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Memory Reinforcement with Scale Effect and its Application to Mutual Symbiosis among Terrestrial Cyanobacteria of Nostochineae, Feather Mosses and Old Trees in Boreal Biome in Boreal Forests

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Abstract

We are concerned with BNF (biological nitrogen fixation) of mutual symbiosis between terrestrial cyanobacteria of Nostochineae and feather mosses in boreal forest theoretically. It has been reported in 2011 that BNF of the cyanobacteria with epiphytic feather mosses on canopy is three times as much as in forest floor there. We present a frequency model with scale effect to realize it qualitatively. BNF ability based on nitrogenase's function has a systematic structural stability, and moreover, it is reinforced with scale merit. It is elucidated in this article that the systematic advantage affects synergistically to environmental nature on canopy of old tree to make BNF much higher than in forest floor in boreal forest of North Pacific area in the American continent.

Keywords: Biological nitrogen fixation; Boreal forest; Cyanobacteria; Mathematical "on-off" switching model with scale effect

Introduction

Cyanobacteria is an important and interesting micro-organism which has improved environment of the earth, as having existed clearly for about 27 billion years at least. These inhabit with a lot of traits in various surroundings, especially, in hot springs of 70°C (158°F) or within Arctic Circle [1]. Generically speaking, cyanobacteria, basically composed of a single cell, have the following characteristics:

1. It is thought as a kind of prokaryotic eubacteria without possessing a nucleus in a cell.
2. It belongs to the group of Gram negative bacteria.
3. It can photosynthesize with oxygen outbreak type.
4. As having an enzyme named the nitrogenase, some species obtain the ability to perform biological nitrogen fixation (called BNF in what follows).

Terrestrial cyanobacteria of Nostochineae (for example, Anabaena, Nostoc, Scytonema, Anabenopsis, Dichothrix and so forth) have a filamentous form constituted of trichome, heterocyst, akinete (dormant spore) cells, and sheaths of the quality of agar surrounding them. In a heterocyst cell, they produce ammonium nitrogen with BNF, separating it spatially away from trichome cells in which it photosynthesizes to release oxygen since nitrogenase is beaten by oxygen. Generally, in ecological system of boreal forest (in, for instance, pacific northwest of North American continent or Scandinavian Peninsula) [2-5], inorganic nitrogen is seems to be insufficient very often, but the terrestrial cyanobacteria with mutualistic symbiosis of feather moss (*Pleurozium schreberi* and *Hylocomium splendens* are dominant species) is an important source of supply of the ammonium nitrogen there.

When feather moss is placed in nitrogen-starved situation, it takes some attractive chemical substances which are slightly different from each other and dependent upon species) (out of itself to induce the filamentous cyanobacteria of Nostochineae to come to itself. Cyanobacteria of Nostochineae will make hormogonia differentiation to change their form to the hormogonia from the usual one and make gliding movement to go toward feather moss by its chemotaxis. In Bay et al., they perform micro ecosystem experiments to study this interaction for *Pleurozium* schreberi and *Hylocomium splendens* in details [6]. Their chemical is mighty enough to enchant it to the incurve of its leafy gametophyte completely. If the cyanobacteria (it is *Nostoc spp.* here) arrives at the "cozy" place, then it goes back to the original form of filament and create the heterocyst cells in which it produces the available ammonium nitrogen with BNF. Recently, this function is thought of as an important role of the mutual symbiosis between the filamentous cyanobacteria of Nostochineae and feather moss in the boreal biome of boreal forest [4,5]. In 2011, they took an attention to a remarkable role of old trees in the boreal forests of pacific northwest of North American continent [5] (Actually, they made investigations in the Clayoquot sound UNESCO Biosphere Reserve, Vancouver Island, or British Columbia in Canada.) They have studied the ability of output of BNF of the filamentous cyanobacteria of Nostochineae (here, it is *Scytonema*) making mutual symbiosis with epiphytic bryophytes in the high canopy of a coastal temperate rain forests there. As a marked result, they found that the stand-level ability of BNF at 30 m height of the canopy is almost three times higher than that of the forest floor. Here, the old trees act as the third sub-member of this mutual symbiosis to reinforce the BNF ability of the main members configuring the mutual symbiosis. The objective of this paper is structural characterization of this mutual symbiosis by a certain mathematical skeleton model (it is a kind of "on"-"off" frequency model with scale effect) and explain the qualitative mechanism of this reinforcement theoretically in view of micro ecosystem analysis by use of it.

