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# Entropy production in living systems: from organisms to ecosystems ☆

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**Abstract**

Entropy production in the human body as a whole can be calculated from observed energetic data. The entropy production in humans thus calculated shows a two-stage character over the human life span, that is an early increasing stage and a later decreasing stage until death. Similar methods for calculating entropy production are also applied to lake ecosystems. Entropy production in two lakes (Lake Biwa in Japan and Lake Mendota in USA) has been calculated, and it is found that entropy production per year per volume of lake water in the eutrophic Lake Mendota is larger than that in the oligotrophic Lake Biwa. Because ecological succession (evolution) in a lake always proceeds from oligotrophy to eutrophy, the present results suggest that processes of ecological succession accompany the increase in entropy production. This situation is parallel to the trend in the early stage of the human life span. Based on the above discussion, a hypothesis is presented on the entropy principle in living systems.

*Keywords:* Ecosystem; Entropy; Human body; Living system

## 1. Introduction

The energy concept has been extensively employed in natural and even social sciences. In the biological sciences, biocalorimetry, bioenergetics and ecological energetics can be mentioned as examples of investigations using the energy concept.

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However, the entropy concept has rarely been studied in biology, although entropy is as significant as energy from a thermodynamical viewpoint because energy is the key concept in the First Law of Thermodynamics and entropy in the Second Law. Furthermore, entropy is the only concept in the physical sciences having directionality with time. Because most biological phenomena have directionality with time in their trends, application of the entropy concept to biology would lead to a deeper understanding of living systems. Thus, it must be emphasised that it is important to study these systems from an entropy viewpoint.

However, there are conceptual and methodological difficulties in the measurement and estimation of the entropy content of living systems. In contrast, an entropy-related quantity, i.e. entropy production, can be estimated by use of some physical methods from observed energetic data of biological objects. In the present paper, entropy productions in humans and in lake ecosystems are calculated, and an hypothesis is presented on entropy production in the process of development, growth and aging of organisms and ecosystems.

## 2. Human body

Consider a naked human subject put in a respiration calorimeter. Energy flows between this subject and its surroundings are due to incoming infrared radiation ($E_{l\downarrow}$), outgoing infrared radiation ($E_{l\uparrow}$), evaporation ($E_{evp}$) and conduction–convection ($E_{con}$). The energy balance equation is expressed as the change of energy content (denoted $\Delta Q$) of the subject equal to the energy inflow minus energy outflow

$$\Delta Q = (E_{l\downarrow} - E_{l\uparrow}) + (-E_{evp} - E_{con}) \tag{1}$$

Energetics of this kind for the human body has been intensively studied in classical works by Hardy and Du Bois and coworkers [1–10].

Associated with these energy flows, there are corresponding entropy flows, that is, entropy flows due to incoming infrared radiation ($S_{l\downarrow}$), outgoing infrared radiation ($S_{l\uparrow}$), evaporation ($S_{evp}$) and conduction–convection ($S_{con}$). Also, there are entropy flows associated with mass flows, that is, entropy flows due to $O_2$ consumption ($S(O_2)$) and $CO_2$ liberation ($S(CO_2)$).

The entropy balance equation is expressed as

$$\Delta S = \Delta_e S + \Delta_i S \tag{2}$$

where $\Delta S$ is the change in entropy content of the subject, $\Delta_e S$ is the net entropy inflow into the subject and $\Delta_i S$ is the entropy production within the subject. Entropy production is the production rate of entropy by irreversibility of the processes, and is non-negative ($\Delta_i S \geqq 0$) according to the Second Law of Thermodynamics (see, for example, the textbooks by Prigogine). Entropy flows are given by

$$\Delta_e S = \Delta_e S(\text{energy}) + \Delta_e S(\text{mass}) \tag{3}$$

where

$$\Delta_e S(\text{energy}) = (S_{1\downarrow} - S_{1\uparrow}) + (-S_{\text{evp}} - S_{\text{con}}) \tag{4}$$

$$\Delta_e S(\text{mass}) = S(O_2) - S(CO_2) \tag{5}$$

Each term in Eq. (4) is expressed as [11,12]

$$S_{1\downarrow} = A^e \times \tfrac{4}{3}\sigma T_c^3 \tag{6}$$

$$S_{1\uparrow} = A^e \times \tfrac{4}{3}\sigma T_s^3 \tag{7}$$

$$S_{\text{evp}} = \frac{E_{\text{evp}}}{T_r} \tag{8}$$

$$S_{\text{con}} = \frac{E_{\text{con}}}{T_s} \tag{9}$$

where $A^e$ is the effective radiating surface area, $\sigma$ is the Stefan-Boltzmann constant, $T_c$ is the temperature of the calorimeter, $T_s$ is the surface temperature of the human body and $T_r$ is the temperature within the body. Each term in Eq. (5) is given by

