$ is somewhat colder than T_e .

Effectively, this equation serves as a parameterization of dynamical heat transfer. Note that in the daisyworld model, dynamics is parameterized as a secondary effect while the biota is featured as a first order effect. For simplicity, we have not modified eq. (8) to account for temporal disequilibria between $T_{i,i}$ and T_e .

Before presenting results of the modified model, we briefly review in Fig. 1, the results of the original daisyworld model of Watson and Lovelock (1983). Their model was integrated for-

ward in time at a fixed solar luminosity L until equilibrium temperature and daisy populations were established. The value of L was incremented and the procedure was repeated until a new steady state was achieved. The daisy area fractions were initialized at the larger of 0.01 or the steady state values at the previous value of L . Fig. 1a,b show that planetary temperature is effectively stabilized at a value close to the optimal growth temperature of the daisies (22.5°) over a wide range of solar luminosity ($\sim 0.75 < L < 1.6$) due to adjustments

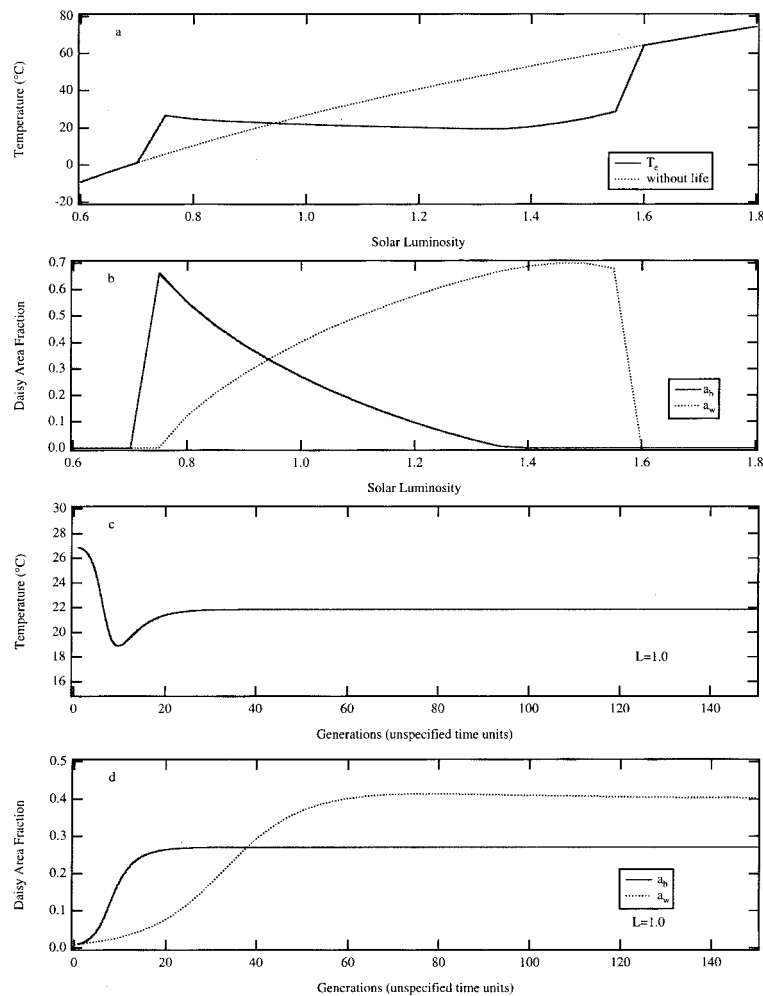


Fig. 1. Results from the original daisyworld model (using eq. (1)) with $\gamma = 0.3$. (a) Stabilization of temperature over range of solar luminosity L . The dotted line shows planetary temperature without life, i.e., at a constant albedo of $A = 0.5$. (b) Steady state black and white daisy populations over range of solar luminosity L . (c) Achievement of steady state temperature at $L = 1$. (d) Achievement of steady state daisy populations at $L = 1$.

in the relative areas of black and white daisies. Fig. 1c,d show that at a given value of L , both T_e and the daisy populations achieve steady state fairly rapidly. Note that time in the original daisyworld model using eq. (1) is expressed in terms of daisy generations and otherwise need not be specified. When eq. (2) is used, time takes on the specific units of the terms S and σ . In the next section, in which we present results from the modified daisyworld model, we have used time units of years unless otherwise specified.

