



Transition from abstract thermodynamic concepts to perceivable ecological indicators



Hua Lin^{a,c}, Houlei Zhang^{b,*}, Qinghai Song^{a,d}

^a Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China

^b School of Energy and Power Engineering, Nanjing University of Science and Technology, Nanjing, Jiangsu 210094, China

^c Ailaoshan Station for Subtropical Forest Ecosystem Studies, China

^d Xishuangbanna Station for Tropical Rainforest Ecosystem Studies, China

ARTICLE INFO

Keywords:

Ecosystem development
Total entropy production
Exergy destruction
Specific entropy production
Surface temperature
Thermodynamics

ABSTRACT

Entropy and exergy are the central concepts in thermodynamics, and many researchers have used them to characterize ecosystem development. However, these concepts are very abstract to outsiders. Direct measurements of the indicators related to entropy and exergy are difficult and involve large errors. Schneider and Kay (1994) bridged thermodynamic concepts, i.e., entropy and exergy, with perceivable ecological indicators, i.e., canopy surface temperature (T_{surf}) and net radiation (R_n) in their maximum exergy destruction principle. However, the connection between entropy and exergy with T_{surf} and R_n was based on the similarity between the ecosystem and the Bénard cell, and not on thermodynamic reasoning. Considering the coherence of entropy production and exergy destruction, we analyzed the relationship between entropy production and T_{surf} and R_n , based on the first and second laws of thermodynamics, and verified it using long-term monitoring data of a tropical seasonal rain forest. We demonstrated that total entropy production (exergy destruction) linearly increased with increasing R_n and decreasing T_{surf} theoretically. Empirical data showed that the total entropy production increased, whereas specific entropy production decreased during the growing season. This indicates that plant growth can enhance exergy conversion efficiency. R_n , T_{surf} , and related indicators can be used as surrogates for thermodynamic indicators to measure ecosystem status and development. The bridge between thermodynamic concepts and measurable ecological indicators will improve the application of thermodynamics in ecology studies and the understanding of thermodynamic processes in ecosystem.

1. Introduction

The direction of ecosystem development (e.g., growth, succession, and recovery) has been a central theme in ecology study. It is not only a theoretical question, but also has implications for current environmental challenges, e.g., prediction of vegetation response to climate change or assessment of deforestation and restoration (Prach and Walker, 2011). Many patterns have been observed across ecosystem development, for example: the transition from r-selected species to K-selected species (MacArthur and Wilson, 1967), gross production/community respiration approaching one, life cycles and information increases (Odum, 1969), and the transition from quantity growth to quality growth (Fath et al., 2004). These measurements reflect the characteristics of ecosystems from a certain perspective. Thermodynamics, on the other hand, provides a comprehensive insight into system development (Chapman et al., 2016; Svirezhev, 2000). Entropy and exergy based concepts have been demonstrated to be useful to

assess ecosystem development, and to integrally characterize ecosystems (Bejan, 2013; Bertram, 2014; Chapman et al., 2016; Fath et al., 2004; Fraser and Kay, 2002; Jørgensen, 2007; Kleidon, 2009). However, these thermodynamic concepts might not seem straightforward for ecologists who are not familiar with thermodynamics due to their relatively abstract ecological meaning.

Schneider and Kay (1994) connected thermodynamic concepts (i.e., exergy destruction) with ecological parameters in their maximum exergy destruction principle. They took ecosystems as dissipation structures that can dissipate temperature gradients more efficiently than bare ground. They emphasized that exergy destruction played key roles in ecosystem characterization, and the more developed ecosystems could gain more energy, while maintaining lower surface temperature (Fraser and Kay, 2002). Net radiation and canopy surface temperature are proxies for the interaction between vegetation and environment, which are perceivable ecological parameters and easy to be measured. Many experiments have supported Schneider and Kay's conclusion

* Corresponding author.

E-mail address: zhanghl@njust.edu.cn (H. Zhang).

(Akbari, 1995; Lin, 2015; Lin et al., 2009; Lin et al., 2011; Maes et al., 2011); however, the Maximum Exergy Destruction principle was proposed based on the similarity between ecosystems and Bénard cells. Quantitative analysis of the relationship among exergy destruction, canopy surface temperature, and net radiation from the view of thermodynamic laws has never been conducted. According to the second law of thermodynamics, exergy destruction is actually proportional to entropy production (Cengel and Boles, 2014).

In the present study, we analyzed the relationship among entropy production (exergy destruction), net radiation, and canopy surface temperature based on thermodynamic laws, and verified it with long-term monitoring data of a tropical seasonal rain forest. We aim to further understand the relationships between thermodynamic concepts and ecological indicators, i.e., R_n and T_{surf} .

2. Materials and methods

2.1. Study sites

All the data were obtained from the meteorology gradient system on a tower in the tropical seasonal rain forest in Menglun, Xishuangbanna, southwestern China (21°57'N, 101°12'E, 750 m asl). The mean canopy height was 35 m. The annual mean temperature of this forest was 19.9 °C and the maximum air temperature was 34.6 °C. Annual precipitation averaged 1557 mm, 85% of which occurred during the rainy season (May–October). The dry season occurred from November to February (Cao et al., 2006).