$S(O_2)$ = (amount of $O_2$ uptake) × (entropy content of $O_2$ gas per unit amount of $O_2$ gas) (10)

$S(CO_2)$ = (amount of $CO_2$ liberation) × (entropy content of $CO_2$ gas per unit amount of $CO_2$ gas) (11)

The change of entropy content is

$$\Delta S = [(\text{energy production}) - (\text{energy elimination})]/T_r \tag{12}$$

In the experiment by Hardy and Du Bois [2] for a naked subject (EFDB) in basal conditions over 1 h, they observed: $A^e = 1.5$ m$^2$, $T_c = 300.55$ K, $T_s = 306.12$ K, $T_r = 310.3$ K, $E_{\text{evp}} = 20.66$ kcal h$^{-1}$, $E_{\text{con}} = 11.00$ kcal h$^{-1}$, $O_2$ uptake = 20.67 g h$^{-1}$, $CO_2$ liberation = 23.16 g h$^{-1}$, energy production = 68.65 kcal h$^{-1}$ and energy elimination = 77.36 kcal h$^{-1}$. Using these observed values, $\Delta_e S$ and $\Delta S$ can be calculated, and then from the entropy balance equation (Eq. (2)) the entropy production $\Delta_i S$ is estimated as [11]

$$\Delta_i S = 0.259 \text{ J s}^{-1} \text{ K}^{-1} \tag{13}$$

Entropy flow due to mass exchange ($\Delta_e S$(mass)) is small compared with the total entropy flow ($\Delta_e S$); $\Delta_e S$(mass) is only ≈2% of $\Delta_e S$, and it is less than the significant figure. Hence, it may not be taken into account. Entropy flow due to $H_2O$ mass flow from the subject (evaporation) has already been taken into account in the entropy flow due to evaporation ($S_{\text{evp}}$) and does not need to be considered.

The entropy production thus calculated is a kind of measure of the degree of activity (physical, chemical and biological) within the subject [11,12], because natural processes are all irreversible and this always causes entropy production according to the Second Law of Thermodynamics (see also the textbooks by Prigogine).

Calculations of entropy production in the temperature range of the calorimeter between 23 and 34°C show [12] that entropy production per surface area of the human body is almost equal to the metabolic entropy production, {metabolic heat production ($E_{mtb}$)}/$T_r$, per surface area. That is

$$\Delta_i S/\text{surface area} \approx (E_{mtb}/\text{surface area})/T_r \tag{14}$$

This would be a natural result because the contribution from mass flow is small as stated above. The metabolic heat production per human surface area at various ages has been measured (for example, Ref. [13]). Hence from Eq. (14), the entropy production per human surface area at various ages can be obtained [12]; it turns out that the entropy production per surface area rises from 0 to 2 years of age, and decreases rapidly from 2 to 25 years of age and then decreases gradually to 85 years of age.

Multiplying the entropy production per surface area obtained in Ref. [12] by the average human surface area [14] gives the entropy production per human individual at various ages. The results are shown in Fig. 1 (0–75 years of age) and Fig. 2 (0–19 years of age). As shown, the entropy production per individual increases rapidly from birth to about 16 years of age for males and to about 14 years of age for females, then gradually decreases thereafter. Thus, the entropy production per individual consists of two phases over the human life span: an early increasing stage and a later decreasing stage. This trend may be called the "two-stage principle". It could be applied universally to other organisms. This result should be compared