3. Results

The main new result of the modified daisyworld model is that, under certain conditions, the model

produces self-sustained temperature oscillations which are closely coupled to oscillations in the populations of black and white daisies (Fig. 2a). Unlike the original model, in which the daisies achieved stable equilibrium populations at a given solar luminosity, the modified daisyworld model alternates between strong dominance by one species and then the other, with relatively short periods in between in which both daisies have comparable populations. At the solar luminosity shown in Fig. 2a ($L=1$), white daisies dominate over a somewhat longer period than black daisies, with the extremes of temperature occurring during the changeover interval. Eq. (8) is critical to the establishment of the oscillations because it yields a warmer local temperature $T_{l,b}$ for black daisies

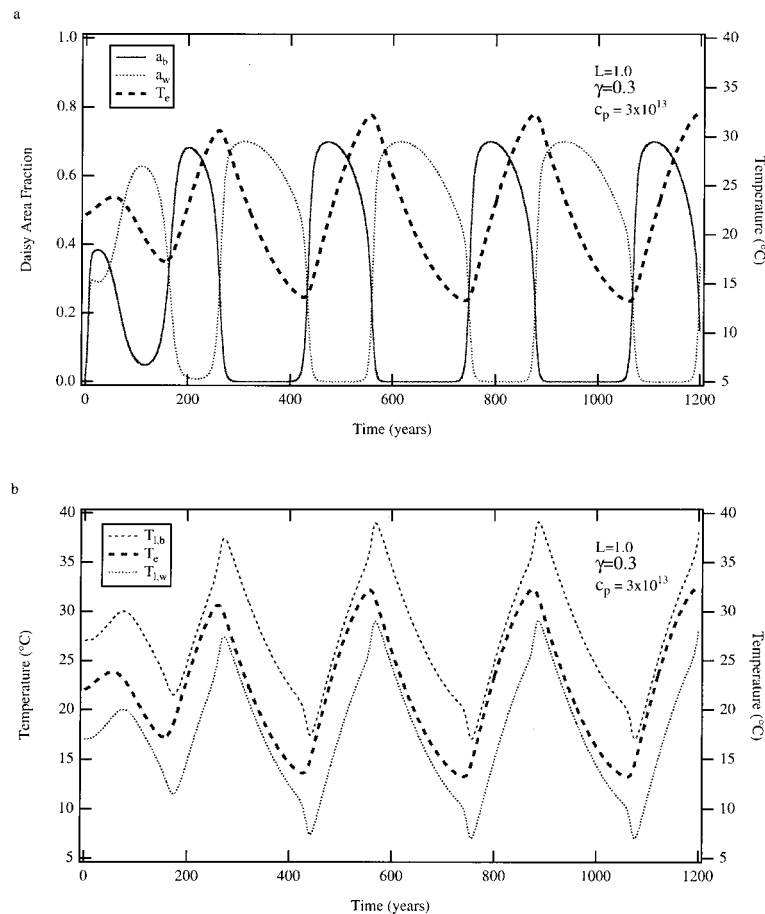


Fig. 2. Oscillations in T_e , a_b , and a_w predicted by the modified daisyworld model (using eq. (2)) with $\gamma = 0.3$. (a) Warm sun conditions, $L = 1.0$, $c_p = 3 \times 10^{13}$. (b) T_e and the local daisy temperatures $T_{l,b}$ and $T_{l,w}$ under warm sun conditions.

and a colder local temperature $T_{l,w}$ for white daisies compared to T_e (Fig. 2b). As T_e cools to below T_{opt} , the white daisy growth rate slows down while the black daisy growth rate is near optimum. An abrupt warming occurs as black daisies proliferate and white daisies die off. However, as T_e becomes increasingly warmer than T_{opt} , the black daisy growth rate slows down while white daisies stage a comeback. This results in a gradual cooling of the planet until the whole cycle repeats again.