2.2. Measurements

The net radiation was measured using a 4-component radiometer (CNR4, Kipp & Zonen, Netherlands) at 41.6 m above the ground. The canopy surface temperature was measured by an infrared thermometer (SI-111, Apogee, USA) installed at 52 m. We used the air temperature (HMP45C, Campbell Scientific Inc., USA) at the same height of the measurements of sensible heat (CSAT3, Campbell, USA) and latent heat (LI-7500, LI-COR Inc, USA) (48.8 m) in the calculation. Soil heat and soil temperature (105T, Campbell Scientific Inc., USA) were measured 5 cm below the soil surface. All variables were automatically sampled at 0.5 Hz, and 30 min averages were obtained as outputs from the data logger (CR5000, Campbell Scientific Inc., USA). For the detailed descriptions of the site and instruments, see Dou et al. (2007).

2.3. Data analysis

The average data from the year 2003 to 2009 were used in the

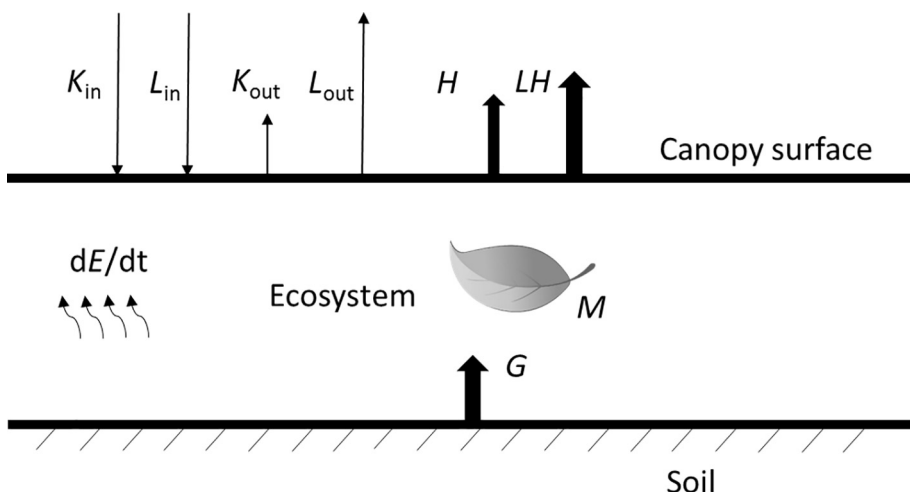


Fig. 1. Energy balance of ecosystem. K_{in} , incoming shortwave radiation; L_{in} , incoming longwave radiation; K_{out} , outgoing shortwave radiation; L_{out} , outgoing longwave radiation; H , sensible heat flux; LE , latent heat flux; G , soil heat flux; M , energy flux owing to metabolic activity; $\frac{dE}{dt}$, energy storage rate of ecosystem.

present study. The total entropy production (\dot{S}_{irrev}) was calculated using the data at half-hour intervals. The daily total entropy production and net radiation were used to analyze seasonal courses. To analyze the relationship between entropy production and canopy surface temperature, we controlled the incoming shortwave radiation (K_{in}) at four levels: 600–610, 650–660, 700–710, and 800–810 $J m^{-2} s^{-1}$, and the incoming longwave radiation (L_{in}) within 450–460 $J m^{-2} s^{-1}$ to satisfy the requirement of identical radiation environment.

3. Theory

According to the second law of thermodynamics, exergy destruction (\dot{E}_d) is proportional to entropy production (Cengel and Boles, 2014)

$$\dot{E}_d = T_0 \dot{S}_{irrev} \quad (1)$$

where T_0 is the temperature at the reference state, which can be taken as a constant. Therefore, exergy destruction is consistent with entropy production, and we only analyzed \dot{S}_{irrev} in the present study.

The entropy budget ($\frac{dS}{dt}$) (i.e., entropy change rate) of the ecosystem is calculated by entropy flux (\dot{S}_{flux}) and entropy production (\dot{S}_{irrev}) due to irreversible processes occurring inside the system:

$$\frac{dS}{dt} = \dot{S}_{irrev} + \dot{S}_{flux} \quad (2a)$$

Thereafter, entropy production is obtained as follows:

$$\dot{S}_{irrev} = \frac{dS}{dt} - \dot{S}_{flux} \quad (2b)$$

The energy storage rate of the ecosystem ($\frac{dE}{dt}$) is determined by the temperature change and heat capacity of the ecosystem (Eq. (3)). In Eq. (3), C is the equivalent heat capacity of the whole forest. Considering the difficulty in measuring C , we calculated $\frac{dE}{dt}$ through energy balance. According to the first law of thermodynamics (i.e., energy conservation law):

$$\frac{dE}{dt} = C \frac{dT_{surf}}{dt} = K_{in} + L_{in} - K_{out} - L_{out} - H - LE - G - M \quad (3)$$

where, K_{in} is shortwave radiation, L_{in} is incoming longwave radiation, K_{out} is outgoing shortwave radiation, L_{out} is outgoing longwave radiation, H is sensible heat flux, LE is latent heat flux, G is soil heat flux, and M is energy flux owing to metabolic activity (Fig. 1). Usually, M is negligible because of the small magnitude (Gu et al., 2007).