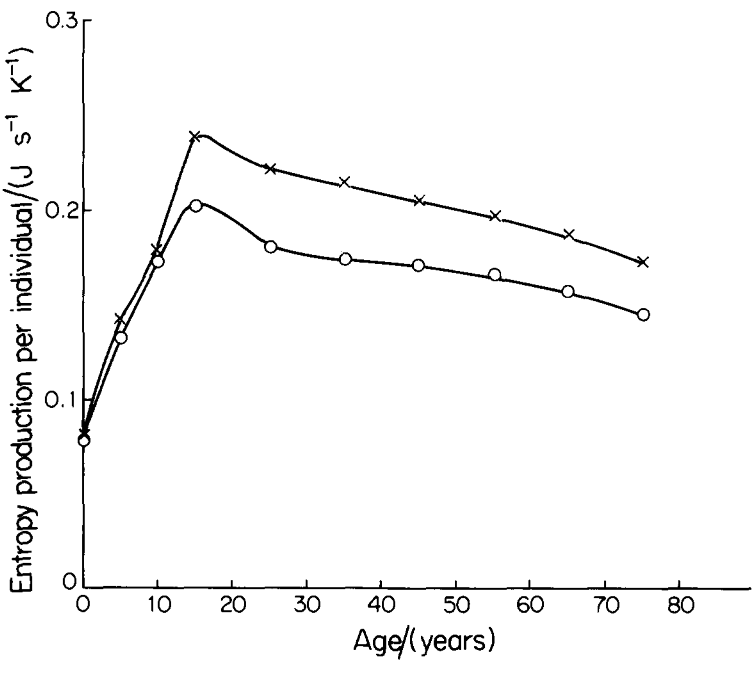


Fig. 1. Entropy production per human individual vs. years of age (0–75) for male and female: ×, male; ○, female.

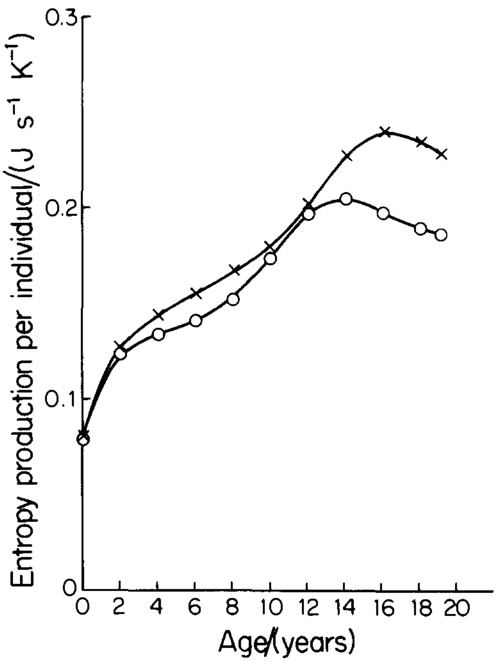


Fig. 2. Entropy production per human individual vs. years of age (0–19) for male and female: ×, male; ○, female.

with Prigogine's well-known minimum entropy production principle [15], which asserts that entropy production always decreases monotonically with time and approaches a minimum stationary level. This is, so to speak, the "uni-stage principle". From Figs. 1 and 2, it is evident that Prigogine's principle does not hold for the human life span.

## 3. Lake ecosystem

Energy flows between a lake and its surroundings are due to direct solar radiation ($E_{dr}$), scattered solar radiation ($E_{sc}$), reflected solar radiation ($E_{rf}$), downward infrared radiation ($E_{I\downarrow}$), upward infrared radiation ($E_{I\uparrow}$), evaporation ($E_{evp}$) and conduction–convection ($E_{con}$). The energy balance equation is written as the change in energy content of a lake ($\Delta Q$) equal to energy inflow minus energy outflow

$$\Delta Q = (E_{dr} + E_{sc} - E_{rf}) + (E_{I\downarrow} - E_{I\uparrow}) + (-E_{evp} - E_{con}) \qquad (15)$$

Associated with the energy flows, there are corresponding entropy flows, i.e. entropy flow due to direct solar radiation ($S_{dr}$) and $S_{sc}$, $S_{rf}$, $S_{I\downarrow}$, $S_{I\uparrow}$, $S_{evp}$ and $S_{con}$ due to scattered solar radiation, reflected solar radiation, etc.