Two important criteria must be met for the oscillations described in Fig. 2 to occur. First, solar luminosity L must be such that both daisies in the original model have viable, not widely disparate populations. Fig. 1b provides a useful guide to the range of L in which oscillations can be expected based on this first criterion. Numerically, we find that this range is approxi-

mately $0.8 < L < 1.2$, with some variation with the parameters c_p and γ . Outside these limits, the modified model predicts steady state, non-oscillatory temperatures and daisy populations similar to those of the original model. At the periphery of the limits, e.g., $L = 1.25$, damped oscillations can occur. The relative sizes of the original steady state daisy populations in Fig. 1b are useful for predicting which daisy species will dominate the oscillatory periods in the modified model. At $L = 0.8$ (cool-sun conditions), in contrast to Fig. 2a, black daisies dominate for longer periods than white daisies and the temperature oscillations are characterized by an abrupt cooling and a more gradual warming.

The second criterion for free oscillations to occur is that the thermal response time τ_{clim} of the daisyworld climate must be within a certain order of magnitude of the timescale for the turnover of the daisy populations. Here, we have assumed that τ_{clim} is proportional to the value of the heat capacity c_p , based on Harvey and Schneider's (1984) work with a simple Earth model, and that daisy turnover is proportional to $1/\gamma$, the inverse of the daisies' death rate. Fig. 3 presents model results using a time unit of 0.001 years and a fixed value of $c_p = 3 \times 10^{13}$, which corresponds to $\tau_{clim} \sim 500$ years on Earth (Harvey and Schneider, 1984). The three curves in Fig. 3, which represent different values of $1/\gamma$ spanning 4 orders of magnitude, show a range of behavior depending on the relative magnitudes of $1/\gamma$ and c_p . When $1/\gamma \sim 4$ months, free oscillations occur as described above. When $1/\gamma \sim 30$ years, oscillations occur initially, but are damped to a steady state solution. The climate appears to adjust quickly enough in this case that the balance between incoming and outgoing radiation is near zero, similar to the original model of Watson and Lovelock. In the third case, when $1/\gamma \sim 1$ day, an interesting phenomenon occurs. As T_e warms during the period of black daisy dominance, $T_{l,b}$ increases to and persists at a point at which a_b reaches a value smaller than the computer can resolve numerically. We have interpreted this to mean extinction of black daisies. Whereas for larger values of $1/\gamma$ the temperature begins to cool before the black daisies die off completely, in the $1/\gamma \sim 1$ day case the relative thermal response time is so slow that they are driven to extinction. Meanwhile, the surviving white daisies eventually cool the planet to 13° ,