Nitrogenase is the enzyme of BNF by which the filamentous cyanobacteria of Nostochineae make the available ammonium nitrogen from atmospheric nitrogen molecules (N_2). If cyanobacteria with BNF are put in nitrogen-starved situation, then Nitrogenase's activation is let higher, and if it is in nitrogen-rich state, then the switch turns off. It is regulated by other proteins which can detect deficiency of nitrogen or oxygen. Lately in 2014, the detail mechanism of this process in molecular level has been revealed for *Leptolyngbya boryana*, which is a diazotrophic cyanobacterium lacking heterocysts [7]. According to this paper, they have discovered that ChlR (chlorophyll regulator) and CnfR (Cyanobacterial nitrogen fixation regulator) are principally controlling nitrogenase's activation. But this species is not exactly in Nostochineae, although it is also a kind of the filamentous diazotrophic cyanobacteria. We assume that the filamentous cyanobacteria of Nostochineae also obtain a certain similar regulation system controlling nitrogenase's activation. Here we excuse that the exact quantitative analysis in a cell level of a certain precise mathematical model based on such kind of remarkable fact of molecular biological experiment is slightly out of the aim of this paper and that will remain one of future challenges. It is remarked only that the "on"-"off" switching mechanism of nitrogenase depends upon the nitrogen starved or rich state in the cyanobacteria of Nostochineae, respectively, and this has the heterocyst cell where that is isolated from any oxygen, and moreover, the mechanism of nitrogenase's activation can possess a property of the so-called Michaelis-Menten type nonlinear reaction. As the model imbedding these characters qualitatively, we consider that the cyanobacteria obtain "on"-"off" two-state, that the system has an enzyme controlling the states, and that production from "on" state makes a kind of negative feedback operation, and moreover we regard the population of the cyanobacteria as scale of the system. This is a sort of a model describing skeleton structure of the system. We use this model to elucidate salient structural features and characteristic behaviors of it from the viewpoint of qualitative comprehension of nature of this ecosystem.

BNF function of the cyanobacteria basically obtains the switching mechanism responding density of ammonium nitrogen around it. One of devices working well to realize it is to create good memory element. It is well-known that a robust device to memorize the "on"-"off" two-state makes its adapting potential ability higher to environment (for example, a molecular realization of circadian rhythm). We present a mathematical frequency model describing such two-state as a skeleton structure of the function. This model also obtains a scale effect, which can depict scale merit of the phenomena. This is derived from the nonlinearity of the reaction after all, and is one of the important structural characters of the system. We will attempt to explain a piece of feature of BNF of the mutual symbiosis between the filamentous cyanobacteria of Nostochineae and feather moss in the boreal biome with old trees by use of this structural character. From the viewpoint of evolutionary ecology, this system is composed of the main two species' mutual symbiosis added by extra sub-species of old tree. Sub-species is almost neutral for itself, but it often gives good effect to the system. Our model will explain this effect theoretically without any ad-hoc hypothesis.

Method or two-state frequency model with scale effect

We basically consider a two-state (*S* and *T*) model. *T* stands for inactive state and *S* for active state. They represent two states of the cyanobacteria concerned with BNF. The number n represents magnitude of scale of the system under consideration, which means scale of population of the cyanobacteria. As n is bigger, the whole number of nitrogenases are increasing, hence the scale of the system is larger. Currently, a variable of a frequency model means rate of "on"-state (or "off"-state) in the whole group, which cannot obtain the ability to give expression to size of scale. But, generally speaking, if the system has nonlinear interaction, then the behavior of the system may change qualitatively, or sometimes drastically, even if the scale varies moderately. The system has at least the Michaelis-Menten type nonlinear reaction, which is an enzyme reaction catalysed by nitrogenase. Therefore our model needs scale variable "n". This is based on the model in the classical work of Professors Asakura et al., where they have originally considered about the problem of temporary reaction and post-adaptation process in a cell [8]. We utilize it as modifying it a little. This two-state frequency model is expected to memorize whether the state is "on" or "off". This switching mechanism is realized by regulation proteins, which is symbolized as A in the model. Hence A_{total} is a given constant which stands for the N-starved degree, and A_{total} is consist of free A and trapping A (the intermediate state i' (from T to S) possesses A temporarily in the catalysis). The total quantity of nitrogenase is denoted by C_{total} and

$$A_{total} = A + \sum_{i=0}^{n} T_i' \ (1)$$

$$C_{total} = \sum_{i=0}^{n} (S_i + T_i) \ (2)$$

We illustrate our model in the following:

Fig. 1

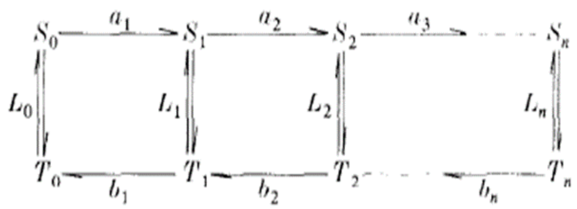

Figure 1: Conceptual figure of two-state frequency model with scale effect.

The intermediate state T'_i is actually arising in reaction process L_i in Figure 1 and this reaction arrive at the equilibrium very rapidly.

Therefore the usual argument leads the following Michaelis-Menten type nonlinearity:

$$A = \frac{A_{total}}{1+\sum_{i=0}^{n}(k_i T_i/\lambda_i)} \qquad (3)$$

Consequently, the model equation is the following:

$$\begin{cases} \frac{dS_0}{dt} = k_0 A T_0 - (\gamma_0 + \alpha_0) S_0 \\ \frac{dS_i}{dt} = k_i A T_i + \alpha_{i-1} S_{i-1} - (\gamma_i + \alpha_i) S_i \\ \frac{dS_n}{dt} = k_n A T_n + \alpha_{n-1} S_{n-1} - \gamma_n S_n \\ \frac{dT_0}{dt} = -k_0 A T_0 + \gamma_0 S_0 + \beta_0 T_1 \\ \frac{dT_i}{dt} = -(k_i A + \beta_{i-1}) T_i + \gamma_i S_i + \beta_i T_{i+1} \\ \frac{dT_n}{dt} = -(k_n A + \beta_{n-1}) T_n + \gamma_n S_n \end{cases} \qquad (4)$$

Here, i = 1, 2, 3, ... , n - 1, and $\alpha_i, \beta_i, k_i, \lambda_i, \gamma_i$ are positive constants. It is easy to understand that the total quantity of C_{total} is preserved. In fact, clearly we understand that $\frac{d}{dt}(\sum_{i=0}^{n}(S_i + T_i))=0$ by summing up all the equations of the system of equations (4).

This paper's aim is a qualitative comprehension of nature of the mutual symbiosis of the ecosystem of the filamentous cyanobacteria of Nostochineae, feather moss, and old trees from the model equation theoretically. Only the above model gives us explanations of some of these (for example, the character of three figures in page 144 in Lindo et al. [5] related to activation of BNF of the cyanobacteria in the forest floor or on the canopy), as we will state it in the following chapter of discussion. Moreover, we would like to understand the intrinsic periodicity of the BNF system of it. For this purpose, we introduce the new variable *B*, which describes the operation inhibiting the activating function of *A*, when the nitrogen-rich situation comes. Originally, this inhibiting operation may be realized by more complex transcription-translation mechanism. We give it with a kind of symbolic variable *B* operating also by Michaelis-Menten type reaction. Here *B* can be regarded as an averaging and abstract variable. We remark that the variable (*AB*) means the state that *B* sticks temporarily *A* to inhibit the activating function of *A* and B_{total} is the total amount of that operation (This is the sum of active *B*, inactive *B*, and (*AB*)).

$$\begin{cases} A_{total} = A + (AB) + J \\ C_{total} = \sum_{i=0}^{n}(S_i + T_i) \end{cases} \qquad (5)$$

$$\begin{cases} \frac{dA}{dt} = \frac{d}{1+J}\left\{m_2 A_{total} - \left(l_2 B + \frac{d}{dt}J\right)A\right\} - m_2 A \\ \frac{d(AB)}{dt} = d\{l_2\, B\, A - m_2\,(AB)\}, \\ \frac{dB}{dt} = d\{l_1 P(B_{total} - (AB) - B) + m_2(AB) - (m_1 + l_2 A)B\}, \end{cases} \qquad (6)$$

where *J* is defined by $J = \sum_{i=0}^{n} \frac{k_i T_i}{\lambda_i}$ and λ_i, k_i (i = 0, 1, 2, ..., n), l_j , m_j (j = 1, 2), d are positive constants.

