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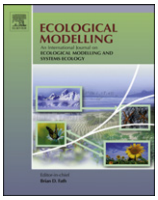

Self-organization of tropical seasonal rain forest in southwest China

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ABSTRACT

How to measure development of ecosystems is both a theoretical and practical question in ecology. Species richness and biomass accumulation are familiar figures of merit, but they cannot be instant watched. Self-organization is a tacit character. However, methods to measure the degree of self-organization of ecosystem are problematic. To this end Lin et al. (2009) have devised indicators of energy capture and dissipation so that self-organization defined via maximum energy dissipation can be quantified easily. Here the method is used to analyze long-term data (2004–2006) of a tropical seasonal rain forest included in the ChinaFLUX program. Three years of average self-organization values were clearly separated by seasonal variation. Reflection and long wave radiation are the main two pathways of energy loss. For tropical seasonal rain forest studied, long wave radiation contributed most to energy loss, and was negatively correlated with energy capture ability (*Rn*/DR). The nocturnal difference between canopy and air temperatures had a strong negative correlation with the long wave radiation loss ratio. However, the long wave radiation loss ratio was slightly lower than the reflection loss ratio in rainy season, when values were very low. Precipitation and wind had significant impact on energy dissipation ability in the hot dry season, but the correlation coefficients between precipitation and wind with thermal response numbers (TRNs) were very low. The results indicated that the self-organization estimation system based on "maximum energy dissipation theory" is applicable for tropical forest.

1. Introduction

Self-organization is one of the most important advances in modern nonlinear and nonequilibrium thermodynamic study. Self-organization phenomenon has been well known in chemical reactions and physical phase transitions as B.Z. reactions (Zhabotinsky, 1964; Rossi et al., 2009; Belousov, 1958) and the Bénard cell (Rayleigh, 1916). Many achievements in self-organization theory have been made in chemistry and physics, due to the advantages of studying controllable systems (Borckmans et al., 1987; Chinake and Simoyi, 1997; Rossi et al., 2008). Ecosystems are usually extremely dynamic and complex, so they present difficulties for the application of self-organization theory.

Self-organization is process in which systems become more highly organized over time without being ordered by outside agents or by external programs (Ashby, 1945). From thermodynamic viewpoint, self-organized systems can spontaneously exchange material, energy and information with environment to reduce the entropy in the system (Nicolis and Prigogine, 1977). Ecosystems acquire different amount of energy from the same insolation when the ecosystems differ from each by their machinery to capture radiation. Potential differences (gradients) are the powers to generate current. For example, voltage drives current and temperature difference drives convection. Similarly, different energy capture ability generates distinct potential difference in ecosystems and drives different evolution process (Annila and Annila, 2008). Energy dissipates when it flows and transforms within a forest ecosystem (Würtz and Annila, 2010). Instead of the elastic scattering of light, ecosystems absorb light through photosynthesis and transduce sunlight (high quality) into infrared thermal energy (low quality). Energy absorption in place of elastic scattering increases the heat-transporting capacity by a factor of $\sim 10^9$ for each atom acting as an absorber (Hoelzer et al., 2006). Schneider and Kay (1994) took ecosystem as Rayleigh–Bénard convection system and proposed that in the same environment, when ecosystems received equal amount of radiation, the more developed or organized ecosystem attempts to capture more solar energy and dissipates this energy against a larger energy gradient. Thus, the more developed ecosystem should have lower canopy temperature. This hypothesis is in accordance with the Stephan–Boltzmann law ($\mathrm{ULR} = \varepsilon\delta T_c^4$), where long wave (infrared) radiation (ULR) is quartic with canopy temperature T_c. That is to say, the lower canopy temperature, the less long wave radiation lost.