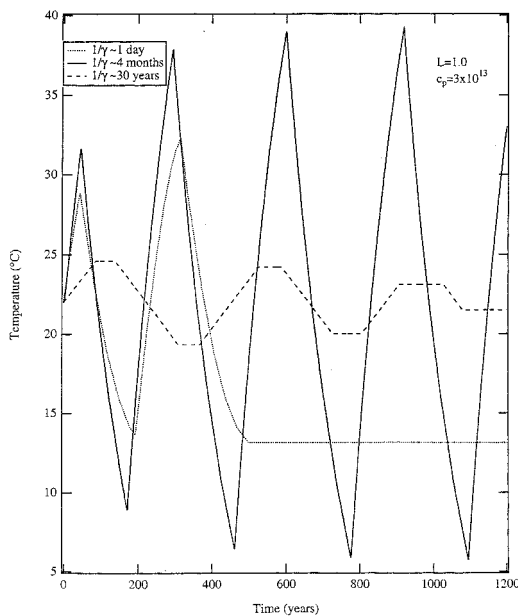


Fig. 3. Oscillations in T_e at $L=1$ and $c_p = 3 \times 10^{13}$, which yields a thermal response time τ_{clim} of ~ 500 years. The three curves show a range of $1/\gamma$, spanning 4 orders of magnitude. At $1/\gamma \sim 4$ months, self-sustained oscillations occur. At $1/\gamma \sim 30$ years, oscillations are damped to a steady state. At $1/\gamma \sim 1$ day, temperature changes slowly, leading to the extermination of black daisies as warm temperatures persist too long. Surviving white daisies cool the planet to 13°C , where T_e and a_w become trapped at fixed values.

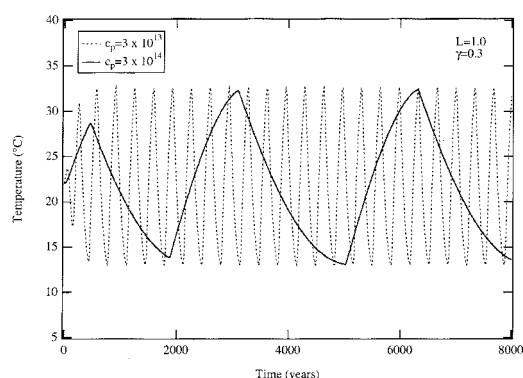


Fig. 4. Sensitivity of the oscillation period to the heat capacity c_p . The period generally increases by a factor of 10 with ten-fold increase in c_p .

beyond which point further cooling would jeopardize their survival. Black daisies no longer exist to lower planetary albedo, and daisyworld remains trapped at an uncomfortably cold temperature.

Provided the criterion described above is met, that is, $1/\gamma$ remains bounded relative to c_p , modifications to the period of the self-sustained temperature oscillations can be achieved by varying c_p . An increase in c_p by a factor of 10 results in a tenfold increase in the oscillation period (Fig. 4).

A final key result of the modified daisyworld model is the maintenance of homeostasis of the mean planetary temperature over a wide range of solar luminosity (Fig. 5). Although the amplitude of the self-sustained temperature oscillations is large ($\sim 20^\circ\text{C}$), the mean value of T_e still falls close to T_{opt} . Thus the fundamental result of the original daisyworld model is preserved in a mean climatic sense. Fig. 5 is similar in some ways to Fig. 1 of Jascourt and Raymond (1992), who rebutted the claim by Zeng et al. (1990) that the occurrence of chaos in a discrete version of daisyworld contradicts homeostasis. Among the other reasons stated in their rebuttal, Jascourt and Raymond showed that the long-term means of the chaotic temperature states predicted by Zeng et al. still exhibit homeostasis.

4. Discussion

The most striking new feature of the modified daisyworld model is the establishment of self-

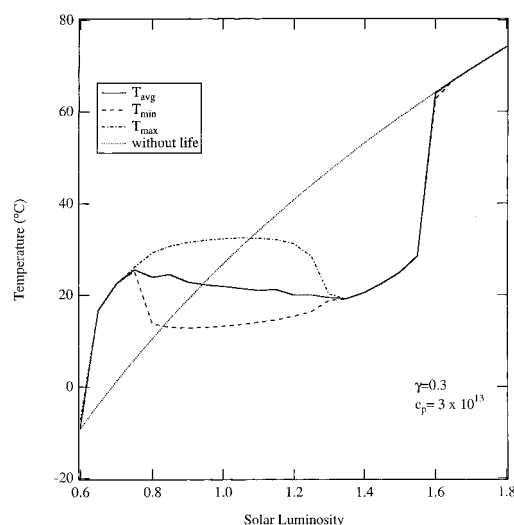


Fig. 5. Stabilization of mean planetary temperature over range of solar luminosity L at $c_p = 3 \times 10^{13}$, $\gamma = 0.3$. The maximum and minimum temperatures shown reflect the amplitude of the temperature oscillations. All averages, maxima, and minima are computed over a 1000 year period after first initializing the model for 1200 years. The dotted line shows temperature without life, i.e., at a constant value of $A = 0.5$.

