

# Ecological exergy analysis: a new method for ecological energetics research

Jizhong Zhou <sup>a,\*</sup>, Shijun Ma <sup>a,1</sup>, George W. Hinman <sup>b</sup>

<sup>a</sup> *Research Center of Eco-Environmental Sciences, Academia Sinica, Beijing, People's Republic of China*

<sup>b</sup> *Environmental Science and Regional Planning, Washington State University, Pullman, WA 99164, USA*

Accepted 24 August 1994

---

## Abstract

A new method for ecological energetics research, ecological exergy analysis, is developed based on the exergy analysis in thermodynamics and the characteristics of living systems. This method takes account of both energy quantity and energy quality. Exergy balance equations for both an animal and a plant are constructed, and methods for estimating different types of exergy in living systems are proposed that consider the complex physical-chemical and physiological-ecological processes. Four ecological exergy efficiency indices for evaluating different ecological processes are proposed based on the exergy balance equations.

*Keywords:* Exergy; Thermodynamics

---

## 1. Introduction

All living systems (organisms, populations, and communities) can be considered as open thermodynamic systems that are not in thermodynamic equilibrium and that continuously utilize and convert energy. Energy transfers and conversions in these systems strictly obey the first and second laws of thermodynamics. Energy change in the organisms in an ecosystem must be accompanied by a corresponding energy change in the environment. For instance, the increase of energy in

plants from photosynthesis is equal to the decrease in solar energy in the environment. Although the total energy remains constant during this conversion process, solar energy is converted into chemical energy and fixed within the plants of the ecosystem. A part of this fixed solar energy is used by the plants to maintain metabolic activities such as osmosis, absorption, transportation, and evaporation. The rest is utilized to construct new tissues and is thereby stored in the plants in the form of internal potential energy. The stored energy can then be transferred along food chains among various kinds of consumers, each transfer being accompanied by an energy loss in the form of heat (i.e., increased entropy). According to the second law, it is impossible for organisms to convert this heat completely into other types of en-

---

\* Corresponding author. Present address: Center for Microbial Ecology, Plant and Soil Sciences Building, Michigan State University, East Lansing, MI 48824-1325, USA.

<sup>1</sup> Deceased.

ergy, such as chemical energy. Thus, an ecosystem continually uses high quality energy and gradually degrades it to heat at ambient temperature, at which point it is no longer available to carry out the processes necessary to maintain life in the ecosystem in its highly organized state.

From the viewpoint of the ultimate results of energy transfers and conversions, living systems are merely complex physical and chemical systems. Therefore, the principles and methods derived in the physical and chemical sciences should be directly applicable to living systems. The wide application of thermodynamics in ecology leads to the formation of ecological energetics, which is a branch of ecology that studies energy transfers, conversions and dynamic equilibria in ecosystems and the relationships between energy flows and organism adaptation. Although ecological energetics only recently became an independent subject, the work leading up to it was carried out in the early development of ecology (Forbes, 1887; Lindman, 1942; Macfadyen, 1948). After 1950, ecological energetics was developed rapidly along two lines: one represented by E.P. Odum and H.T. Odum who emphasized the energy flows through trophic levels of ecosystems (Odum and Odum, 1955; Teal, 1957; Odum, 1960); another represented by Slobodkin who focused on the energy dynamics of a single population or food chain (Trama, 1957; Richman, 1958; Slobodkin, 1959, 1960, 1961, 1962). In the 1960s, the pattern of energetics studies as a quantitative description of energy flow had been established (Engelmann, 1961; Wiegert, 1961, 1964, 1968; Scott, 1965; Johnson and Maxell, 1966; Phillipson, 1966). Gates (1962, 1966, 1967, 1968) used an analytical approach involving the laws of physics and chemistry to study interactions between organisms and their environment. Since 1970, the emphasis of ecological energetics has shifted to the construction of predictive models of energy flow (Wiegert, 1973, 1975; Zucchetto, 1975; Patten, 1976, 1983, 1984, 1985; Odum, 1983, 1984a, 1984b, 1988; White, 1984a,b; Limburg, 1985; Parikh, 1985). Instead of considering energy flow, Aoki studied entropy flow and entropy production in animals (Aoki, 1987a), plants (Aoki, 1987b,c) and lake ecosystems (Aoki, 1987d, 1989), applied the en-

tropy concept to the network theory of ecological systems at steady state and presented entropy laws in network systems (Aoki, 1988). Also related to irreversibility, another quantity, exergy, which is the potential-work measure of the departure from equilibrium, was introduced into ecology (Jørgensen and Mejer, 1977) and its ecological applications and implications were discussed (Mejer and Jørgensen, 1979; Jørgensen and Mejer, 1981; Jørgensen, 1986, 1988, 1990, 1992a, 1992b, 1992c, 1992d; Herendeen, 1989; Aoki, 1992, 1993; Salomonsen, 1992).

In an attempt to consider energy quality and find a common denominator in ecosystems, H.T. Odum (1983) proposed the concepts of transformity, the joules of one type of energy required to generate a joule of another type, and emergy, the energy of one type required to generate that of another. The emergy flow of a system is obtained by multiplying energy flow by different weighting factors, i.e., transformities. As a result, emergy does not really concern energy loss caused by irreversible processes and, therefore, does not deal with energy quality in the sense of thermodynamics.

From the methodological viewpoint, most studies only consider energy quantity, not energy quality. In fact, all energy transfer and conversion processes are accompanied by changes in both energy quantity and quality. To some extent, the change in energy quality is more important in living systems than the change in energy quantity. Therefore, it is important for ecologists to develop new methods to deal with energy quality as well as quantity. In this paper, a new method is presented – ecological exergy analysis, which is a modification and improvement, in light of living system characteristics, of the exergy analysis method of thermodynamics.

## 2. Exergy flows in living systems

Energy exchanges between an organism and its environment occur in the following way: (1) heat exchange, (2) work exchange, and (3) matter exchange (Fig. 1).