The entropy balance equation is expressed in the same form as Eq. (2): $\Delta S = \Delta_e S + \Delta_i S$. Entropy flow ($\Delta_e S$) is written as

$$\Delta_e S = (S_{dr} + S_{sc} - S_{rf}) + (S_{l\downarrow} - S_{l\uparrow}) + (-S_{evp} - S_{con}) \tag{16}$$

Each term of this equation is given by [16]

$$S_{dr} = (2.31 \times 10^{-4}\ \mathrm{K}^{-1})\, E_{dr} \tag{17}$$

$$S_{sc} = \frac{4}{3}\frac{E_{sc}}{T_o} X(\varepsilon) \tag{18}$$

where $T_o$ is the temperature of the sun

$$\varepsilon = E_{sc}/\sigma T_o^4$$

$$X(\varepsilon) = \frac{45}{4\pi^4}\frac{1}{\varepsilon}\int_0^\infty y^2[(x+1)\ln(x+1) - x\ln x]\,\mathrm{d}x$$

$$x = \varepsilon/(\mathrm{e}^y - 1)$$

$$S_{rf} = \frac{4}{3}\frac{E_{rf}}{T_o} X(\varepsilon') \qquad \varepsilon' = E_{rf}/\sigma T_o^4 \tag{19}$$

$$S_{l\downarrow} = \frac{4}{3}\frac{E_{l\downarrow}}{T_{atm}} X(\varepsilon'') \tag{20}$$

where $T_{atm}$ is the effective temperature of the atmosphere and $\varepsilon'' = 0.94$.

$$S_{l\uparrow} = \frac{4}{3}\varepsilon'''\sigma T^3 X(\varepsilon''') \tag{21}$$

where $T$ is the mean temperature of the lake surface and $\varepsilon''' = 0.94$.

$$S_{evp} = \frac{E_{evp}}{T} \tag{22}$$

and

$$S_{con} = \frac{E_{con}}{T} \tag{23}$$

Contributions to the entropy flow from water inflow into a lake and water outflow from a lake seem to be nearly equal on average and cancel each other, so are not considered here. The change in entropy content of a lake ($\Delta S$) is

$$\Delta S = (\text{the change in heat storage in a lake})/T_m \tag{24}$$

where $T_m$ is the mean temperature of lake water. All of the above entropy-related quantities can be estimated from experimentally observed data using the above equations. Then, from the entropy balance equation, the entropy production ($\Delta_i S$) in a lake can be obtained: $\Delta_i S = \Delta S - \Delta_e S$.

Let us consider two lakes as examples: Lake Biwa and Lake Mendota. Lake Biwa is located at 34°58′–35°31′ N, 135°52′–136°17′ E (near Kyoto, Japan) and consists of a northern basin (the main part) and a southern basin (the smaller part). The northern basin is oligotrophic and the southern basin is nearly eutrophic. Only the northern basin is considered here. Lake Biwa is the most studied lake in Japan, and its energy budgets have been studied in detail by Ito and Okamoto [17] and Kotoda [18]. Lake Mendota, another example, is located at 43°04′ N, 89°24′ W (near Madison, Wisconsin, USA), and is a eutrophic lake. It is the most studied lake in the USA, and its energy budgets have been investigated by Dutton and Bryson [19] and Stewart [20].

From the observed monthly energy budgets of the two lakes, the monthly entropy production per $m^2$ of lake surface in each lake was calculated using the methods described above (for details, the reader is referred to Refs. [16] and [21]). The results, entropy production plotted against absorbed solar radiation energy, are shown in Fig. 3 (Lake Biwa) and Fig. 4 (Lake Mendota), where the entropy production is in units of MJ $m^{-2}$ per month $K^{-1}$ and the absorbed solar radiation energy in units of MJ $m^{-2}$ per month. As shown, the entropy production in month $j$ (denoted as $(\Delta_i S)_j$) is a linear function of the absorbed solar radiation energy in month $j$ (denoted as $E_j$)

$$(\Delta_i S)_j = a + bE_j \tag{25}$$

The first term on the right-hand side is the entropy production independent of solar radiation energy and the second term is the entropy production dependent on solar