sustained oscillations in the three prognostic variables a_b , a_w , and T_e . The daisyworld results provide a unique demonstration that internally driven oscillations can arise in a coupled physical-biological system, with the caveat that they occur on a highly simplified planet. These results naturally prompt the question of whether such oscillations might occur in the real world. To explore this question, we will consider the daisyworld results in the context of various real-world oscillations observed on Earth and of attempts to simulate these oscillations using simple intrinsic models.

Real-world oscillations are well documented in both biological and climatic records. Commonly observed oscillations in biology include predator and prey populations which vary with the same period but are somewhat out of phase. Such oscillations have been reproduced reasonably well by the Lotka-Volterra model (Goel et al., 1971). Although qualitatively different from the feedback-stabilized daisyworld model, the Lotka-Volterra model, a simple open-loop system of two coupled ODEs describing the internal dynamics of interacting species, also gives rise to limit cycles. In

addition to such purely biological oscillations, many real-world oscillations have been observed in Earth's climate record over a wide range of timescales. One well-known example is the El Niño–Southern Oscillation (ENSO) with a periodicity of about 2–5 years. The ENSO has been modeled fairly successfully as an internal oscillation of the coupled physical atmosphere–ocean mixed layer system (Suarez and Schopf, 1988; Battisti and Hirst, 1989; Penland and Sardeshmukh, 1995), although some studies have suggested that processes over continental land masses also should be considered (Barnett et al., 1988). Additional examples of climatic oscillations include the recently discovered millennial-scale oscillation in northern hemisphere temperature (of amplitude $\sim 2^\circ\text{C}$) (Keigwin, 1996; Bond et al., 1997) and Earth's ice age or glaciation cycles, with a dominant periodicity of 100,000 years and amplitude of $\sim 10^\circ\text{C}$.

Earth's glaciation cycles are commonly attributed to externally forced Milankovitch variations, i.e., small changes in Earth's orbital parameters. However, climate models driven by Milankovitch forcings have had difficulty accurately reproducing the observed cycles, particularly the dominant 100 000 year peak (Ghil and Le Treut, 1981; Pollard, 1982). The shortcomings of externally forced models have led to efforts to explain Earth's glaciation cycles through the internal dynamics of coupled energy balance–cryosphere models (EBCMs).

EBCMs are of particular interest to our discussion since they resemble the modified daisyworld model in several important ways. EBCMs generally include two or more ODEs of the following form (Kallen et al., 1979; Ghil and Le Treut, 1981; Ghil and Childress, 1987):

$$c_p \, dT_e/dt = f(T_e, A(I)), \quad (9)$$

$$c_i \, dI/dt = f(T_e, I). \quad (10)$$

Eq. (9) is analogous to eq. (2) in the modified daisyworld model, except that planetary albedo A is now a function of a purely physical variable I , the equatorward extent of the northern hemisphere ice sheet. The growth in the ice sheet in turn is a function of I and temperature, and has a characteristic relaxation time governed by c_i . When the timescales of the ice sheets and Earth's climate system, represented by c_i and c_p , respectively,

are comparable, internally forced EBCMs can generate self-sustained temperature oscillations of the correct amplitude ($\sim 10^\circ\text{C}$) but of distinctly shorter period ($\sim 10^4$ years) than observed in Earth's climate record (Kallen et al., 1979; Ghil and Le Treut, 1981). The essential problem is that the thermal response time of Earth's climate system, dominated by the ocean, is too short to reproduce internally forced oscillations on timescales of 10^5 years (Ghil, 1981). This is true even if the ocean is treated as a deep isothermal reservoir, and the problem is exacerbated if c_p is assumed to be governed by the relatively shallow ocean mixed layer. The mixed layer assumption in fact can damp out internal oscillations altogether, since the timescales of the climate and the ice sheets become too disparate (Harvey and Schneider, 1984).