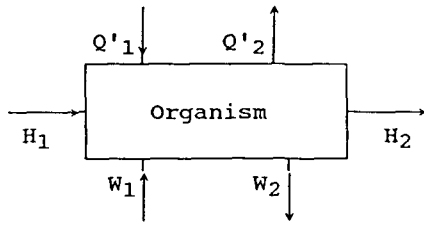


Fig. 1. Energy exchange between an organism and its environment. The explanation for the symbols is in the text.

From Fig. 1, the energy balance equation at constant pressure is

$$\Delta H_s = (H_1 - H_2) + (Q'_1 - Q'_2) + (W_1 - W_2) = \Delta H + \Delta Q' + \Delta W \quad (1)$$

where  $H_1$  and  $H_2$  are the enthalpy content of ingested matter and egested-excreted matter.  $Q'_1$  is the directly absorbed heat,  $Q'_2$  is the dissipated heat,  $W_1$  is the work (excluding PdV work) of the environment on the organisms (e.g., wind on plants, tides on fishes, airstreams on insects and birds), which ultimately tends to zero,  $W_2$  is the work (also excluding PdV work) of organisms acting on their environments (e.g., animals feeding), which is very small compared to the total amount of energy exchange so that it may be neglected (Wiegert, 1968). As a result, the net work exchange between an organism and its environment,  $\Delta W = W_1 - W_2$ , may be omitted.  $\Delta H_s$  is the overall enthalpy change of the organism.

In comparison with the classical equation for the energy budget

$$P = I - R - F. \quad (2)$$

Wiegert (1968) found that  $\Delta H_s$ ,  $H_1$  and  $H_2$  are equivalent to the energy of production ( $P$ ), ingestion ( $I$ ) and egestion-excretion ( $F$ ). The net heat exchange,

$$\Delta Q = (Q'_1 - Q'_2) = (Q_1 - Q_2 - R),$$

is approximately equal to the negative of the energy of respiration ( $R$ ) because, within a longer period, the net direct heat exchange,  $(Q_1 - Q_2)$ , (i.e., radiation, conduction, convection and latent heat transfer excluding respiration) between an organism and its environment tends to zero. Otherwise, the organism will die from over- or under-heating (Wiegert, 1968).

### 2.1. Animal exergy balance

All living systems consume energy as well as exergy because exergy is the part of the energy which can be utilized to do work. The exchange of energy and exergy in an animal is represented in Fig. 2. It should be noted that  $Q_1$  and  $Q_2$  include only the direct heat exchange and do not include respiration.

As is shown in Fig. 2, an animal ingests food from its environment. Under the action of a series of enzymes, some of the ingested energy is assimilated and some is egested. Of the assimilated energy, a part is transformed into animal tissue and storage materials (i.e., production), most is used to maintain respiration, and a small portion is excreted in feces and urine. Energy flows are accompanied by exergy flows, which are necessary to keep the system functioning. For convenience, the exergy contained in the ingested food is referred to as ingestion exergy ( $E_I$ ) and that in feces and urine as egestion-excretion exergy ( $E_F$ ). The exergy embodied in production is called production exergy ( $E_P$ ) and that embodied in respiration is named respiration exergy ( $E_R$ ). An animal may absorb the heat exergy ( $E_{Q_1}$ ) as well as heat from its environment through radiation, and it may release heat exergy ( $E_{Q_2}$ ) as well as heat to its environment through radiation, conduction, convection, and latent heat transfer. Assume the net direct heat exergy exchange to be  $E_Q = E_{Q_2} - E_{Q_1}$ . When  $E_Q > 0$ , an animal releases heat exergy to its environment, otherwise it absorbs heat exergy from its environment. Furthermore, an animal may exchange mechanical work with its environment but, as mentioned above, the net work exchange usually is very small

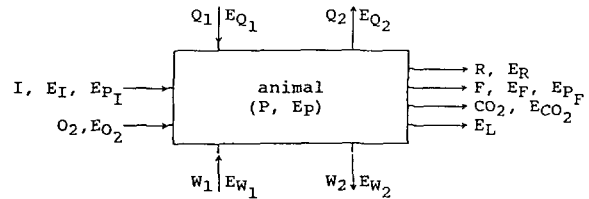


Fig. 2. The energy and exergy exchanges between an animal and its environment. The explanation for the symbols is in the text.

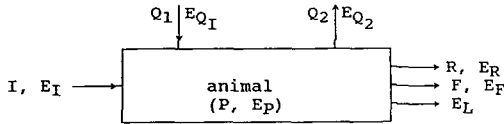


Fig. 3. Simplified energy and exergy exchange between an animal and its environment. The explanation for the symbols is in the text.

and may be neglected so that the net exergy exchange of mechanical work, ( $E_W = E_{W_2} - E_{W_1}$ ), may also be omitted. In addition, during the process of ingestion, egestion and excretion, the ingested food and egested-excreted waste materials may possess physical exergy ( $E_{P_i}$  and  $E_{P_f}$ ) due to the difference of temperature and pressure between the animal and its environment. For most animals, however, this difference may be small so that physical exergy may also be omitted. Finally, animals exchange gases ( $O_2$  and  $CO_2$ ) with their environments through respiration and the body surface so that they may exchange diffusion exergy ( $E_{O_2}$  and  $E_{CO_2}$ ). However, we assume that the diffusion exergy is very small, or the net exchange of diffusion exergy is zero. From the above, we obtain the animal exergy balance equation (Fig. 3):

$$E_I = E_P + E_R + E_F + E_Q + E_L \quad (3)$$

where  $E_L$  is exergy loss (Appendix).

As mentioned previously, the net direct heat exchange between an animal and its environment may be ignored, and thus the net direct heat exergy exchange can be omitted. Therefore

$$E_I = E_P + E_R + E_F + E_L. \quad (4)$$

## 2.2. Plant exergy balance

The plant exergy equation is constructed in a similar way, i.e.,

$$E_S = E_P + E_R + E_Q + E_L \quad (5)$$

or

$$E_S = E_P + E_R + E_L \quad (6)$$

where  $E_S$  is the photosynthetically active radiation exergy. The other terms have the same meaning as in Eq. 3.

## 3. Estimation of the different types of exergy

### 3.1. Chemical exergy

Generally speaking, exergy can be classified into two main types: physical and chemical exergy (Appendix). Ingestion, production and egestion-excretion exergy are chemical exergy and they can be estimated by the following methods.