The ecosystem can be considered an incompressible substance, therefore, the entropy budget in Eq. (2a) can be further expressed as (Cengel and Boles, 2014):

$$\frac{dS}{dt} = \frac{dE/dt}{T_{surf}} \quad (4)$$

According to the energy balance in Eq. (3), entropy flux (\dot{S}_{flux}) can be calculated as:

$$\dot{S}_{flux} = \dot{S}_{K_{in}} + \dot{S}_{L_{in}} - \dot{S}_{K_{out}} - \dot{S}_{L_{out}} - \dot{S}_H - \dot{S}_{LE} - \dot{S}_G \quad (5a)$$

where the right side is the entropy production contributed by K_{in} , L_{in} , K_{out} , L_{out} , H , LE , and G respectively.

The entropy fluxes of radiation are equal to the radiation components divided by the absolute temperature of emission sources. We used the brightness temperature 5760 K as the surface temperature of the sun (T_{sun}) (Holdaway et al., 2010). The entropy flux of sensible heat is calculated by the sensible heat divided by the air temperature at the system boundary (T_{air}). The entropy flux of latent heat includes the entropy flux associated with the change in the state of water from liquid to vapor ($\frac{LE}{T_{air}}$) and the mixing of saturated air with dry air (\dot{S}_{LEmix}). Considering that \dot{S}_{LEmix} is much less than $\frac{LE}{T_{air}}$, we neglected \dot{S}_{LEmix} (Holdaway et al., 2010). The entropy flux of soil heat is calculated by the soil heat flux divided by the soil temperature at the system boundary (T_{soil}). Moreover, we neglected the entropy production associated with precipitation, subsurface transport of water and photosynthesis due to their small magnitudes (Brunsell et al., 2011; Kleidon and Schymanski, 2008). Therefore, entropy flux can be expressed as:

$$\dot{S}_{flux} = \frac{K_{in}}{T_{sun}} + \frac{L_{in}}{T_{sky}} - \frac{K_{out}}{T_{surf}} - \frac{L_{out}}{T_{surf}} - \frac{H}{T_{air}} - \frac{LE}{T_{air}} - \frac{G}{T_{soil}} \quad (5b)$$

Combined with Eqs. (2b), (4) and (5b), \dot{S}_{irrev} is given by

$$\dot{S}_{irrev} = \frac{dE/dt}{T_{surf}} - \frac{K_{in}}{T_{sun}} - \frac{L_{in}}{T_{sky}} + \frac{K_{out}}{T_{surf}} + \frac{L_{out}}{T_{surf}} + \frac{H}{T_{air}} + \frac{LE}{T_{air}} + \frac{G}{T_{soil}} \quad (6)$$

The magnitude of $\frac{dE}{dt}$ largely depends on the time scale of the data and energy closure of the system. Because we used the data at half-hour interval, the dynamic part of $\frac{dE}{dt}$ could not be neglected. Combining Eqs. (3) and (6) and eliminating $C \frac{dT_{surf}}{dt}$, we obtained the simplified form of \dot{S}_{irrev} :

$$\begin{aligned} \dot{S}_{irrev} = & K_{in} \left(\frac{1}{T_{surf}} - \frac{1}{T_{sun}} \right) + L_{in} \left(\frac{1}{T_{surf}} - \frac{1}{T_{sky}} \right) + H \left(\frac{1}{T_{air}} - \frac{1}{T_{surf}} \right) \\ & + LE \left(\frac{1}{T_{air}} - \frac{1}{T_{surf}} \right) + G \left(\frac{1}{T_{soil}} - \frac{1}{T_{surf}} \right) \end{aligned} \quad (7)$$

T_{sky} is estimated by the Stephan–Boltzmann law $L = \epsilon\sigma T^4$, where L is the long wave radiation flux, ϵ is the emissivity of the sky (approximately 0.73 according to Chen et al. (1991)), σ is Boltzmann constant, and T is the surface temperature.

$$T_{sky} = \left(\frac{L_{in}}{5.67 \times 10^{-8} \times 0.73} \right)^{1/4} \quad (8)$$

The total entropy production of an ecosystem can not reveal the thermodynamic efficiency, due to the change of biomass or net radiation of the ecosystem. Specific entropy production (s) thus was used to characterize exergy conversion efficiency.

$$s = \frac{\dot{S}_{irrev}}{R_n} \quad (9)$$

4. Results

4.1. Seasonal courses of thermodynamic indicators

Seasonal daily entropy production peaked in May, and showed a reduction in July, and the lowest value occurred in January (Fig. 2A). The entropy production induced by K_{in} and L_{in} (\dot{S}_{in} , the first two terms on the right side of Eq. (7)) was the main contribution to the total

entropy production, and followed the same trend as \dot{S}_{irrev} (Fig. 2B). As compared with \dot{S}_{in} , the entropy production induced by LE , H , and G (\dot{S}_e , the last three terms on the right side of Eq. (7)) was much less (Fig. 2B), therefore, the contribution of \dot{S}_e to the total entropy production could be neglected. Because K_{in} , L_{in} , T_{sun} , and T_{sky} were assumed to be constant, \dot{S}_{irrev} was positively correlated to the reciprocal of T_{surf} according to Eq. (10).

$$\dot{S}_{irrev} \approx \frac{1}{T_{surf}} (K_{in} + L_{in}) - \left(\frac{K_{in}}{T_{sun}} + \frac{L_{in}}{T_{sky}} \right) \quad (10)$$

Generally, the specific entropy production was lower during the rainy season and higher during the dry season ($P < 0.001$) of the tropical seasonal rain forest. It decreased from April and reached the lowest level during August and September (Fig. 3A). The entropy budget of the forest was positive and stable throughout the year (Fig. 3B).