Both the EBCM and daisyworld results demonstrate the importance of the climatic heat capacity c_p . On Earth, c_p depends on the relatively inflexible properties of specific heat and density of water, and on the characteristic depth D of the ocean volume assumed to dominate Earth's thermal response. D has been estimated to range from the relatively shallow mixed layer (< 100 m) to the deep ocean (> 3000 m), which leads to some uncertainty in the appropriate value of c_p (Harvey and Schneider, 1984). In addition, c_p is quite different for an ocean-dominated planet than a terrestrial planet and is also temperature sensitive (Thompson and Schneider, 1979). The value of $c_p = 3 \times 10^{13}$ that we have used in most of our calculations is appropriate for a planet like Earth, assuming the climatic heat capacity is dominated by a deep ocean. In theory, an entirely terrestrial planet like daisyworld would have a much smaller heat capacity. To justify using such a large value of c_p in our daisyworld model, reducing the parameter p (fraction of potentially fertile ground) from 1.0 to a more Earth-like value of 0.3 might seem appropriate, since it would allow that the remaining 70% of the planet be covered by a deep ocean. However, in the current model formulation this would imply that life has no control over ocean albedo. Such an assumption would be incorrect, since ocean algae have been shown to influence cloudiness and thus albedo by producing precursors for cloud condensation nuclei (CCN) (Falkowski et al., 1992). A more complete treatment of this question is beyond the scope of the present study, and the discussion above suggests

the need for a coupled hydrological cycle in the daisyworld model.

The EBCM and daisyworld results also demonstrate the importance of the comparability of characteristic ODE timescales. In Fig. 3, we assumed that c_p and $1/\gamma$ were proportional to the timescales for climate and daisies, respectively. Although not directly analogous to c_1 in EBCMs, $1/\gamma$ provides some measure of the timescale associated with changes in the areal coverage of daisies, or of the ecosystems they might represent in a geophysiological interpretation. Assuming a likely range of c_p on Earth and allowing some flexibility in the timescale for ecological shifts, we estimate that the periodicity of a hypothetical real-world internal oscillation arising from a coupled physical-biological mechanism would fall in the range of a few years to a few thousand years. Such a periodicity is too short to explain Earth's glaciation cycles, but possibly could contribute, at least on the basis of timescale considerations, to shorter-periodicity phenomena such as the ENSO or the northern hemisphere millennial oscillation.

Clearly one must use caution in attempting to attribute oscillations observed on Earth to the type of feedback mechanism described for the fictitious daisyworld. However, a literal interpretation of the daisyworld life-albedo-climate feedback as a significant geophysiological process may not be unreasonable. One possible example of a real-world life-albedo-climate oscillatory mechanism involves the dramatic alteration of albedo due to ecological shifts at northern hemisphere high latitudes and the associated feedbacks on climate. Winter/spring albedo at these latitudes ranges from 0.8–0.85 for snow-covered tundra to only 0.1–0.15 for snow-covered boreal forest (Klinger, 1991). Although this difference is smaller in summer, when most solar radiation reaches the northern high latitude region, the cold season differences still may significantly affect Earth's radiation balance and exert a broader scale influence on climate (Barnett et al., 1988; Bonan et al., 1992; Gallimore and Kutzbach, 1996). Furthermore, boreal forests shift to tundra on a timescale of 100–1000 years, likely due to climatic influences (Sirois, 1992; Klinger and Short, 1996). Such a timescale is comparable to Earth's thermal response time, which, as discussed earlier, is a prerequisite for internal self-sustained oscillations to arise in a coupled system.