Shieh and Fan (1982) suggested the estimations of exergy contents in structurally complicated materials as:

$$\begin{aligned} E_{ch}^n = & 340.124[C] + 5.25[N] + 5996.25[H] \\ & + 1062.45[O] + 2147.45[S] + 2733.411[F] \\ & + 2085.698[Cl] + 1022.642[Br] \\ & + 684.466[I] - 298.15S_{ash}^n W_{ash} \\ & - \Delta H^n \text{ (kcal/kg)} \end{aligned} \quad (7)$$

where  $E_{ch}^n$  is the chemical exergy content of complex materials (kcal/kg) under standard conditions ( $P^n = 1 \text{ atm}$ ,  $T^n = 298.15 \text{ K}$ ). [C], [H], [O], [N], [S], [F], [Cl], [Br] and [I] are respectively the contents of carbon, hydrogen, oxygen, nitrogen, sulfur, fluorine, chlorine, bromine and iodine per kg of complex materials.  $W_{ash}$  is the weight of ash per kg of material and  $S_{ash}^n$  is the specific entropy of ash.  $S_{ash}^n$  is assumed to have a value of 0.17152 kcal/(kg of ash, K), which is an average of the values of  $S_{ash}^n$  for 12 types of coal.  $\Delta H^n$  is the negative of the heat of combustion of a combustible structurally complicated material.

When  $\Delta H^n$  is not available, the specific exergy can be estimated by the following equation (Shieh and Fan, 1982):

$$\begin{aligned} E_{ch}^n = & 8177.79[C] + 5.25[N] + 27892.63[H] \\ & + 4364.33[S] - 3173.66[O] + 5763.41[F] \\ & + 2810.57[Cl] + 1204.3[Br] + 692.5[I] \\ & - 298.15S_{ash}^n W_{ash} + 0.15[O]\{7837.667[C] \\ & + 33888.889[H] - 4236.1[O] + 3828.75[S] \\ & + 4447.37[F] + 1790.9[Cl] + 681.97[Br] \\ & + 334.86[I]\} \text{ (kcal/kg)}. \end{aligned} \quad (8)$$

From Eqs. 7 and 8, we can obtain the specific chemical exergy under the standard conditions.

The specific chemical exergy under any other condition can be calculated as (Shieh and Fan, 1982)

$$E_{ch}(T,P) = E_{ch}^n + \int_{T^n}^T C_P(1 - T_0/T)dT + \int_{P^n}^P [V - (T - T_0)(\partial V/\partial T)_P]dP \tag{9}$$

where  $C_P$  is the specific heat capacity at constant pressure in kcal/kg · K, and  $T_0$  is the temperature of the environment. When the pressure effect is negligibly small, Eq. 9 becomes

$$E_{ch}(T,P) = E_{ch}^n + \int_{T^n}^T C_P(1 - T_0/T)dT. \tag{10}$$

### 3.2. Heat exergy

While a system is reaching thermal equilibrium with its environment, heat exergy exchange as well as heat exchange occurs. The heat exergy of a system is defined as the maximum work that can be done under given conditions by heat transferred out of the system in a reversible way (Zhao and Qian, 1984; Yang, 1986).

From thermodynamics, the gain in heat exergy ( $E_Q$ ) by a system receiving heat  $Q$  from the environment can be estimated by

$$E_Q = Q - T_0(S_2 - S_1) = Q - T_0\Delta S \tag{11}$$

and the gain in anergy by

$$A_Q = T_0(S_2 - S_1) \tag{12}$$

where  $T_0$  is the temperature of environment,  $S_1$  and  $S_2$  are the entropies of the system in states 1 and 2, and  $\Delta S$  is the production of entropy in the system.

Eq. 11 is the general form of heat exergy.

The processes of heat exchange between an organism and its environment are very complicated. Heat transfer in various forms (radiation, conduction, convection and latent heat transfer) relates not only to the temperature of the organism and its environment but also to many other factors such as radiation intensity and surface reflectivity, surface textures, wind velocity, prop-

erties of fluid media, and air pressure. In addition, the four heat transfer processes are accompanied by the processes of active absorption or release by respiration, drinking, egesting, excreting and sweating, so that heat exchange is not only a complicated physical and chemical process but also a complex living process. It is technically difficult and tedious to precisely estimate the heat of different transfers. But, for an organism, the ultimate result of various transfers is the absorption or rejection of heat, however complicated these processes are. The absorption or rejection of heat ultimately leads to the increase or decrease of the body temperature so that the heat exchange may be approximately estimated based on the temperature of the organism and its environment.

Assume the body temperature of an organism at times  $t_1$  and  $t_2$  to be  $T_1$  and  $T_2$  and the temperature of its environment to be  $T_0$ . If  $T_1 < T_2$ , then the net heat absorbed by the organism from its environment is

$$Q = C_P(T_2 - T_1). \tag{13}$$

The increase in entropy of the organism during the process of heat absorption is

$$\Delta S = \int_{T_1}^{T_2} (1/T)dQ = \int_{T_1}^{T_2} (C_P/T)dT = C_P \ln(T_2/T_1). \tag{14}$$

From Eq. 11, the heat exergy absorbed by the organism from its environment during the interval of  $t_1$  and  $t_2$  is

$$E_Q = Q - T_0\Delta S = C_P(T_2 - T_1) - T_0C_P \ln(T_2/T_1). \tag{15}$$

If  $T_2 < T_1$ ,  $Q$  and  $E_Q$  are negative, the organism releases heat exergy as well as heat to its environment. In addition, if we consider different processes of heat transfers in detail, the net heat absorbed or released by an organism can be computed as (Gates and Schmerl, 1975)

$$Q = \int \dot{Q}_{abs} dt = \int (\dot{Q}_{rad} + \dot{Q}_{conv} + \dot{Q}_{cond} + \dot{Q}_{vapor}) dt. \tag{16}$$

If we substitute Eq. 16 into 15, we may also obtain the value of heat exergy, but this approach leads to the complications described above.