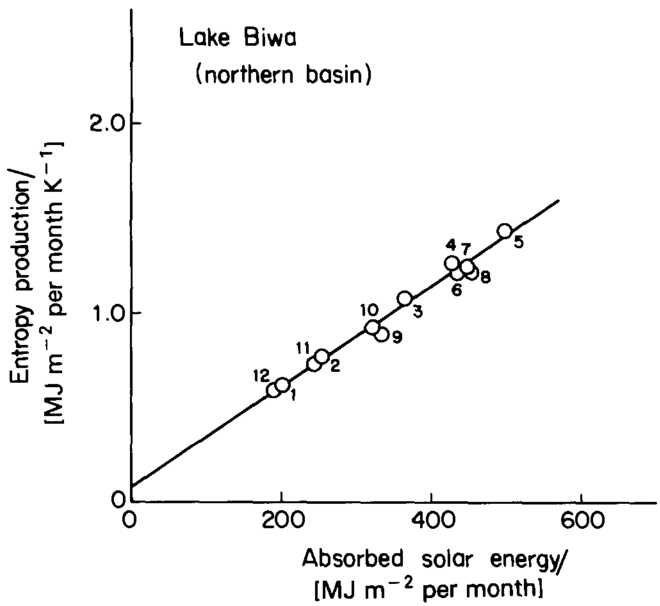


Fig. 3. Monthly entropy production in the northern basin of Lake Biwa per $m^2$ of the lake surface plotted against monthly solar radiation energy absorbed by 1 $m^2$ of the lake surface. The numbers near the circles are the months.

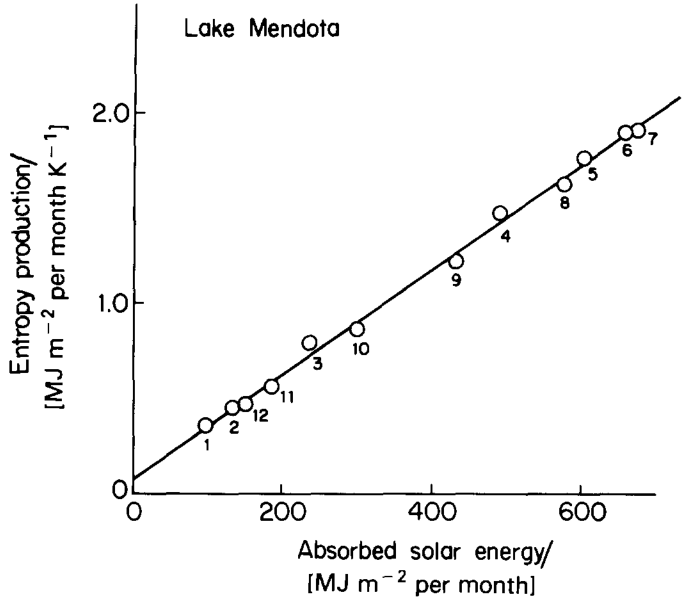


Fig. 4. Monthly entropy production in Lake Mendota per m$^2$ of the lake surface plotted against monthly solar radiation energy absorbed by 1 m$^2$ of the lake surface. The numbers near the circles are the months.

radiation energy. The former is due to decomposition of organic matter like dead plankton and other organisms by bacteria in the lake water; this decomposition produces heat and hence entropy production. The latter is due to absorption of solar radiation by fine suspended particles in lake water and subsequent conversion of solar radiation energy to heat energy; this process causes entropy production. The parameters $a$ and $b$ for both the lakes are shown in Table 1. Entropy production per year is

$$\sum_{j=1}^{12} (\Delta_i S)_j = 12a + b \sum_{j=1}^{12} E_j \tag{26}$$

and entropy production per year normalized by absorbed solar radiation energy per year is

Table 1
The parameters $a$ and $b$ in Eq. (25) for Lake Biwa and Lake Mendota

| | $a$/ (MJ m$^{-2}$ per month K$^{-1}$) | $b$/ K$^{-1}$ |
|---|---|---|
| Lake Biwa | 0.0704 | $2.670 \times 10^{-3}$ |
| Lake Mendota | 0.0702 | $2.789 \times 10^{-3}$ |

$$\frac{\sum_{j=1}^{12}(\Delta_i S)_j}{\sum_{j=1}^{12} E_j} = \frac{12a}{\sum_{j=1}^{12} E_j} + b \tag{27}$$