Lin et al. (2009) developed thermodynamic indicators of energy capture and dissipation to quantify the degree of self-organization. These indicators of ecosystem's operational self-organization are

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particularly useful for studies of complex terrestrial ecosystems. Tropical seasonal rain forest is the primary vegetation distributed in lowlands and wet valleys in Xishuangbanna, China. It has multiple vertical structures and high species diversity. These attributes of the complex forest ecosystem make the use of information, ascendency or exergy storage perspectives to study self-organization inapplicable. Therefore, the method based on maximum energy dissipation theory (Schneider and Kay, 1994) shows predominant advantage. From 2003, the ChinaFLUX research project was launched in a permanent tropical seasonal rain forest plot. Long-term ecological monitoring data have been collected, allowing for the calculation of several years' self-organization possible. The present study provides a model to simulate long-term self-organization dynamics with data commonly obtained in long-term ecological research networks. Besides, this study tests the sensitivity and applicability of these indicators to seasonal variation of tropical seasonal forest.

2. Methods

2.1. Study site

Xishuangbanna is on the northernmost edge of tropical Asia, where the tropical and subtropical floras intermingle. Annual mean temperature is 21.8 °C and the average minimum annual temperature is 7.5 °C. Annual precipitation averages 1557 mm, of which 85% occurs during the May–October rainy season. The November–April dry season comprises both a cool dry season from November to February and a hot dry season from March to April. The cool dry season is characterized by relatively low temperatures and heavy fog during the night and throughout the morning. The hot dry season is dry and hot during the afternoon with fog occurring in the morning only. Tropical seasonal rain forest is the most luxuriant forest in Xishuangbanna and is mainly distributed in the wet valleys, usually with small streams or on the low hills and flats below 1000 m altitude. The study site (21°57′ N, 101°12′ E, 750 m asl) is located in Menglun, Xishuangbanna, and is a permanent plot dedicated to long-term ecological research, managed by Xishuangbanna Tropical Botanical Garden. The plot is also part of the ChinaFLUX long-term ecological monitoring project. The overstory can exceed 40 m in height, the upper-midstory is between 16 and 30 m and the lower-midstory are classified as plants under 16 m. Shrubs and herbs are abundant in the understory. Dominant species are *Pometia tomentosa*, *Barringtonia macrostachya* and *Gironniera subaequalis* (Cao et al., 1996). The soil in the area is laterite (Cao et al., 2006).

2.2. Instruments and measurements

All measurements were made on a 72 m meteorological tower constructed in the study site. Our data were obtained from the record of a meteorology gradient system which is installed on the tower with air temperature and relative humidity sensors (HMP45C) installed at heights of 4.2, 16.3, 26.2, 36.5, 42.0, 48.8 and 69.8 m. Canopy temperature (T_c) was measured with an infrared thermometer mounted at 52 m. Net radiation (Rn), global radiation (DR), reflective radiation (UR), upward long wave radiation (ULR) and downward long wave radiation (DLR) was measured with a 4-component method (CM11, KIPP & ZONEN, Netherlands) at 41.6 m above the ground. All variables were automatically sampled at 0.5 Hz, and the 30 min averages were calculated and output to data loggers. Monitoring was initiated in November 2002, and the data from 2004 to 2006 were used for this study. Leaf area index (LAI, the ratio of total upper leaf surface of vegetation divided by the surface area of the land on which the vegetation grows) started to be measured with LAI-2000 (LI-COR, Lincoln, America) every month since Dec., 2003.

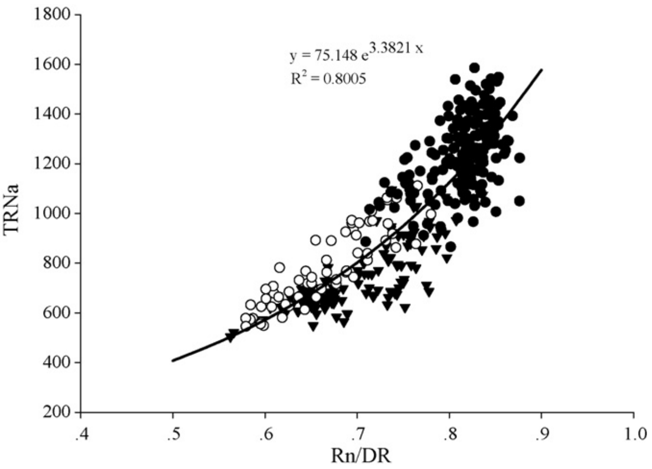

Fig. 1. Average annual pattern of self-organization. (▼) Cool dry season; (○) hot dry season; (●) rainy season.