For homoiothermal animals, although heat exchange occurs, the body temperature remains constant. The net heat exchange and net entropy exchange are equal to zero so that the net exergy exchange also equals zero.

### 3.3. *Respiration exergy*

Respiration is a fundamental and important life process which provides not only energy for all life activities but also the necessary raw materials for all biosyntheses. It is the metabolic center of matter such as carbohydrates, lipids and proteins. During the process of respiration, all respiratory substrates can be degraded into  $\text{CO}_2$  and  $\text{H}_2\text{O}$  through the Krebs cycle by the action of a series of enzymes. A part of energy stored in respiratory substrates dissipates into heat. The rest is fixed to ATP, which is used, on the one hand, to do internal work such as osmosis, absorption, secretion, transportation and muscle constriction, and, on the other hand, to construct cellular structural materials. The energy which is used to do internal work ultimately dissipates into heat. Therefore, some of the chemical energy in ATP is transformed into heat, and the rest into the chemical energy contained in the tissues and the stored materials.

According to the definition of exergy, respiration exergy ( $E_R$ ) is defined as the part of energy stored in respiratory substrates that is transformed into the chemical energy contained in ATP, which drives all life processes.

From biochemistry, we know that 40% of energy stored in carbohydrates and lipids can be transformed into the chemical energy in ATP. However, it is difficult to find out how much energy stored in proteins can be fixed in ATP after complete oxidation because the ways by which amino acids join in the Krebs cycle are different. Based on the properties of metabolism and various kinds of substrates, we may assume that, generally, proteins are not taken as the substrates of respiration when there are sufficient carbohydrates and lipids in the body of the organ-

ism. The direction of amino acid metabolism in higher plants and most of bacteria is composition not decomposition (Lehninger, 1975). Generally speaking, animals rarely take amino acids as their respiratory substrate under the conditions of sufficient sugar and fat, little supply of exogenous amino acids, and great requirement for amino acids. In this case, for animals to take amino acids as their respiratory substrate is not economical and favorable. Even if there is only a small amount of amino acids as respiratory substrate, we may consider the energy efficiency of amino acids for complete oxidation as the same as that of carbohydrates and lipids (Bell, 1985). Thus, respiration exergy can be estimated as

$$E_R = 0.4R. \quad (17)$$

### 3.4. *Photosynthetically active radiation exergy*

The light incident on a green plant may (1) be reflected at the interface between the plant and the air (catoptric light), (2) pass through the green plant without being absorbed by it (transmission light), or (3) enter the green plant and be absorbed by it. The ratio of reflection, transmission, and absorption of light to the incident radiation depends on the incident angle, plant shape, growth period, population dynamics, and etc. (Bell, 1985). Not all solar radiation can be absorbed by green plants to elicit photosynthesis. Solar radiation in the wave length range 380–710 nm is defined as photosynthetically active radiation, which can lead to photosynthesis of green plants.

Photosyntheses are very complicated processes. Photosynthetic molecules in chloroplasts are excited by absorbing the energy of photons. A few of the excited pigment molecules return to the ground state after releasing heat or light energy in the process called fluorescence or phosphorescence. The energy in most of the excited pigment molecules is transferred along the sequence of pigment molecules to the reaction center of the pigment system. From there, the excited electrons of the energy-trapping molecules in the reaction center are transferred along the carrier chain to  $\text{NADP}^+$ . Meanwhile, non-cyclic

photophosphorylation is initiated, and assimilatory power (ATP and NADPH) is formed with the release of O<sub>2</sub>. At the expense of ATP and NADPH, CO<sub>2</sub> and H<sub>2</sub>O are reduced to carbohydrates through the Calvin cycle.

From the definition of exergy and the processes of photosynthesis, photosynthetically active radiation exergy is defined as the amount of incident energy which theoretically leads to an increase of the free energy of plants.

Let  $\lambda$  be the wavelength of light,  $f(\lambda)$  be the spectral distribution function of the incident radiation, and  $A(\lambda)$  be the absorptance of the body storing the light energy of wavelength  $\lambda$ . In a narrow spectral interval  $(\lambda, \lambda + d\lambda)$ , the flux of the incident energy is  $f(\lambda)d\lambda$  and the flux of absorbed energy is  $A(\lambda)f(\lambda)d\lambda$ .

Photosynthesis includes a series of photophysical, photochemical and biochemical processes. Not all of this primary stored energy (i.e., absorbed energy) is utilized by green plants for the formation of carbohydrates because various types of energy losses may occur on further transformation of the energy. Let  $\epsilon$  be the fraction of the primarily stored energy that ultimately remains in green plants, i.e., the ratio of free energy increase of the green plant to the amount of absorbed light energy. It is called energy yield (Bell, 1985). Thus, for light of wavelength  $(\lambda, \lambda + d\lambda)$ , the amount of stored energy is

$$\epsilon A(\lambda)f(\lambda)d\lambda. \tag{18}$$

From the definition of photosynthetically active radiation exergy, we have

$$E_s = \int_{380}^{710} \epsilon A(\lambda)f(\lambda)d\lambda. \tag{19}$$

Energy yield is the product of the overall quantum efficiency ( $\alpha$ ) and the overall energy efficiency ( $\beta$ ) (Bell, 1985). The overall quantum efficiency of the photosynthetic processes as a whole is the proportion of the quanta eliciting the reduction of CO<sub>2</sub> into carbohydrates to the primarily absorbed quanta. Let  $\alpha_i$  be the quantum efficiency of the  $i$ th sequential process, then  $\alpha = \Pi\alpha_i$ . The overall energy efficiency is the fraction of the energy of one quantum that can be fixed into carbohydrates. Assume  $\beta_i$  to be the energy

efficiency of the  $i$ th sequential process. Thus,  $\beta = \Pi\beta_i$ .