Degree of activation of nitrogenase, *P*, is defined by $P = \sum_{i=0}^{n} iS_i$, which means how many nitrogenases are made activated totally. We remark that (4), (6) and (5) are a consistent system of equations, although it seems to be surplus, apparently. In fact, we can derive the conservation law of A_{total} in (5) by use of (6) easily. We remark that the right hand side of (6) has the terms dependent upon T_i or (dT_i /dt), which come from the implicit change of *A* because of shift of chemical equilibrium according to *A*'s and *B*'s varying explicitly. These terms need for conservation law of A_{total} of (5).

Finally in this section, we present some stochastic process simulations. We use Poisson process corresponding to our frequency model with scale effect. Some results of these are the following figures. We remark that *n* means magnitude of population of the cyanobacteria, and we consider of "1" of the unit in the model system as approximate 2000 individuals of the cyanobacteria population in actual data in [5].

Results

How does *P* varies? We investigate *P*'s behavior according to change of A_{total} in (3). Initial conditions of (4) are T_0 = 1.0, T_i = 0.0, and S_j = 0.0 (i = 1, 2, 3, ... , n and j = 0, 1, 2,..., n). We increase the value of A_{total} from 0.01 to 10.0 step by step as a width of step is 0.01, and we plot the value of *P* after enough time goes by. Then an each initial state is successively made the final state just in the previous simulation. Inversely, we decrease the value of A_{total} from 10.0 to 0.01 in the opposite manner, and plot it in the same figure. We repeat the same kind of numerical experiment in each possibly modifying magnitude number. Moreover, we exactly solve the stationary problem of (4) in another way, and we make an infinitesimal stability analysis for each stationary solution. Figures 2, 3, 4 and 5 and we see a bistable region existing and hysteresis occurring when the magnitude number is bigger than two. In the figures, curves outside bistable region stand for stable branches of stationary solution, and a curve inside bistable region stands for unstable branch. The stable branches overlap completely with the final states in solving the time evolution equation, but the unstable branch goes inversely up (or down) the interior of in the bistable region, although at the end points the final states are jumping up (or down) to the nearest stable states in the same parameters.

Fig. 2

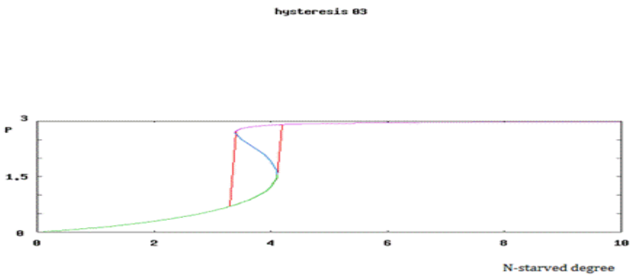

Figure 2: 3-magnitude.

Fig. 3

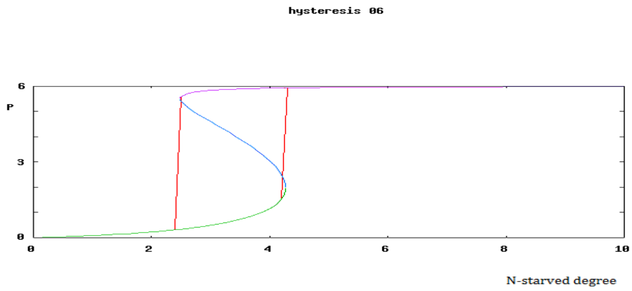

Figure 3: 6-magnitude.