2.3. Data analysis

Occasionally, measurements of the climatic variables failed for unexpected reasons. In those cases, a linear interpolation approach was used to insert missing data which were within a 2 h time gap. Missing data for longer time periods were interpolated based on specific regression equations of the concerned factors.

Thermal response number of canopy temperature (TRNc) and canopy air temperature (at 36.5 m) (TRNa) were calculated as $\sum_{t_1}^{t_2} Rn(\Delta t)/\Delta T$, where $\sum_{t_1}^{t_2} Rn(\Delta t)$ is the net radiation Rn over the time interval Δt, and ΔT is temperature variation over Δt, chosen here to be 1 day. The average canopy height is 35 m, so we used wind speed, relative humidity (RH) at 42 m and air temperature at 69.8 m to analyze the fluctuation of environmental factors.

3. Results

3.1. Self-organization patterns

The 3-year average energy dissipation ability was exponentially related to energy capture ability ($R^2 = 0.80$), indicating that the higher energy capture ability, the rate of energy dissipation increases. However after Rn/DR reaches a maximum, TRN can continue to increase. There was an obvious seasonal pattern in self-organization, with the three seasons (rainy, cool dry, hot dry) easily distinguished (Fig. 1). Self-organizations in the rainy season were all located on the top of the regression line indicating that the forest was highly self-organized during this period. Self-organizations in the hot dry season concentrated in the left bottom. And those in cool dry season occupied the right middle (Fig. 1). TRNas in cool dry season were significantly higher than in the hot dry season (one-way ANOVA, $P = 0.016$).

3.2. Seasonal fluctuation of climate factors and leave area index (LAI)

Climate factors fluctuated with the seasons. The hot dry season was characterized by high diurnal temperature and large daily extreme temperature difference, accompanied with low relative humidity. The diurnal temperature was lower in the wet season than in the hot dry season because of the cooling effect of rainfall, but nocturnal temperature was higher compared to the other seasons. The forest had the lowest daily extreme temperature difference and highest relative humidity in the rainy season. In terms of humidity, cool dry season is a transition season between rainy

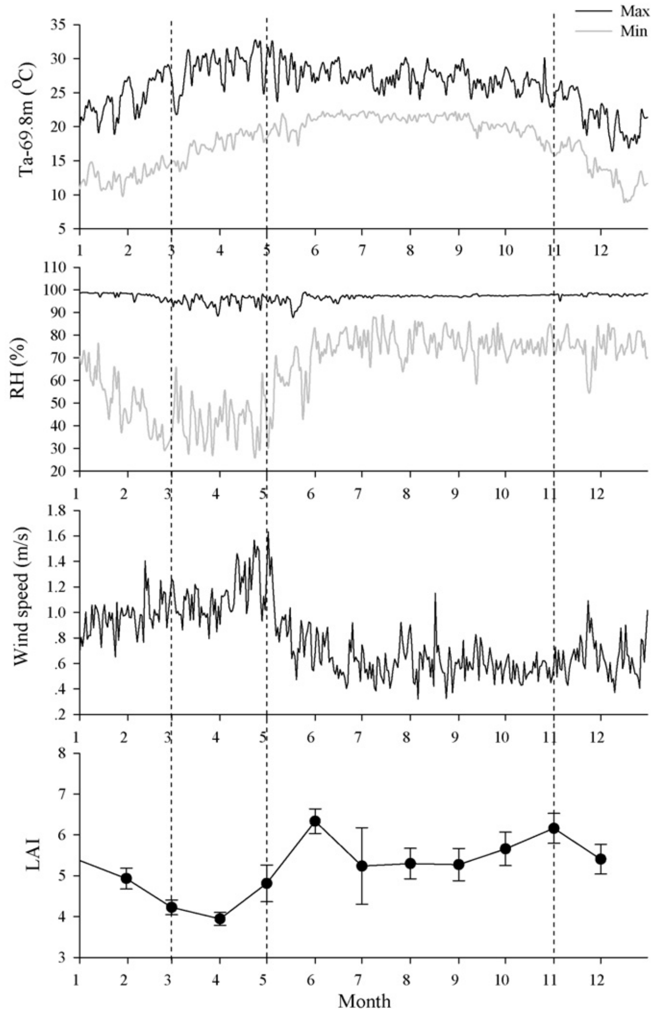

Fig. 2. Average annual fluctuations of environmental factors and LAI.