An absorbed quantum may be inefficient for several reasons. In the first place, the excitation energy may not reach the reaction center. In particular, some quanta may be re-emitted as fluorescent light. Even if the energy reaches the reaction center, it may not be trapped by the latter, and this will further reduce the efficiency. Some of the energy may be lost in the charge separation processes. In addition, since the two photosystems must operate in a concerted manner, some of the excitation energy may be lost in the electron transport along the carrier chain to NADP<sup>+</sup>, which involves at least 10 partial processes. The formation of the assimilatory powers (ATP and NADPH) at the expense of the energy trapped in the reaction center is probably less efficient than 100%. Finally, the numerous stages in the biochemical pathway of the Calvin cycle may also lead to inefficient utilization of the assimilatory power for the reduction of CO<sub>2</sub>. The quantum efficiency of various stages of photosynthesis under optimal conditions is summarized in Table 1 (Bell, 1985).

From Table 1, the maximum overall quantum efficiency is

$$\alpha = \Pi\alpha_i = 0.629 \text{ to } 0.696. \tag{20}$$

Bell (1985) concluded that the total energy loss per quantum in the various processes of photosynthesis is  $(11 + 1 + 24/n + 28/n)$ , where  $n$  is the quantum requirement for the reduction of one CO<sub>2</sub> molecule. Theoretically, the minimum

Table 1  
Quantum efficiency of various stages of photosynthesis

Processes	Upper limit of quantum efficiency ( $\alpha_i$ )
Retention of absorbed quantum	0.95
Migration of excitation energy to reaction center	0.95
Trapping of excitation energy	0.95
Charge separation	0.95
Transport of electron along carrier chain to NADP	0.8–0.9
PGA reduction and RDP regeneration	0.95

quantum requirement is eight. Based on the red quantum, the input energy is  $8 \times 42 = 336$  kcal. The energy loss for reduction of one  $\text{CO}_2$  molecule is  $12 \times 8 + 24 + 28 = 148$  kcal. The increase of free energy is  $336 - 148 = 188$  kcal. If all quanta are used with 100% efficiency, the overall energy efficiency  $\beta = 188/336 = 0.56$ .

From above, we know that the maximum energy yield is 0.35 to 0.39 (i.e.,  $0.619 \times 0.56 = 0.35$ ,  $0.696 \times 0.56 = 0.39$ ). This is consistent with the experimentally observed value of maximum energy efficiency (0.35 to 0.40) (Bell, 1985). We take the mean value of 0.37 as the estimation of energy yield in Eq. 19, i.e.  $\epsilon = 0.37$ .

**4. Ecological exergy efficiency**

Similar to an ecological efficiency index, which is calculated on the basis of an energy balance equation, an ecological exergy efficiency, which is the index to evaluate the thermodynamic perfectness of different ecological processes, can be estimated based on the ecological exergy balance equation.

*4.1. Ecological process exergy efficiency*

The exergy efficiency of any thermodynamic process can be estimated based on the exergy input and output of the system (Appendix). From Eq. 3, the ecological process exergy efficiency of an animal system can be obtained

$$\eta_e^1 = \frac{E_I - E_L}{E_I} = \frac{E_P + E_R + E_F + E_Q}{E_I} \tag{21}$$

$\eta_e^1$  measures the thermodynamic perfectness of ecological processes.

*4.2. Assimilation exergy efficiency*

If the heat exergy and egestion-excretion exergy are taken as external exergy loss (Appendix), the total exergy loss is

$$E_L^1 = E_F + E_Q + E_L \tag{22}$$

Thus, the exergy balance Eq. 3 becomes

$$E_I = E_P + E_R + E_L^1 \tag{23}$$

Assimilation exergy efficiency is estimated as

$$\eta_e^2 = \frac{E_I - E_L^1}{E_I} = \frac{E_P + E_R}{E_I} \tag{24}$$

$\eta_e^2$  measures the ability for organisms to assimilate exergy.

*4.3. Production exergy efficiency*

Modifying exergy balance Eq. 3 as

$$E_I - E_F - E_Q = E_P + E_R + E_L \tag{25}$$

If respiration exergy is considered as an external exergy loss, then the total exergy loss is

$$E_L^2 = E_R + E_L \tag{26}$$

Production exergy efficiency

$$\eta_e^3 = \frac{(E_I - E_F - E_Q) - E_L^2}{E_I - E_F - E_Q} = \frac{E_P}{E_I - E_F - E_Q} \tag{27}$$

$\eta_e^3$  measures the ability of organisms to produce exergy.

*4.4. Respiration exergy efficiency*

Relative to the metabolic processes themselves, production exergy can be considered as an external exergy loss, then the total exergy loss is

$$E_L^3 = E_P + E_L \tag{28}$$

From the definition of exergy efficiency and Eq. 25, we have

$$\eta_e^4 = \frac{(E_I - E_F - E_Q) - E_L^3}{E_I - E_F - E_Q} = \frac{E_R}{E_I - E_F - E_Q} \tag{29}$$

$\eta_e^4$  expresses the fraction of the assimilated exergy which organisms use to maintain their life activities.

**5. Discussion**

An ecological exergy analysis method is developed on the basis of the exergy analysis method



in thermodynamics in light of the features of living systems. This method takes account of both energy quantity and energy quality in the sense of thermodynamics. It should have significant applications in theory and practice when experiments are carried out that can be used to evaluate the exergy coefficients developed. So far applicable experimental data do not appear to be available.

An ecosystem is a large energy convector consisting of many components. With the help of the ecological exergy analysis method, the weak energy transfer and conversion links in the ecological network can be identified, and this method, therefore, appears to supply a theoretical basis for the management of ecosystems. Ecological exergy efficiency is a unified measure of the ultimate thermodynamic limitations on various ecological processes so that it can be taken as the objective function in the optimization of an ecosystem. In particular, thermo-economic analysis, which is derived from a combination of exergy analysis and economic analysis (Yang, 1986), is a powerful method to deal with problems in multiple complex systems. Based on thermal economics, it appears to be possible to realize the unity of ecological benefits and economic benefits in a single research method. However, the application of thermal economics to multiple complex ecosystems depends on the estimation of exergy flows. From the exergy flows at the level of organisms, it is easy to obtain exergy flows at the level of ecosystems. This paper lays a foundation for the application of thermal economics to ecosystems.