Fig. 4

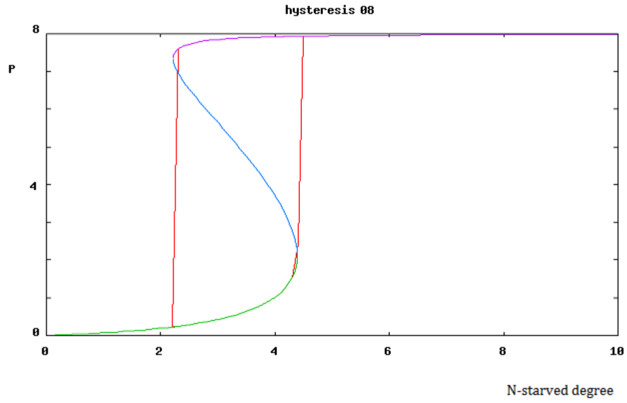

Figure 4: 8-magnitude.

These are not overlapped with each other at all. We solve the system (4), (5), and (6), numerically. We ensure that it has a time periodic solution shown in Figure 9 and Figure 10. These are generated by the corresponding hysteresis loop to bifurcations of hysteresis type of Figure 4 and Figure 5.

As detailed data of each month was not found about population and BNF activity of the cyanobacteria, some samples time series of data of population from May to December (it is not activated in winter season), and BNF activity is plotted by use of the hysteresis graph.

According to Lindo et al. [5], the ratio of populations is approximately (forest floor):(15 m canopy):(30 m canopy)=3:8:12 (per dwt moss), therefore it is utilized. As June is the spore-forming season, the activity is slightly high. In warm season (around September), the population is much higher than the other seasons. The "BNF-switch" is completely "on" on 30m canopy, although it almost remains "off" in the forest floor and 15m canopy (Figures 6, 7 and 8).

Fig. 5

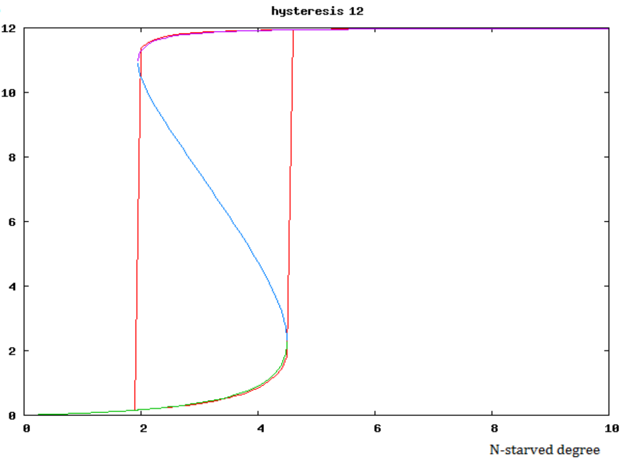

Figure 5: 12-magnitude.

Fig. 6

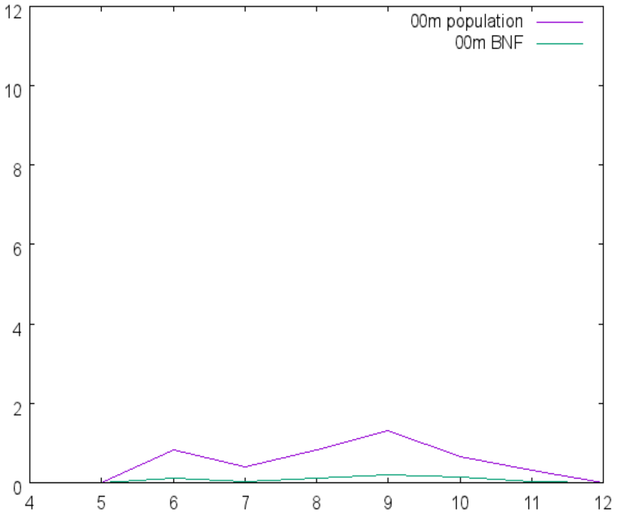

Figure 6: Forest floor.

The activity is let low in the end of October because the switch turns off with nitrogen-rich condition. A piece of intrinsic oscillatory property is appearing here. (The simulations: Figures 9, 10, 11 and 12 mean the essential oscillation of the system.) In winter season, the activity is disappearing.