and hot dry seasons. Temperature is also lower during the cool dry season. The nocturnal temperature reaches below 15 °C from December to February, and is associated with defoliation for some tree species. Accordingly, LAI started decreasing in November and reached a minimum in April (Fig. 2).

3.3. Factors affecting energy capture ability

The lowest energy capture ability occurred during the hot dry season, which coincided with the period of lowest LAI. This result and the slight increase of reflection rate during the hot dry season demonstrate a structural limitation of energy capture (Fig. 3). Although LAI in the cool dry season was not significantly lower than in the rainy season (Fig. 2), low temperature reduced the physiological energy capture ability of the canopy. Long wave radiation loss rates were high during hot dry and cool dry seasons. For the tropical seasonal rain forest, long wave radiation contributed to the major part of energy loss during hot dry and cool dry season. I/DR was lower than UR/DR during rainy season, but the values were very low (Fig. 3). So long wave radiation ratio has a strong negative relationship with energy capture ability (Pearson correlation = −0.862, $P < 0.001$). During day the forest canopy was heated by radiation, but at night it was cooler than the air because of the long wave radiation loss. Accordingly, there was a larger nocturnal temperature difference between the canopy and air in cool dry and hot dry season than in rainy season (Fig. 4). Nocturnal temperature difference was strongly negatively correlated with I/DR (Pearson correlation = −0.897, $P = 0.000$).

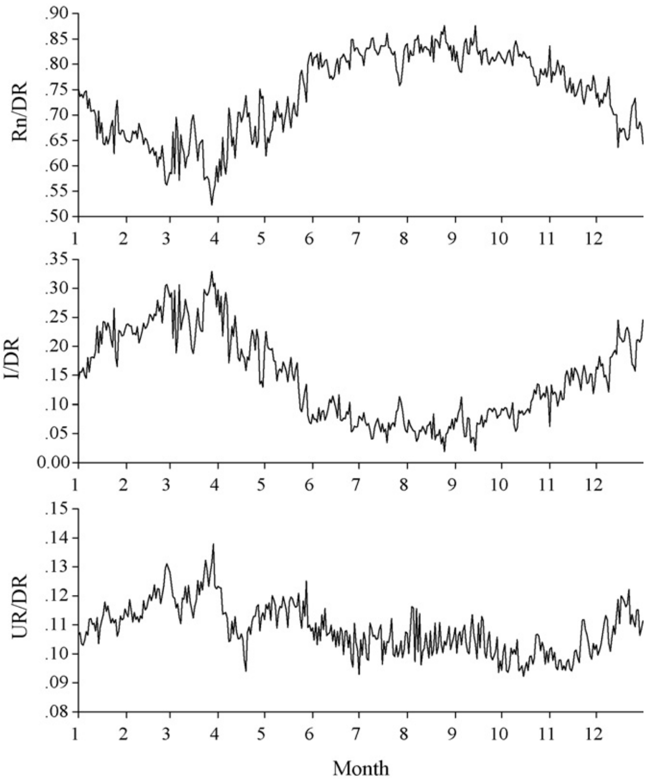

Fig. 3. Average annual fluctuations of net radiation/global radiation (*Rn*/DR), net long wave radiation/global radiation (I/DR) and reflective radiation/global radiation (UR/DR).