Fig. 5 shows the entropy production in Lake Biwa per year per $m^2$ of lake surface. The absorbed solar radiation energy per year per $m^2$ of lake surface is 4153 MJ. Consider a water column from the lake surface to the bottom, the cross section of which is 1 $m^2$. This water column consists of a light zone and a dark zone. The entropy production dependent on solar radiation in the light zone is 11.1 MJ $K^{-1}$ per year, and the entropy production independent of solar radiation is 0.8 MJ $K^{-1}$ per year, which is distributed over the whole water column because organic matter and bacteria are distributed from the surface to the bottom. Numbers in parentheses are corresponding values normalized by absorbed solar radiation energy in units of kJ $K^{-1}$ per year for entropy production and MJ $year^{-1}$ for absorbed solar energy. Fig. 6 shows distributions of entropy production in Lake Mendota in a similar manner.

Thus, it is possible to make a comparative study between the two lakes. Consider entropy production per year, per MJ of absorbed solar radiation energy, and per $m^3$ of the lake water column. Entropy production densities per year normalized by absorbed solar radiation energy are shown in Table 2 in units of kJ $K^{-1}$ $m^{-3}$ per year. As shown, in any of the categories, entropy productions in the eutrophic

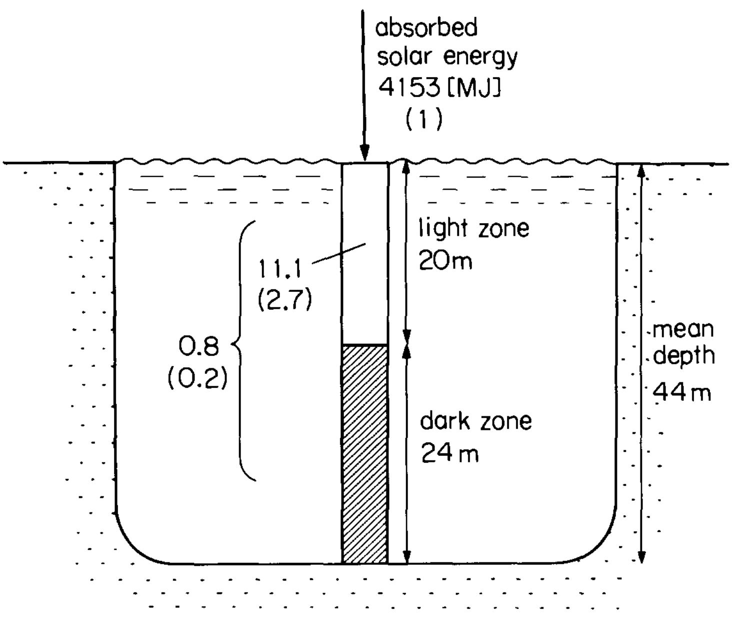


Fig. 5. Pattern of entropy production per year in the northern basin of Lake Biwa. Explanations are given in the text.

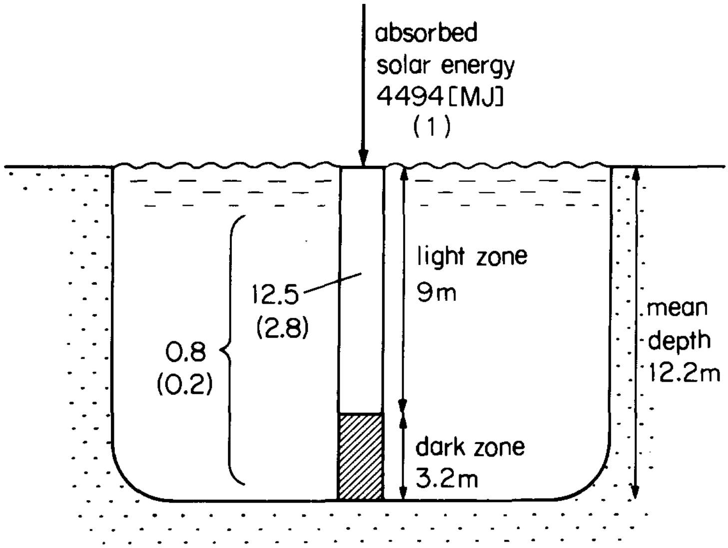


Fig. 6. Pattern of entropy production per year in Lake Mendota, parallel to Fig. 5.