Interestingly, Watson and Lovelock (1983) did not interpret the results of the original daisyworld model literally in terms of the biota's effect on surface albedo. Rather, they emphasized the rôle of the biota in regulating atmospheric CO_2 , a greenhouse gas which is believed to have been a dominant influence determining Earth's mean temperature over geologic time (Walker et al., 1981). Lovelock and Kump (1994) explored the idea of biota- CO_2 feedbacks in a simple geophysiological model, which also included a parameterization of CCN production by ocean algae. Their model predicted stabilizing negative feedbacks between life and climate under glacial conditions. However, these feedbacks broke down under warmer conditions, leading Lovelock and Kump to propose that other climate-regulating mechanisms must operate in the warm regime. This result, together with our results and discussion, points to the idea that the hydrological cycle may provide the additional feedbacks needed for understanding Earth's climate variability. Water in its various phases is critical in determining both surface (ice, snow) and atmospheric (clouds) albedo, and liquid water (ocean) predominantly determines Earth's climatic heat capacity. Furthermore, atmospheric water vapor is even more important than CO_2 in determining Earth's greenhouse forcing (Raval and Ramanathan, 1989; Rind et al., 1991). The biota and the hydrological cycle are well known to be fundamentally coupled (see additional remarks below), making geophysiological models ideal tools for investigating life-climate-hydrological cycle feedback mechanisms.

5. Concluding remarks

We have shown that when the diagnostic equation for temperature in the original daisyworld model is replaced with a differential equation that allows for disequilibria in the planetary radiation balance, self-sustained temperature oscillations can arise from the internal dynamics of the coupled physical-biological system. Considered in the context of geophysiology, our results point to a new line of investigation into whether the daisyworld model can be modified further to more realistically simulate Earth conditions and behaviors, including natural limit cycles and possible chaos. A critical step toward meeting this goal would

involve introducing a hydrological cycle that is fundamentally coupled to life and climate. Such a step would be consistent with the idea that geophysics, the study of the dynamics of the whole-Earth system, is analogous to human physiology,

the study of the metabolism of individual organisms. Indeed the noted Scottish geologist James Hutton stated as early as 1785 that the planetary hydrological cycle can be compared to the circulation of blood in the human body (Lovelock, 1995).