4.2. Relationship between thermodynamic indicators and ecological parameters

The empirical data showed that entropy production decreased linearly with increasing T_{surf} , and that higher K_{in} produced more entropy (Fig. 4A). Entropy production linearly increased with net radiation (Fig. 4B).

5. Discussion

Our results showed that exergy destruction, entropy production, net radiation, and surface temperature are highly correlated. The same trend between entropy production, net radiation, and vegetation growth has also been observed in empirical studies (Aoki, 1989; Brunsell et al., 2011). As compared with exergy destruction and entropy production, net radiation and canopy surface temperature are more perceivable. Moreover, the measurements of net radiation and canopy surface temperature are more direct and accurate than those of the related indicators of entropy and exergy.

There have been many studies about the net radiation of ecosystems, which has been accepted as an integral index for assessing ecosystem status (Holst et al., 2005; Lafleur et al., 1998; Mccaughy, 1985; Moore, 1976). However, canopy surface temperature was generally studied as one of the important parameters correlated with energy conversion (Caselles et al., 1992; Richards, 2005; Wang et al., 2011) or as an indicator of drought stress (Pandey et al., 1984; Rashid et al., 1999; Suralta et al., 2013). Few studies related canopy surface temperature with ecosystem development until the maximum exergy destruction principle was proposed (Schneider and Kay, 1994; Schneider and Sagan, 2005). Under a given radiation environment, from the perspective of the first law of thermodynamics, a cooler surface emits less longwave radiation into the atmosphere than a warmer surface (Bastable et al., 1993; Dou et al., 2006; Wang et al., 2007), thus, more energy can be gained by the system (i.e., larger R_n). From the perspective of the second law of thermodynamics, a cooler surface radiates energy at a lower exergy level, thus the system can gain more exergy (Kay et al., 2001). Therefore, the canopy surface temperature reflects the efficiencies of both the first and the second laws of thermodynamics. Canopy surface temperature is primarily determined by radiation conditions, and it is impacted by multiple physical and physiological processes (e.g., G , H , and LE). Latent heat is induced by evapotranspiration, a process that cools the canopy. Sensible heat is related to the temperature difference and thermal conductance between canopy surface and atmosphere. It cools the canopy when the canopy is hotter than the air, whereas the opposite occurs when the canopy is cooler than the air. The direction of soil heat flux is determined by the temperature gradient between soil and air. The rate of temperature increase is related to the heat storage capacity of the forest, which is

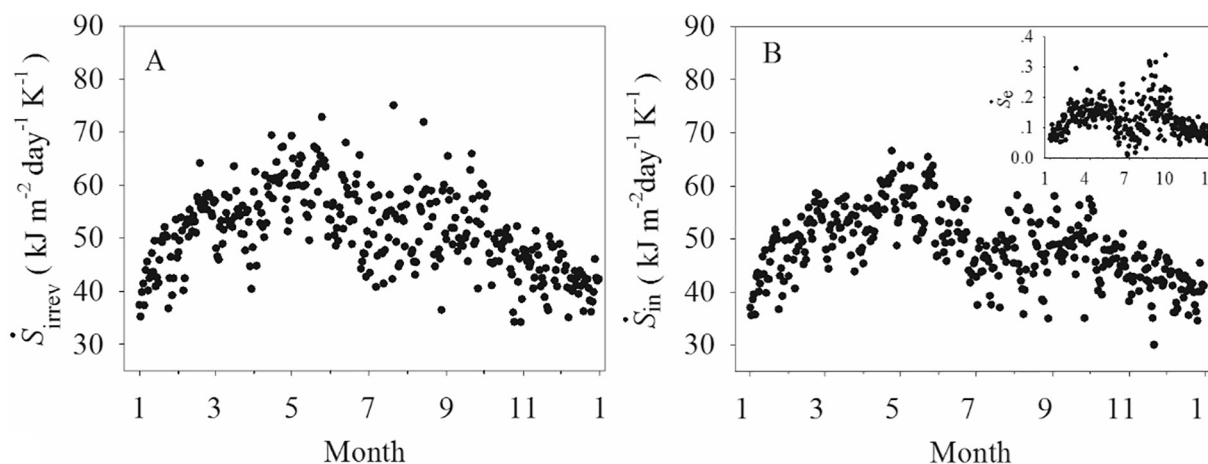


Fig. 2. Seasonal courses of A) total entropy production (\dot{S}_{irrev}) and B) entropy production induced by K_{in} and L_{in} (\dot{S}_{in}); the small figure on the top right shows the entropy production induced by LE , H , and G (\dot{S}_G).