3.4. The relationship between TRNc and TRNa

The TRNa was calculated using the canopy air temperature at 36.5 m and was significantly higher than TRNc ($P < 0.05$) (Fig. 5). The difference between TRNa and TRNc was positively correlated with TRNa (Pearson correlation = 0.765, $P = 0.000$), and TRNc and TRNa exhibited the same seasonal trend. The strong linear positive relationship ($R^2 = 0.94$; Fig. 6) between the two variables indicates that TRNc can be calculated from TRNa

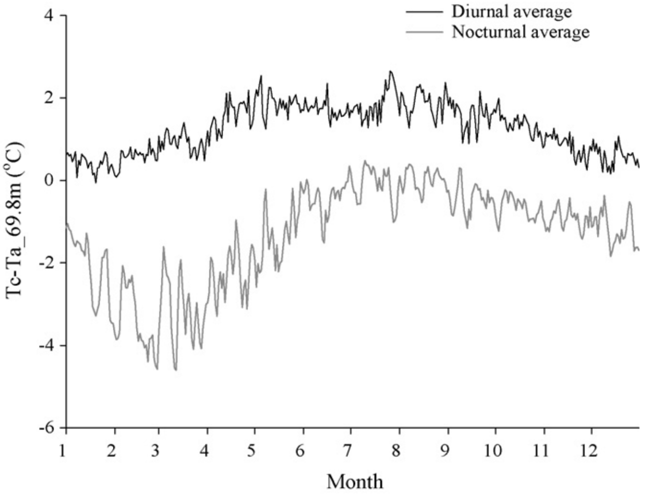

Fig. 4. Diurnal and nocturnal averaged temperature difference between canopy and air at 69.8 m.

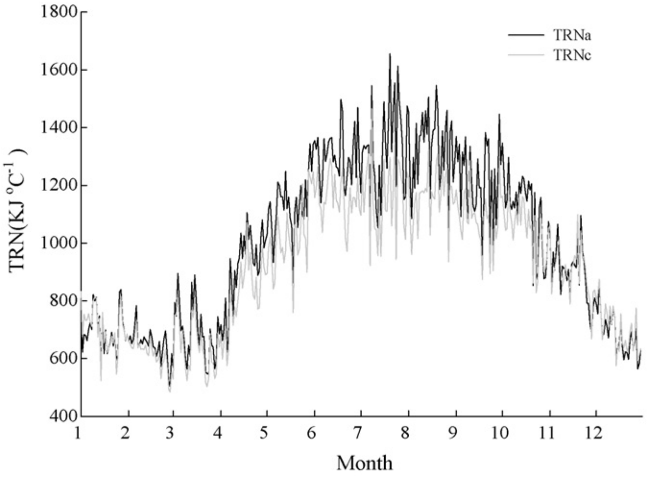

Fig. 5. Average annual fluctuations of TRNa and TRNc.

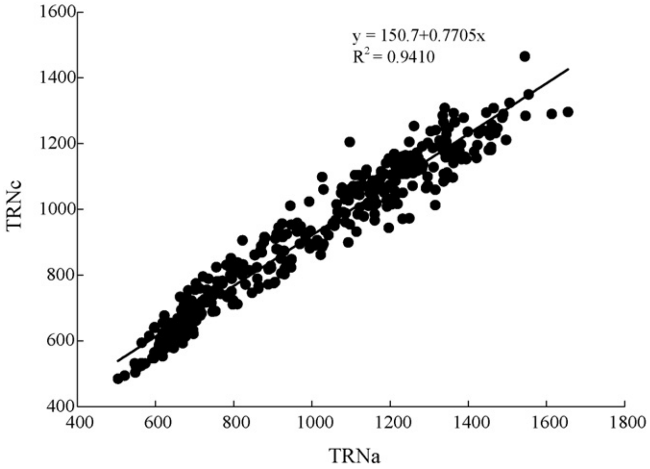

Fig. 6. Regression relationships between TRNa and TRNc.

with the equation: TRNc = 150.7 + 0.7705 × TRNa for the studied forest.

3.5. The impact of wind and precipitation on TRN

Precipitation and wind significantly correlated with TRNa and TRNc in the hot dry season, although the correlation coefficients were quite low. During the hot dry season, self-organization was weaker than in the other seasons, and was more sensitive to environmental conditions (Table 1).