REFERENCES

- Barnett, T. P., Dumenil, L., Schlese, U. and Roeckner, E. 1988. The effect of Eurasian snow cover on global climate. *Science* **239**, 504–507.
- Battisti, D. S. and Hirst, A. C. 1989. Interannual variability in a tropical atmosphere–ocean model: Influence of the basic state, ocean geometry and nonlinearity. *J. Atmos. Sci.* **46**, 1687–1712.
- Bonan, G. B., Pollard, D. and Thompson, S. L. 1992. Effects of boreal forest vegetation on global climate. *Nature* **359**, 716–718.
- Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal, P., Priore, P., Cullen, H., Hajdas, I. and Bonani, G. 1997. A pervasive millennial-scale cycle in North Atlantic holocene and glacial climates. *Science* **278**, 1257–1266.
- Budyko, M. I. 1969. The effect of solar radiation variations on the climate of the Earth. *Tellus* **21**, 611–619.
- Falkowski, P. G., Kim, Y., Kolber, Z., Wilson, C., Wirick, C. and Cess, R. 1992. Natural versus anthropogenic factors affecting low-level cloud albedo over the North Atlantic. *Science* **256**, 1311–1313.
- Gal-Chen, T. and Schneider, S. 1976. Energy-balance climate modeling: Comparison of radiative and dynamic feedback mechanisms. *Tellus* **28**, 108–121.
- Gallimore, R. G. and Kutzbach, J. E. 1996. Role of orbitally induced changes in tundra area in the onset of glaciation. *Nature* **381**, 503–505.
- Ghil, M. and Childress, S. 1987. *Topics in geophysical fluid dynamics: atmospheric dynamics, dynamo theory, and climate dynamics*. Springer-Verlag, New York.
- Ghil, M. and Le Treut, H. 1981. A climate model with cryodynamics and geodynamics. *J. Geophys. Res.* **86**, 5262–5270.
- Goel, N. S., Maitra, S. C. and Montroll, E. W. 1971. On the Volterra and other nonlinear models of interacting populations. *Rev. Modern Phys.* **43**, 231.
- Harvey, L. D. D. and Schneider, S. H. 1984. Sensitivity of internally generated climate oscillations to ocean model formulation. *Proceedings of the Symposium on Milankovitch and Climate*. NATO ASI Series (eds. Berger, A., Imbrie, J., Hays, J., Kukla, S. and Saltzman, B.). D. Reidel, Hingham, Mass., 653–667.
- Jascourt, S. D. and Raymond, W. H. 1992. Comments on “Chaos in daisyworld” by X. Zeng et al. *Tellus* **44B**, 243–246.
- Kallén, E., Crafoord, C. and Ghil, M. 1979. Free oscillations in a climate model with ice-sheet dynamics. *J. Atmos. Sci.* **36**, 2292–2302.
- Keigwin, L. D. 1996. The little ice age and medieval warm period in the Sargasso Sea. *Science* **274**, 1504–1508.
- Klinger, L. F. 1991. Peatland formation and ice ages: A possible gaian mechanism related to community succession. *Scientists on Gaia* (eds. Schneider, S. H. and Boston, P. J.). The MIT Press, Cambridge, MA, 247–255.
- Klinger, L. F. and Short, S. K. 1996. Succession in the Hudson Bay Lowland, Northern Ontario, Canada. *Arctic and Alpine Res.* **28**, 172–183.
- Lovelock, J. E. 1995. Geophysics, the science of Gaia. *Rev. of Geophys.* **27**, 215–222.
- Lovelock, J. E. and Kump, L. R. 1994. Failure of climate regulation in a geophysiological model. *Nature* **369**, 732–734.
- Peixoto, J. P. and Oort, A. H. 1992. *Physics of climate*. Am. Inst. of Phys., College Park, MD.
- Penland, C. and Sardeshmukh, P. D. 1995. The optimal growth of tropical sea surface temperature anomalies. *J. Climate* **8**, 1999–2024.
- Pollard, D. 1982. A simple ice sheet model yields realistic 100 kyr glacial cycles. *Nature* **296**, 334–338.
- Raval, A. and Ramanathan, V. 1989. Observational determination of the greenhouse effect. *Nature* **342**, 758–761.
- Rind, D., Chiou, E.-W., Chu, W., Larsen, J., Oltmans, S., Lerner, J., McCormick, M. P. and McMaster, L. 1991. Positive water vapour feedback in climate models confirmed by satellite data. *Nature* **349**, 500–503.
- Sellers, W. D. 1969. A global climatic model based on the energy balance of the earth–atmosphere system. *J. Applied Meteorology* **8**, 392–400.
- Sirois, L. 1992. The transition between boreal forest and tundra. *A systems analysis of the global boreal forest* (eds. Shugart, H. H., Leemans, R. and Bonan, G. B.). Cambridge University Press, New York, 196–215.
- Suarez, M. J. and Schopf, P. S. 1988. A delayed action oscillator for ENSO. *J. Atmos. Sci.* **45**, 3283–3287.
- Thompson, S. L. and Schneider, S. H. 1979. A seasonal zonal energy balance climate model with an interactive lower layer. *J. Geophys. Res.* **84**, 2401–2414.
- Walker, J. C. G., Hays, P. and Kasting, J. F. 1981. A negative feedback mechanism for the long-term stabilization of earth’s surface temperature. *J. Geophys. Res.* **86**, 9776–9782.
- Watson, A. J. and J. E. Lovelock. 1983. Biological homeostasis of the global environment: the parable of daisyworld. *Tellus* **35B**, 284–289.
- Zeng, X., Pielke, R. A. and Eykholt, R. 1990. Chaos in daisyworld. *Tellus* **42B**, 309–318.