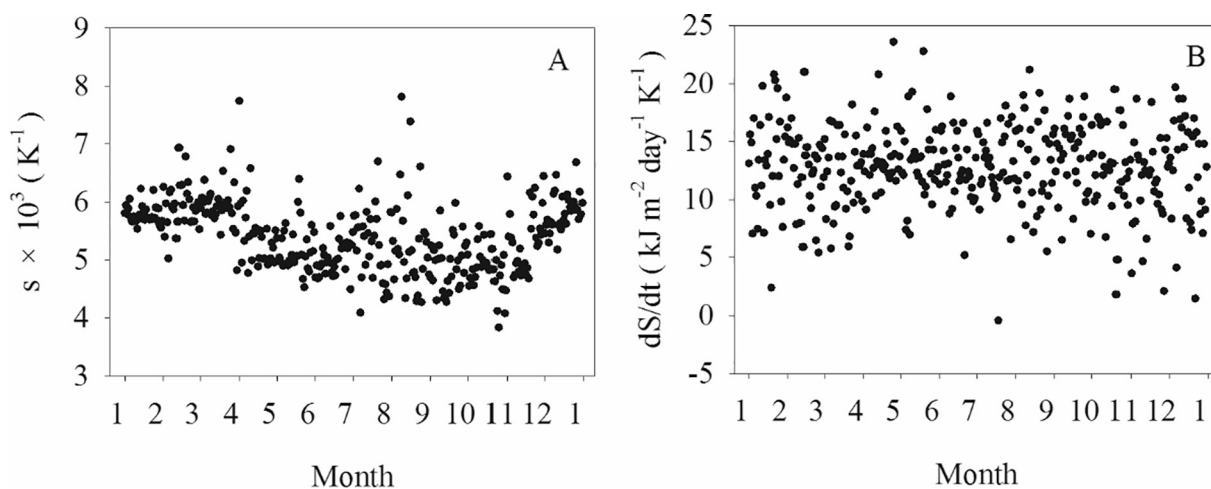


Fig. 3. Seasonal courses of A) specific entropy production (s) and B) entropy budget ($\frac{dS}{dt}$).

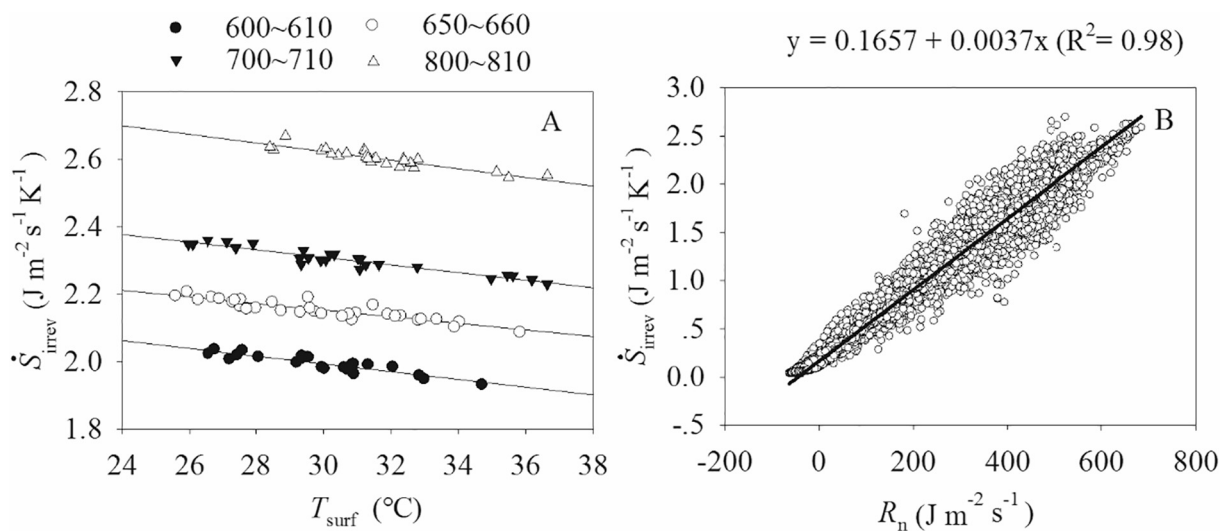


Fig. 4. A) Relationship between total entropy production (\dot{S}_{irrev}) and canopy surface temperature (T_{surf}) of the tropical seasonal rain forest under four levels of incoming shortwave radiation (K_{in}): 600–610, 650–660, 700–710, and 800–810 $J m^{-2} s^{-1}$. Incoming longwave radiation (L_{in}) was controlled at 450–460 $J m^{-2} s^{-1}$. Significant regression lines were shown in the figure ($P < 0.05$). B) Relationship between \dot{S}_{irrev} and net radiation (R_n).

largely determined by the biomass of the ecosystem (Gates, 2003). Thus, canopy temperature holistically reflects all these processes, and it has higher potential for characterizing the ecosystem than that of any of the heat fluxes. For example, evapotranspiration is efficient for cooling the canopy; however, its trend along ecosystem development is not consistent (Amiro et al., 2006; Engel et al., 2005; Jin et al., 2012; Licata et al., 2008; Lin et al., 2017). However, we have observed mono-increasing thermal response number (TRN, calculated by $R_n/\Delta T$) with ecosystem growth, succession, and recovery for twelve chronosequences of vegetation (Lin et al., 2017). It indicates that the more developed ecosystem can gain more energy, yet maintain lower canopy temperature.