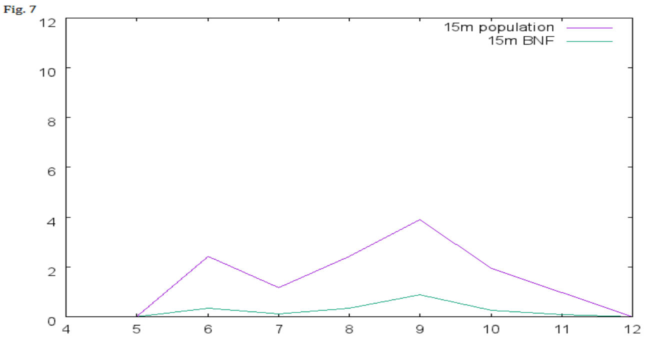

Figure 7: 15 m canopy.

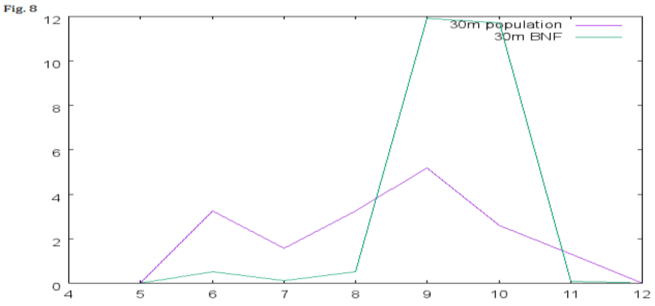

Figure 8: 30 m canopy.

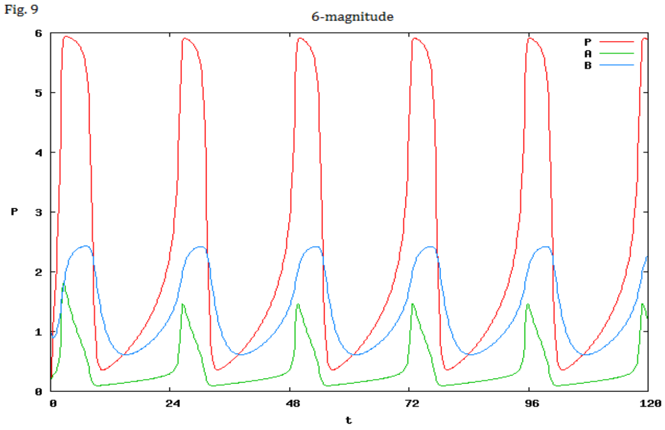

Figure 9: 6-magnitude deterministic process.

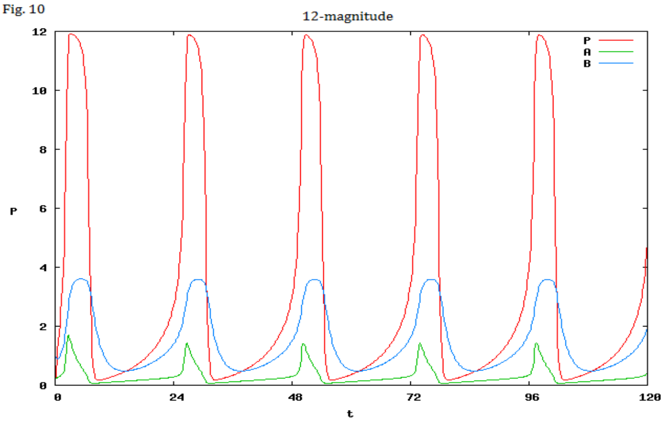

Figure 10: 12-magnitude deterministic process.

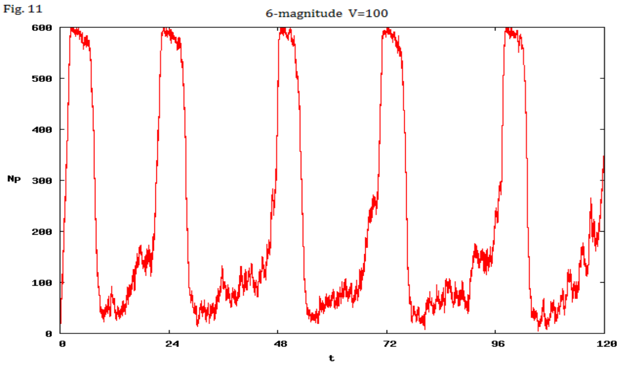

Figure 11: 6-magnitude stochastic process.