Mejer and Jørgensen (1979) proposed a formula to calculate exergy for a system with an inorganic net flow and passive outflow based on information theory and thermodynamics. Strictly speaking, this formula is appropriate for the exergy calculation of a pure substance such as phosphorus but may be not proper for the exergy calculation of complex biological materials because their free energies of formation ( $\Delta G_f^0$ ) are unknown. In addition, the equilibrium values used in this formula are not from the equilibrium defined in thermodynamics (Yang, 1986) so that the calculated exergy for a system with an inorganic netflow and passive outflow is not the ex-

ergy in the sense of thermodynamics. The method developed here provides a way to investigate exergy flow and exergy production in biological systems in the sense of thermodynamics.

Eqs. 7 and 8 to estimate chemical exergy may have some limitations in estimating exergy of biological materials because some biologically important and abundant elements such as phosphorus are not considered. Further modifications of this formula to include other biologically important and abundant elements are needed. In addition, the content of halogens except chlorine in biological materials appears to be very small (Morowitz, 1968) so that the contribution of exergy from these halogens to the total exergy in biological materials may be very small and can be ignored.

An ecosystem consists of many components which interact with each other through the networks of flows of energy as well as exergy, matter and information. Aoki (1992) applied network analysis to ecological systems based on the concepts of exergy content, exergy input–output and exergy loss but did not present how to estimate them in complicated ecosystems. With the help of the method developed here, it is possible to apply the exergy network analysis theory to complex ecosystems and develop mathematical models to simulate the dynamic changes of ecosystems based on the quantity of exergy.

Exergy depends on the states of both system and environment so that exergy is not a state variable (Yang, 1986). However, under a given environmental condition, exergy is only dependent on the state of the system (Yang, 1986) so that it can be treated as a state variable to describe the changes of the system. Many different environmental state models have been proposed to be used as reference (or datum) states in the estimation of exergy (Yang, 1986). The environmental state model used to obtain Eqs. 7 and 8 appears to be superior to other environmental models (Shieh and Fan, 1982; Yang, 1986). This environmental state model, however, may also be not proper for living systems because the equilibrium state in ecosystems appears to be different from that in physical and chemical systems. Alternatively we could stipulate a datum state for

calculating chemical exergy based on chemical and physical conditions of ecological equilibrium and thus develop a more universal method to deal with ecological problems.

Based on the concept of exergy and evolutionary theory, Jørgensen (1992a) proposed a tentative ecological law of thermodynamics, which states that “a system with a through-flow of exergy will attempt to utilize the flow to increase the exergy of system, and the organization of the system that is able to give the system the highest exergy will be selected”. The method developed here provides a way to measure the exergy flow in living systems. By comparing the exergy flows and fitness of different living systems, this tentative law can be directly tested by experimentation.

Respiration exergy is a particular form of exergy. It differs from ingestion, production and egestion-excretion exergy. Although most of the respiration exergy ultimately is dissipated into heat after doing internal work, the description of the process differs from the corresponding description of the flow of the part of respiration energy that is not embodied in ATP. Respiration exergy indicates not only the intensity of metabolism but also the ways and strategies by which organisms utilize and distribute available energy.

In this paper, thermodynamic exergy has been used as the measure of energy quality to describe the physical-chemical processes in organisms. However, in the analysis of ecosystems, especially compound ecosystems (e.g. rural and urban systems), there are three levels of energy quality to be considered relative to the three major processes: physical-chemical process, biological-ecological process and economic process. In order to deal with problems in compound ecosystems, energy quality must be considered at all three levels, and the energy quality in the levels of biological-ecological and economic processes must be based on the level of the physical-chemical process. As noted above, the ecological exergy analysis method presented in this paper concerns the energy quality at the level of the physical-chemical process, i.e., in the sense of thermodynamics. Perhaps, the concept of transformity suggested by Odum (1983) could be used to tackle the concept

of energy quality at the level of the biological-ecological process, but transformity should be estimated according to exergy rather than energy. However, there are some difficulties to estimate the exergy of different energy forms in compound ecosystems that include industrial products, human labor, and animal power. How to estimate the exergy of these different energy forms and how to consider, for the purpose of finding a common denominator in ecosystems, energy quality at the three levels need further study.

### Acknowledgements

We wish to thank Professors James M. Tiedje, David Pimentel, Alan A. Berryman, Robert Herendeen, Lan Zhongxiong, Ding Yanqin, Niu Wenyun, Chen Changming, and Wu Kunjun for their valuable suggestions about the text. Jizhong Zhou wishes to acknowledge the contributions and encouragement of Professor Ma to his education in Beijing and to express his regret and sorrow at Professor Ma's untimely death in an automobile accident in Beijing in 1991.

### Appendix 1

#### Exergy and exergy efficiency

The second law of thermodynamics places limits on energy conversion processes, especially those involving conversions of heat into other energy forms. Under given environmental conditions, the exergy of a system is defined as that part of the energy that can be utilized to do work, and anexergy signifies that part which cannot do work (Zhao and Qian, 1984; Yang, 1986). Thus,

$$\text{Energy} = \text{Exergy} + \text{Anexergy}. \quad (\text{A1})$$

Exergy is dependent on the states of both system and environment. The state in which a thermodynamic system stands in complete thermodynamic equilibrium with its environment is defined as the datum state of exergy (Zhao and Qian, 1984; Yang, 1986). Complete thermody-

dynamic equilibrium for a system requires that there are no unbalanced forces, variations in temperature, potential chemical reactions, and possible diffusion processes within the system, and between it and the environment. The exergy of any system in the datum state is zero. Any system which is not in the datum state has exergy.

Exergy ( $E$ ) can be divided into physical exergy ( $E_{ph}$ ) and chemical exergy ( $E_{ch}$ ), i.e.,

$$E = E_{ph} + E_{ch}. \tag{A2}$$

Physical exergy of a system is the maximum work which can be done by the system when it is brought into mechanical and thermal equilibrium, but not chemical equilibrium, through reversible physical processes, whereas chemical exergy of a system is the maximum work that can be provided by the system when it is changed from incomplete to complete thermodynamic equilibrium through one or more reversible chemical processes.