Furthermore, the temporal and spatial pattern of R_n and T_{surf} are strongly dependent on weather conditions, e.g., incoming radiation, wind, and relative humidity (Maes and Steppe, 2012). Exclusion of the effects of changing conditions is a critical problem hindering the enhancement of their sensitivity to ecosystem status. Therefore, R_n/K_{in} , $R_n/(K_{\text{in}} + K_{\text{out}})$, thermal buffer capacity (TBC), and TRN have been proposed as surrogates for R_n and T_{surf} (Aerts et al., 2004; Lin et al., 2017; Maes et al., 2011). For instant measurements, $R_n/(K_{\text{in}} + K_{\text{out}})$ was recommended if all of the measurements were performed simultaneously (Maes et al., 2011). TRN at daily scale is more resistant to environmental impacts and more discriminative than R_n , T_{surf} , and R_n/K_{in} (Lin et al., 2017).

It is important to distinguish among the concepts of total entropy production, entropy flux, entropy budget, and specific entropy production. Schrödinger (1962) suggested that living organisms could maintain their low entropy (i.e., highly ordered) state by operating as open thermodynamic systems. Prigogine (1968) proposed that when there is an increase in input energy, the system will enhance overall energy dissipation (entropy production). It seems that these two viewpoints are in conflict; however, they represent two different concepts. The low entropy state in Schrödinger's statement referred to the "entropy budget" determined by the balance of entropy production and entropy flux, while the energy dissipation in Prigogine's statement was the "total entropy production". In the present study, the entropy budget remained stable throughout the year, because the increased entropy production was offset by outflow entropy flux. Many observations have confirmed the increase in total entropy production during the course of ecosystem succession, because more energy was dissipated in the ecosystem with the accumulation of biomass (Holdaway et al., 2010; Lin, 2015; Stoy et al., 2014). The entropy budget was reported decreasing with increasing vegetation fraction due to strong outgoing entropy fluxes (Brunsell et al., 2011). Although the total entropy production increased in the rainy season, the growth of biomass reduced the increment per unit of energy gain; consequently, the specific entropy production decreased in the rainy season. It represented an evidence for the maximum power or efficiency theory (Lotka, 1922; Odum and Pinkerton, 1955; Nielsen and Ulanowicz, 2000) and the least irreversibility theory which is known as the entropy generation minimization (EGM) method in the physics and engineering fields (Bejan, 1982; Bejan, 2013). As exergy destruction is proportional to entropy production, there are several ways to calculate exergy conversion efficiency, e.g., biomass-specific exergy, biomass-specific entropy production (Aoki, 1989; Prigogine, 1968; Jørgensen et al., 2000), radiation-specific exergy, or radiation-specific entropy production as applied in the present study. The system with higher exergy conversion efficiency should have lower specific entropy production and higher specific exergy. Any one of these indicators can be chosen based on the availability of data.

6. Conclusions

Our research provides theoretical and empirical support for the linearly negative relationship between total entropy production and canopy surface temperature, and the linearly positive relationship

between entropy production and net radiation. We therefore can use more perceivable and feasible indicators, i.e., canopy surface temperature, net radiation or indicators that combines the two variables, e.g., TRN, to characterize ecosystem status and development. Entropy production, entropy budget, and specific entropy production showed different trend with ecosystem development. It is important to distinguish these concepts, although all of them can be used to characterize ecosystem status. Our study improves the understanding of thermodynamic processes in the ecosystem and the application of thermodynamics in ecology study.

Acknowledgements

This study was funded by the Applied Fundamental Research Program of Yunnan Province (2013FB078), National Natural Science Foundation of China (NSFC, 31200307) and the CAS 135 Program (No. 2017XTBG-F01). We thank Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (XSTRE) and Chinaflux for data management.