4. Discussion

The tropical seasonal rain forest studied is located on the northern edge of the tropics, and has clear seasonal patterns. Some defoliation begins in the cool dry season in November. Although we can observe the phenomenon, it is difficult to determine changes of ecosystem function quantitatively because of "triple uncertainty" (Barkmann and Windhorst, 2000): (1) we do not have sufficient knowledge of how the ecological fabric of most ecosystems on earth is woven, nor can we be confident that our models already account for all relevant risk events or risk categories (epistemic uncertainty). (2) Because of system complexity and system stochastic, we do not know how environmental change will alter the global ecological baselines (stochastic uncertainty). (3) We do not know how the ecological needs and demands of humankind will change in the long run (social uncertainty).

There are various indicators to measure ecosystem self-organization. Some researchers hold that certain relationships occur between biodiversity and ecosystem function (Tilman et al., 1997; Wardle et al., 1997; Hooper and Vitousek, 1997). However, there is no simple correlation between diversity and the actual degree of ecological self-organization. On the other hand, biomass and productivity reflect the status of exergy storage which is an important index to measure the distance from thermodynamic equilibrium (Jørgensen, 2002). Biomass and productivity can also buffer gradients of change in the ecosystem. Productivity/respiration rate (P/R), productivity/biomass (P/B), and respiration rate/biomass (R/B) were proposed as indicators of self-organization. P/R represents the ratio of input and output. With ecosystem development, input and output will theoretically reach a dynamic equilibrium, so P/R approaches to 1. P/B reflects the turn over rate; the more developed ecosystem has a lower P/B rate (Odum, 1969, 1971). R/B is supposed to measure the entropy increase rate (Aoki, 2006). Although useful, these indicators are highly time and labor intensive to acquire the data necessary to calculate self-organization when used to study forests. Alternatively, Rn/DR indicates the energy capture ability, and TRN, canopy temperature T_c and transpiration/evaporation are indicators of energy dissipation (Schneider and Kay, 1994; Kutsch et al., 2001). Although Kutsch et al. (2001) obtained unexpected results using Rn/DR and T_c, as an indicator of self-organization, the discrepancy was likely due to their study methods. They calculated Rn as: $Rn = (1-\alpha)\phi K$, where α represents the albedo of the site, ϕ the coefficient representing the slope of the site, and K the total radiation (W m^{-2}). They neglected the long wave radiation loss which is a major portion of the energy balance as showed in Fig. 3. Reflection ratio has a close relationship with vegetation coverage, as lower ratios may occur for dense grassland than that of sparse forest (Lin, 2009). Also, T_c is not only affected by evaportranspiration but also by incoming radiation. Due to these factors, it is likely impossible to find two

Table 1
Two-tailed partial correlation analysis (SPSS 13.0) results of the wind and precipitation impact on TRN ($P < 0.05$ is considered significant difference).

Year	Season	Significance				Correlation			
		Precipitation		Wind		Precipitation		Wind	
		TRNc	TRNa	TRNc	TRNa	TRNc	TRNa	TRNc	TRNa
2004	Cool dry								
2005		0.005	0.001			0.256	0.300		
2006									
2004	Hot dry	0.001	0.001	0.001		0.412	0.405	0.414	
2005		0.000		0.010	0.000	0.497		0.343	0.452
2006		0.000	0.000	0.003	0.000	0.559	0.539	0.382	0.520
2004	Rainy								
2005									
2006			0.048		0.002		0.150		0.237

ecosystems under the same radiation environment. Therefore, TRN is a more intrinsic variable than T_c when comparing several ecosystems. For poorly self-organized ecosystems, TRN is vulnerable to the environmental factors. This suggests that when comparing poorly self-organized ecosystems, the impact of wind and precipitation should be avoided. Still, more studies are necessary which assess the effects of environmental conditions on TRN. The long-term self-organization found here was in accordance to the short term results reported by Lin (2009). The tropical seasonal rain forest was highly self-organized in the rainy season. The distances between seasonal self-organization values in the rainy season and the other two seasons were much longer than the distance between the hot dry and cool dry season. The results from this study indicate that using TRN and energy capture ability (Rn/DR) is a suitable method for the rapid assessment of ecosystem self-organization, and also for remote monitoring.