In reversible processes, no anexergy is created and the total amount of exergy in a system plus its surroundings remains constant. In irreversible processes, some of the exergy is inevitably transformed into anexergy. This decrease is the exergy loss caused by the irreversible process and is denoted as  $E_L$ . The exergy loss caused by irreversible processes within a system is called internal exergy loss, denoted by  $(E_L)_{in}$  and that which is associated with flows into and out of the environment from and to the system is called external exergy loss, denoted by  $(E_L)_{out}$ . From a thermodynamic viewpoint, all real processes in the natural world are irreversible. Any irreversible process inevitably causes a decrease of exergy and an increase of anexergy. Therefore, there is no conservation of exergy in any realistic process. In order to establish an exergy balance equation, exergy loss must be added to the right hand side of the equation giving a general exergy balance equation for any thermodynamic system:

$$\begin{aligned} &\text{Input of exergy} \\ &= \text{Output of exergy} \\ &\quad + \text{Exergy change of the system} \\ &\quad + \text{Exergy loss.} \end{aligned} \tag{A3}$$

Internal exergy loss can be estimated from the

entropy parameter (Zhao and Qian, 1984):

$$(E_L)_{in} = T_0 \Delta S_{i,s} \tag{A4}$$

where  $T_0$  is the environmental temperature and  $\Delta S_{i,s}$  is the entropy increase of a system caused by irreversible processes.

Exergy loss may also be estimated from the exergy balance Eq. A3:

$$\begin{aligned} \text{Exergy loss} &= \text{Input of exergy} - \text{Output of exergy} \\ &\quad - \text{Exergy change of the system.} \end{aligned} \tag{A5}$$

It should be noted that the estimation of exergy loss from the exergy balance equation includes the *external exergy loss* if it occurs.

The ability of a system to utilize exergy can be measured by exergy efficiency ( $\eta_e$ ); i.e.,

$$\eta_e = E_{gain} / E_{pay}. \tag{A6}$$

$E_{gain}$  is the exergy increase of the system, and  $E_{pay}$  is the difference between the input and output of exergy. From Eq. 5

$$E_L = E_{pay} - E_{gain}. \tag{A7}$$

Therefore

$$\eta_e = \frac{E_{pay} - E_L}{E_{pay}} = 1 - \frac{E_L}{E_{pay}} = 1 - \zeta \tag{A8}$$

where  $\zeta$  is the coefficient of exergy loss.

In the light of the second law, it is impossible for the exergy efficiency of a system or process to be larger than 1. A reversible process is occurring when  $\eta_e = 1$  and an irreversible process when  $\eta_e < 1$ . Exergy efficiency reflects the difference between a realistic process and a reversible (ideal) process, i.e., the degree of thermodynamic perfection of the realistic process. Therefore, exergy efficiency indicates the possibility of improving systems or processes and can be used as a unified measure of the thermodynamic perfection of a system or process.

## References

- Aoki, I., 1987a. Entropy balance of a white-tailed deer during a winter night. *Bull. Math. Biol.*, 49: 321–327.

- Aoki, I., 1987b. Entropy budgets of deciduous plants leaves and a theorem of oscillating entropy production. *Bull. Math. Biol.*, 49: 235–248.
- Aoki, I., 1987c. Entropy budgets of soybean and bur oak leaves at night. *Physiol. Plant.*, 71: 293–295.
- Aoki, I., 1987d. Entropy balance in lake Biwa. *Ecol. Model.*, 37: 235–248.
- Aoki, I., 1988. Entropy laws in ecological networks at steady state. *Ecol. Model.*, 42: 289–303.
- Aoki, I., 1989. Hological study of lakes from an entropy viewpoint – lake Mendota. *Ecol. Model.*, 45: 81–93.
- Aoki, I., 1992. Exergy analysis of network systems at steady state. *Ecol. Model.*, 62: 183–193.
- Aoki, I., 1993. Inconclusive Kullback index – a macroscopic measure in ecological systems. *Ecol. Model.*, 66: 289–299.
- Bell, L.N., 1985. Energetics of the Photosynthesizing Plant Cell. Harwood Academic Publ., Chur.
- Engelmann, M.D., 1961. The roles of soil arthropods in the energetics of an old field community. *Ecol. Monogr.*, 31: 221–238.
- Forbes, S.A., 1887. The lake as a microcosm. Republished 1925. *Ill. Natl. Hist. Surv. Bull.*, 23: 537–550.
- Gates, D.M., 1962. Energy Exchange in the Biosphere. Harper and Row, New York.
- Gates, D.M., 1966. Spectral distribution of solar radiation at the earth's surface. The spectral quality of sunlight, skylight and global radiation varies with atmospheric conditions. *Science*, 151: 523–529.
- Gates, D.M., 1967. Thermal balance of the biosphere. *Proc. 4th Int. Biometeorol. Congr. Biometeorol.*, 3: 29–39.
- Gates, D.M., 1968. Relationships between plants and atmosphere. *Am. Nat.*, 23: 133–140.
- Gates, D.M. and Schmerl, R.B., 1975. Perspectives of Biophysical Ecology. Springer-Verlag, New York.
- Herendeen, R., 1989. Energy intensity, residence time, exergy and ascendancy in dynamic ecosystems. *Ecol. Model.*, 48: 19–44.
- Johnson, D.R. and Maxell, M., 1966. Energy dynamics of Colorado pikas. *Ecology*, 47: 1059–1061.
- Jørgensen, S.E., 1986. Structural dynamic model. *Ecol. Model.*, 31: 1–9.
- Jørgensen, S.E., 1988. Use of models as experimental tool to show that structural changes are accompanied by increased exergy. *Ecol. Model.*, 41: 117–126.
- Jørgensen, S.E., 1990. Ecosystem theory, ecological buffer capacity, uncertainty and complexity. *Ecol. Model.*, 52: 125–133.
- Jørgensen, S.E., 1992a. Exergy and ecology. *Ecol. Model.*, 63: 185–214.
- Jørgensen, S.E., 1992b. Parameters, ecological constraints and exergy. *Ecol. Model.*, 62: 163–170.
- Jørgensen, S.E., 1992c. Development of models able to account for changes in species composition. *Ecol. Model.*, 62: 195–208.
- Jørgensen, S.E., 1992d. Integration of Ecosystem Theories: A Pattern. Kluwer Academic Publishers, Boston.
- Jørgensen, S.E. and Mejer, H., 1977. Ecological buffer capacity. *Ecol. Model.*, 3: 39–61.
- Jørgensen, S.E. and Mejer, H., 1981. Exergy as key function in ecological models. In: W.J. Mitsch, R.W. Bosserman and J.M. Klopatek (Editors), *Energy and Ecological Modelling*. Elsevier, Amsterdam, pp. 587–590.
- Lehninger, A.L., 1975. *Biochemistry – The Molecular Basis of Cell Structure and Function*. Worth Publishers Inc.
- Limburg, K.E., 1985. Increasing complexity and energy flow in models of food webs. *Ecol. Model.*, 29: 5–26.
- Lindman, R.L., 1942. Seasonal food-cycle dynamics in a senescent lake. *Am. Midl. Nat.*, 26: 636–673.
- Macfadyen, A., 1948. The meaning of productivity in biological systems. *J. Anim. Ecol.*, 17: 75–80.
- Mejer, H. and Jørgensen, S.E., 1979. Exergy and ecological buffer capacity. In: S.E. Jørgensen (Editor), *State of the Art of Ecological Modelling*. ISEM, Copenhagen, pp. 829–846.
- Morowitz, H.J., 1968. *Energy Flow in Biology*. Academic Press, New York.
- Odum, E.P., 1960. Organic production and turnover in old field succession. *Ecology*, 41: 34–49.
- Odum, H.T., 1983. *Systems Ecology*. John Wiley and Sons, New York.
- Odum, H.T., 1984a. Energy analysis evaluation of coastal alternatives. *Water Sci. Technol.*, 16: 717–734.
- Odum, H.T., 1984b. Embodied energy, foreign trade, and welfare of nations. In: A.-M. Jansson (Editor), *Integration of Economy and Ecology, and Outlook for the Eighties*. ASCO Laboratory, University of Stockholm, Stockholm, Sweden.
- Odum, H.T., 1988. Self-organization, transformation, and information. *Science*, 242: 1132–1139.
- Odum, H.T. and Odum, E.P., 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok atoll. *Ecol. Monogr.*, 27(3): 291–320.
- Parikh, J., 1985. Modelling energy and agriculture interactions. I. A rural energy systems model. *Energy*, 10: 793–804.
- Patten, B.C., 1976. *System Analysis and Simulation in Ecology*. Academic Press, New York.
- Patten, B.C., 1983. On the quantitative dominance of indirect effects in ecosystems. In: W.K. Lauenroth, G.V. Skogerboe and M. Flug (Editors), *Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling*. Elsevier, Amsterdam.
- Patten, B.C., 1984. Energy cycling, length of food chains, and direct vs. indirect effects in ecosystems. *Can. Bull. Fish. Aquat. Sci.*, 213: 119–138.
- Patten, B.C., 1985. Energy cycling in the ecosystems. *Ecol. Model.*, 28: 1–71.
- Phillipson, J., 1966. *Ecological Energetics*. Edward Arnold Ltd., London.
- Richman, S., 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.*, 28: 373–391.
- Salomonsen, J., 1992. Examination of properties of exergy,