References

- Aerts, R., Wagendorp, T., November, E., Behailu, M., Deckers, J., Muys, B., 2004. Ecosystem thermal buffer capacity as an indicator of the restoration status of protected areas in the northern Ethiopian highlands. *Restor. Ecol.* 12, 586–596.
- Akbari, M.H., 1995. Energy-Based Indicators of Ecosystem Health. Department of Crop Science, University of Guelph, Guelph, Canada.
- Amiro, B.D., Barr, A.G., Black, T.A., Iwashita, H., Kljun, N., McCaughey, J.H., Morgenstern, K., Murayama, S., Nestic, Z., Orchansky, A.L., Saigusa, N., 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. *Agric. For. Meteorol.* 136, 237–251.
- Aoki, I., 1989. Hological study of lakes from an entropy viewpoint – Lake Mendota. *Ecol. Model.* 45, 81–93.
- Bastable, H.G., Shuttleworth, W.J., Dallarosa, R.L.G., Fisch, G., Nobre, C.A., 1993. Observations of climate, albedo, and surface radiation over cleared and undisturbed Amazonian forest. *Int. J. Climatol.* 13, 783–796.
- Bejan, A., 1982. *Entropy Generation Through Heat and Fluid Flow*. Wiley-Interscience, New York, USA.
- Bejan, A., 2013. Entropy generation minimization, exergy analysis, and the constructal law. *Arab. J. Sci. Eng.* 38, 329–340.
- Bertram, J., 2014. Maximum entropy models of ecosystem functioning. In: *Bayesian Inference and Maximum Entropy Methods in Science and Engineering*, Maxent 2013, pp. 131–136.
- Brunsell, N.A., Schymanski, S.J., Kleidon, A., 2011. Quantifying the thermodynamic entropy budget of the land surface: is this useful? *Earth Syst. Dyn.* 2, 87–103.
- Cao, M., Zou, X.M., Warren, M., Zhu, H., 2006. Tropical forests of Xishuangbanna, China. *Biotropica* 38, 306–309.
- Caselles, V., Sobrino, J.A., Coll, C., 1992. A physical model for interpreting the land surface-temperature obtained by remote sensors over incomplete canopies. *Remote Sens. Environ.* 39, 203–211.
- Cengel, Y.A., Boles, M.A., 2014. *Thermodynamics: An Engineering Approach*. McGraw-Hill Education, New York, USA.
- Chapman, E.J., Childers, D.L., Vallino, J.J., 2016. How the second law of thermodynamics has informed ecosystem ecology through its history. *Bioscience* 66, 27–39.
- Chen, B., Kasher, J., Maloney, J., Clark, D., May, W., 1991. Determination of the clear sky emissivity for use in cool storage roof and roof pond applications. In: *American Solar Energy Society – Proceedings*, Denver, USA.
- Dou, J.X., Zhang, Y.P., Zhao, S.J., Song, Q.H., 2006. Characteristics of radiation at different heights with the canopy of a tropical seasonal rain forest in Xishuangbanna, SW China. *J. Beijing For. Univ.* 28, 15–21.
- Dou, J.X., Zhang, Y.P., Yu, G.R., Zhong, S.J., Song, Q.H., 2007. Inter-annual and seasonal variations of energy and water vapour flux above a tropical seasonal rain forest in Xishuangbanna, SW China. *Acta Ecol. Sin.* 27, 3100–3109.
- Engel, V., Jobbagy, E.G., Stieglitz, M., Williams, M., Jackson, R.B., 2005. Hydrological consequences of eucalyptus afforestation in the Argentine pampas. *Water Resour. Res.* 41, W10409.
- Fath, B.D., Jørgensen, S.E., Patten, B.C., Straskraba, M., 2004. Ecosystem growth and development. *Biosystems* 77, 213–228.
- Fraser, R.A., Kay, J.J., 2002. *Exergy Analysis of Eco-Systems: Establishing a Role for the Thermal Remote Sensing*. Taylor & Francis, London, UK.
- Gates, D.M., 2003. *Biophysical Ecology*. Springer Verlag, Heidelberg and Berlin/New York, USA.
- Gu, L., Meyers, T., Pallardy, S.G., Hanson, P.J., Yang, B., Heuer, M., Hosman, K.P., Liu, Q., Riggs, J.S., Sluss, D., Wullschlegel, S.D., 2007. Influences of biomass heat and biochemical energy storages on the land surface fluxes and radiative temperature. *J. Geophys. Res.* 112, D02107.
- Holdaway, R.J., Sparrow, A.D., Coomes, D.A., 2010. Trends in entropy production during ecosystem development in the Amazon Basin. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 1437–1447.
- Holst, T., Rost, J., Mayer, H., 2005. Net radiation balance for two forested slopes on