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Contributions: Hua Lin was involved in conceiving the study, data analysis and writing the paper. Min Cao applied this project, get fund from national natural science foundation of China and revised the paper. Yiping Zhang provided the data and gave valuable suggestions on data analysis.

References

Annila, A., Annila, E., 2008. Why did life emerge? J. Astrobiol. 7, 293–300.

Ashby, W.R., 1945. The physical origin of adaptation by trial and error. J. Gen. Psychol. 32, 13–25.

Aoki, I., 2006. Min–max principle of entropy production with time in aquatic communities. Ecol. Complex 3, 56-53.

Barkmann, J., Windhorst, W., 2000. Hedging our bets: the utility of ecological integrity. In: Joergensen, S.E., Muller, F. (Eds.), Handbook of Ecosystem Theories and Management. Lewis, Boca Raton, pp. 497–517.

Belousov, B.P., 1958. A Periodic Reaction and its Mechanism. Sbornik Referatov po Radiatsonno Meditsine. Medgiz, Moscow, pp. 145–147.

Borckmans, P., Dewel, G., Walgraef, D., Katayama, D., 1987. The search for turing structures. J. Stat. Phys. 48, 1031–1044.

Cao, M., Zhang, J.H., Feng, Z.L., Deng, J.W., Deng, X.B., 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, Southwest China. Trop. Ecol. 37, 183–192.

Cao, M., Zou, X.M., Warren, M., Zhu, H., 2006. Tropical forests of Xishuangbanna, China. Biotropica 38, 306–309.

Chinake, C.R., Simoyi, R.H., 1997. Experimental studies of spatial patterns produced by diffusion–convection–reaction systems. J. Chem. Soc. Faraday Trans. 93, 1345–1350.

Hoelzer, G.A., Pepper, J.W., Smith, E., 2006. On the logical relationship between natural selection and self-organization. J. Evol. Biol. 19, 1785–1794.

Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277, 1302.

Jørgensen, S.E., 2002. Integration of Ecosystem Theories: A Pattern. Kluwer Academic Publishers, Netherlands.

Kutsch, W.L., Steinborn, W., Herbs, M., Baumann, R., Barkmann, J., Kappen, L., 2001. Environmental indication: a field test of an ecosystem approach to quantify biological self-organization. Ecosystems 4, 49–66.

Lin, H., 2009. Study on the self-organization ability of different plant communities in Xishuangbanna—based on thermodynamic theory. Forest function and dynamic research group. Xishuangbanna tropical botanical garden, Mengla. p. 44.

Lin, H., Cao, M., Stoy, P.C., Zhanga, Y., 2009. Assessing self-organization of plant communities—a thermodynamic approach. Ecol. Model. 220, 784–790.

Nicolis, G., Prigogine, I., 1977. Self-organization in Non-equilibrium System, From Dissipative Structures to Order Through Fluctuations. Wiley, New York.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Odum, E.P., 1971. Fundamentals of Ecology. Saunders, Philadelphia.

Rayleigh, L., 1916. On convection currents in a horizontal layer of fluid when the higher temperature is on the other side. Philos. Mag. J. 32, 529–543.

Rossi, F., Liria, M., Liveri, T., 2009. Chemical self-organization in self-assembling biomimetic systems. Ecol. Model. 220, 1857–1864.

Rossi, F., Lombardo, R., Sciascia, L., Sbriziolo, C., Liveri, M.L.T., 2008. Spatio-temporal perturbation of the dynamics of the ferroin catalyzed Belousov–Zhabotinsky reaction in a batch reactor caused by sodium dodecyl sulfate micelles. J. Phys. Chem. B 112, 7244–7250.

Schneider, E.D., Kay, J.J., 1994. Life as a manifestation of the second law of thermodynamics. Math. Comput. Model. 19, 25–48.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Wardle, D.A., Zackrisson, O., Hornberg, G., Gallet, C., 1997. The influence of island area on ecosystem properties. Science 277, 1296.

Würtz, P., Annila, A., 2010. Ecological succession as an energy dispersal process. Biosystems 100, 70–78.

Zhabotinsky, A.M., 1964. Periodic liquid phase reactions. Proc. Acad. Sci. USSR 157, 392–395.