- power and ascendancy along a eutrophication gradient. *Ecol. Model.*, 62: 171–181.
- Scott, D., 1965. The determination and use of thermodynamic data in ecology. *Ecology*, 46: 673–680.
- Shieh, J.H. and Fan, L.T., 1982. Estimation of energy (enthalpy) and energy (availability) contents in structurally complicated materials. *Energy Resour.*, 6: 1–46.
- Slobodkin, L.B., 1959. Energetics in *Daphnia pulex* populations. *Ecology*, 40: 232–243.
- Slobodkin, L.B., 1960. Ecological energy relationships at the population level. *Am. Nat.*, 94: 213–236.
- Slobodkin, L.B., 1961. Preliminary ideas for a predictive theory of ecology. *Am. Nat.*, 95: 147–153.
- Slobodkin, L.B., 1962. Energy in animal ecology. In: I.B. Cragg (Editor), *Advances in Ecological Research*, Vol. 1 Academic Press, New York, pp. 69–101.
- Teal, J.M., 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.*, 27: 283–302.
- Trama, F.B., 1957. The transformation of energy by an aquatic herbivore *Stenonema pulchellum* (Ephemeroptera). Ph.D. dissertation, Michigan State University, East Lansing, MI.
- White, E.G., 1984a. A multispecies simulation model of grassland products and consumers. II. Producers. *Ecol. Model.*, 24: 241–262.
- White, E.G., 1984b. A multispecies simulation model of grassland products and consumers. III. Consumers. *Ecol. Model.*, 24: 263–279.
- Wiegert, R.G., 1961. Respiratory energy loss and activity pattern in the meadow vole, *Microtus pennsylvanicus*. *Ecology*, 42: 245–253.
- Wiegert, R.G., 1964. Populations of energetics of meadow spittlebugs (*Philaenus spumarius* L.) as affected by migration and habitat. *Ecol. Monogr.*, 34: 217–241.
- Wiegert, R.G., 1968. Thermodynamic considerations in animal nutrition. *Am. Zool.*, 8: 71–81.
- Wiegert, R.G., 1973. A general ecological model and its use in simulating algal–fly energetics in a thermal spring community. In: P.W. Geier, L.R. Clark, D.L. Anderson and H.A. Nix (Editors), *Insects: Studies in Population Management*. Ecological Society of Australia (Memoir 1), Canberra, pp. 85–102.
- Wiegert, R.G., 1975. Simulation modeling of the algal–fly heterogeneity, time delays and model condensation. In: B.C. Patten (Editor), *Systems Analysis and Simulation in Ecology*, Vol. 3. Academic Press, New York.
- Yang, D.-H., 1986. Exergy Analysis and Energy Rank Analysis. Science Press, Beijing (in Chinese).
- Zhao, G.-C. and Qian, L.-L., 1984. Exergy Analysis and its Applications. Higher Education Press, Beijing (in Chinese).
- Zucchetto, J., 1975. Energy-economic theory and mathematical models for combining the systems of man and nature. Case study: the urban region of Miami, Florida. *Ecol. Model.*, 1: 241–268.