- opposite sides of a valley. *Int. J. Biometeorol.* 49, 275–284.
- Jørgensen, S.E., 2007. Description of aquatic ecosystem's development by eco-exergy and exergy destruction. *Ecol. Model.* 204, 22–28.
- Jørgensen, S.E., Patten, B.C., Straškraba, M., 2000. Ecosystems emerging: 4. Growth. *Ecol. Model.* 126, 249–284.
- Jin, Y.F., Randerson, J.T., Goulden, M.L., Goetz, S.J., 2012. Post-fire changes in net shortwave radiation along a latitudinal gradient in boreal North America. *Geophys. Res. Lett.* 39, L13403.
- Kay, J.J., Allen, T., Fraser, R., Luvall, J.C., Ulanowicz, R., 2001. Can we use energy based indicators to characterize and measure the status of ecosystems, human, disturbed and natural? In: *Proceedings of the International Workshop: Advances in Energy Studies: Exploring Supplies, Constraints and Strategies, 23–27 May 2000, Porto Venere, Italy*, pp. 2121–2133.
- Kleidon, A., 2009. Maximum entropy production and general trends in biospheric evolution. *Paleontol. J.* 43, 980–985.
- Kleidon, A., Schymanski, S., 2008. Thermodynamics and optimality of the water budget on land: a review. *Geophys. Res. Lett.* 35, 67–78.
- Lafleur, P.M., McCaughey, J.H., Bartlett, P.A., Strachan, I.B., 1998. Observations of the micrometeorology of two forests in eastern Canada: 1. Interannual variations in summer radiation and energy balance. *Can. J. For. Res.* 28, 514–523.
- Licata, J.A., Gyenge, J.E., Fernandez, M.E., Schlichter, T.A., Bond, B.J., 2008. Increased water use by ponderosa pine plantations in northwestern Patagonia, Argentina compared with native forest vegetation. *For. Ecol. Manage.* 255, 753–764.
- Lin, H., 2015. Thermodynamic entropy fluxes reflect ecosystem characteristics and succession. *Ecol. Model.* 298, 75–86.
- Lin, H., Cao, M., Stoy, P.C., Zhang, Y.P., 2009. Assessing self-organization of plant communities – a thermodynamic approach. *Ecol. Model.* 220, 784–790.
- Lin, H., Cao, M., Zhang, Y.P., 2011. Self-organization of tropical seasonal rain forest in southwest China. *Ecol. Model.* 222, 2812–2816.
- Lin, H., Fan, Z., Shi, L., Arain, A., McCaughey, H., Billesbach, D., Siqueira, M., Bracho, R., Oechel, W., 2017. The cooling trend of canopy temperature during the maturation, succession, and recovery of ecosystems. *Ecosystems* 20, 406–415.
- Lotka, A.J., 1922. Contribution to the energetics of evolution. *Proc. Natl. Acad. Sci. U.S.A.* 8, 147–151.
- MacArthur, R.H., Wilson, E.O., 1967. *Theory of Island Biogeography*. Princeton University Press, Princeton, USA.
- Maes, W.H., Pashuysen, T., Trabucco, A., Veroustraete, F., Muys, B., 2011. Does energy dissipation increase with ecosystem succession? Testing the ecosystem exergy theory combining theoretical simulations and thermal remote sensing observations. *Ecol. Model.* 222, 3917–3941.
- Maes, W.H., Steppe, K., 2012. Estimating evapotranspiration and drought stress with ground-based thermal remote sensing in agriculture: a review. *J. Exp. Bot.* 63, 4671–4712.
- McCaughey, J.H., 1985. A radiation and energy-balance study of mature forest and clear-cut sites. *Bound. Lay. Meteorol.* 32, 1–24.
- Moore, C.J., 1976. Comparative study of radiation balance above forest and grassland. *Q. J. R. Meteorol. Soc.* 102, 889–899.
- Nielsen, S.N., Ulanowicz, R.E., 2000. On the consistency between thermodynamical and network approaches to ecosystems. *Ecol. Model.* 132, 23–31.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Odum, H.T., Pinkerton, R.C., 1955. Times speed regulator – the optimum efficiency for maximum power output in physical and biological systems. *Am. Sci.* 43, 331–343.
- Pandey, R.K., Herrera, W.A.T., Pendleton, J.W., 1984. Drought response of grain legumes under irrigation gradient: 2. Plant water status and canopy temperature. *Agron. J.* 76, 553–557.
- Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession. *Trends Ecol. Evol.* 26, 119–123.
- Prigogine, I., 1968. *Introduction to Thermodynamics of Irreversible Processes*, 3rd ed. Interscience Publishers, New York, USA.
- Rashid, A., Stark, J.C., Tanveer, A., Mustafa, T., 1999. Use of canopy temperature measurements as a screening tool for drought tolerance in spring wheat. *J. Agron. Crop Sci.* 182, 231–237.
- Richards, K., 2005. Urban and rural dewfall, surface moisture, and associated canopy-level air temperature and humidity measurements for Vancouver, Canada. *Bound. Lay. Meteorol.* 114, 143–163.
- Schneider, E.D., Kay, J.J., 1994. Life as a manifestation of the 2nd law of thermodynamics. *Math. Comput. Model.* 19, 25–48.
- Schneider, E.D., Sagan, D., 2005. *Into the Cool: Energy Flow, Thermodynamics, and Life*. University of Chicago Press, Chicago, USA.
- Schrödinger, E., 1962. *What is Life? The Physical Aspect of the Living Cell*. Cambridge University Press, Cambridge, UK.
- Stoy, P.C., Lin, H., Novick, K.A., Siqueira, M.B.S., Juang, J.Y., 2014. The role of vegetation on the ecosystem radiative entropy budget and trends along ecological succession. *Entropy-Switz* 16, 3710–3731.
- Suralta, R.R., Gaid, L.L., Julaton, M.C.N., Vizmonte, P.T., 2013. Relationship between root system developmental responses and soil water uptake, and canopy temperature estimates based on thermal image in rice under drought stress. *Philipp. Agric. Sci.* 96, 301–307.
- Svirezhev, Y.M., 2000. Thermodynamics and ecology. *Ecol. Model.* 132, 11–22.
- Wang, X., Zhou, G.Y., Sun, G., Zhou, C.Y., Wang, C.L., 2007. Study on outside radiation flux of coniferous and broad-leaved mixed forest ecosystem at Dinghushan in south China. *J. Zhejiang Univ.* 328–337.
- Wang, Z.H., Bou-Zeid, E., Smith, J.A., 2011. A spatially-analytical scheme for surface temperatures and conductive heat fluxes in urban canopy models. *Bound. Lay. Meteorol.* 138, 171–193.