Lake Mendota are larger than those in the oligotrophic Lake Biwa. Hence, it is possible to propose an entropy principle for eutrophication (or more generally ecological succession), namely that entropy production will increase with the process of eutrophication (or ecological succession).

Eutrophication in a lake is an irreversible process: the process always proceeds with time from oligotrophy to eutrophy, and not conversely. Hence, from the above entropy principle for eutrophication, the entropy production in a lake will increase with time. However, more generally, what is the situation for the overall trend in ecological succession? An hypothesis has already been presented [16]: entropy production increases with time in an early stage (growing stage) of succession, is kept almost stationary in an intermediate stage, and decreases in a later stage (senescent stage) of ecological succession. Thus, processes of ecological succession will consist of multi-phases and are not uni-directional. This trend is analogous to

Table 2
Entropy production densities per year normalized by absorbed solar radiation energy in units of kJ $K^{-1}$ $m^{-3}$ per year for Lake Biwa and Lake Mendota, and the ratios of Lake Mendota to Lake Biwa

| | Whole water column | Solar energy dependent | Solar energy independent |
|---|---|---|---|
| Lake Biwa | 0.07 | 0.13 | 0.005 |
| Lake Mendota | 0.24 | 0.31 | 0.015 |
| L. Mendota/L. Biwa | 3.7 | 2.3 | 3.3 |

the life span of humans as stated in the previous section. In this respect, the ecosystem may be regarded as a "superorganism" [22] and, conversely, the organism as a "mini-ecosystem" [23]. This multi-phase tendency is parallel to the classical hypothesis by Lindeman [24] on productivity in lake ecosystems.

## 4. Second Law of Thermodynamics in living systems

Thus far, the entropy principle, that is the Second Law of Thermodynamics, has been considered in living systems.

In isolated systems, the entropy content of systems always increases with time and approaches a maximum value (the well-known "textbook-level" principle). In open systems very near to thermodynamic equilibrium, the minimum entropy production principle holds [15], and entropy production always decreases with time approaching a minimum stationary level. These are both established principles. However, living systems are not isolated and not near to equilibrium. Hence, these two principles cannot be applied to living systems. What is the entropy principle for living systems?

From the discussion in this paper, it is possible to propose an hypothesis that entropy production in a living system which is open and far from equilibrium, consists of two or more phases: an early increasing stage, a later decreasing stage and an intermediate stage, as shown schematically in Fig. 7. In Fig. 7, point A is the beginning of living systems, e.g. fertilization in organisms, formation of the lake

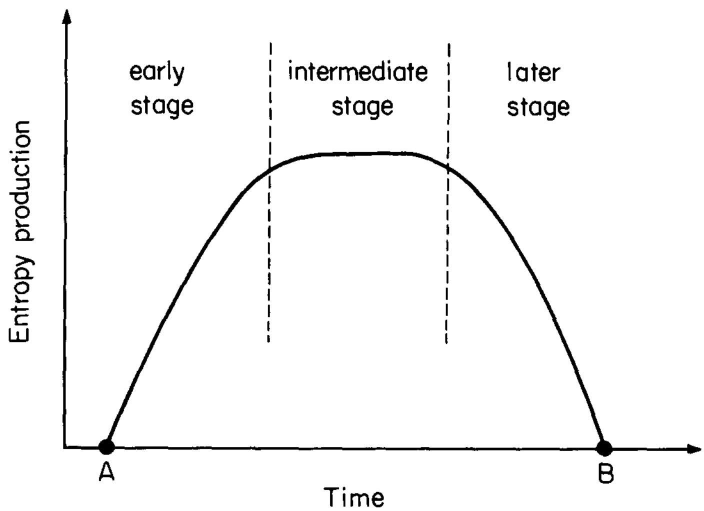


Fig. 7. A hypothetical entropy principle for living systems. Scales are arbitrary. Explanations are given in the text.

in lake ecosystems, and point B is the end (death) of them. The early increasing stage is the phase of development and growth of the systems, the later decreasing stage is the phase of senescence, and the intermediate stage is the transitional or stationary one. The validity of this hypothesis can be examined by experiments for various organisms and ecosystems by the use of methods similar to those shown in this paper.

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