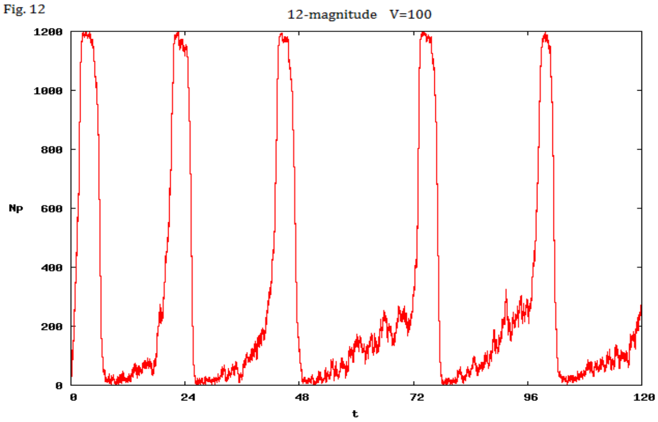

Figure 12: 12-magnitude stochastic process.

Discussion and Conclusion

We understand the character of BNF of *Scytonema* symbiotic with feather moss epiphytic on canopy and in floor in boreal forest in Lindo et al. [5] by our model equation theoretically. Our frequency model with scale effect has a hysteresis type bifurcation, whose width is wider as the scale is larger. This means that the system obtains characteristic memory reinforcement with scale effect intrinsically. The point is that this reinforcement is derived naturally from the structure of the system, and that it is not added with ad-hoc device. Here in the model *n* means magnitude of population of the cyanobacteria. Feather moss is generally perennial and it has certain validity as a substantial amount of population is increasing discretely in the fixed season in a year and the population of cyanobacteria is accompanied with it. In this paper, the forest floor is corresponding to 3-magnitude, 15 m canopy to 8-magnitude of population, and 30 m canopy to 12-magnitude for the theoretical value to agree with the actual measured value in Lindo et al. [5] qualitatively. As an important conclusion of this paper, we explain the strong nonlinear correlation between the population of the cyanobacteria and its BNF activity on forest floor and on canopy.

In Figure 6, Figure 7 and Figure 8, we see the realization of this character. From 00 m to 30 m, the population is larger and larger moderately, as in the paper Lindo et al. [5]. At 30 m canopy the BNF activity is much bigger than the others also as in Lindo et al. [5]. Especially, in August and September this character is remarkable. This is given from bifurcation structure of the equilibrium state of our model system. In the actual field work's measurement [5] canopy 30 m BNF is approximately three times as much as forest floor's in total amount in the year. Our model explains it qualitatively well. The memory reinforcement means that, if the switch is on once, then it hardly turns off. It realizes this type of nonlinear correlation naturally without any ad-hoc additional device.

We totally add the turns-off effect in nitrogen-rich state to make simulation, which means that the BNF function has essentially a kind of periodicity. So far we do not understand fine molecular mechanism of this "switch-off" effect, but we predict such a certain effect. The real data behaves more irregularly, but this is because of effect of rain-fall or of spore-forming [5].

Originally our model system has structural scale effect, and moreover, for instance, if rain-fall affects it, then it spurs on the nonlinear correlation positively. This is because the transport effect of ammonia nitrogen by through-fall rain in trees is stronger on higher canopy than near forest floor. Therefore the feather moss' behavior of mutual symbiosis in higher canopy with larger population is reasonable, and old trees realize it naturally and their raison d'être is realized well.

Synergetic positive effect between the structural stability and the environmental nature makes times of creating symbiosis of them is fewer, and it operates the symbiosis relation for it to be more radiated in boreal biome. In this case feather moss calls the cyanobacteria, only when it is necessary, so the constructing cost is low. But maintenance cost might be running up, if it assembled the cyanobacteria into symbiosis and dismissed it repeatedly a number of times. But such a fruitless repetition cannot occur in the mutual symbiosis on the canopy at least.

As June is the spore-forming season, the BNF activity is higher a little. In the cozy season of September, the more and more increasing the population is, the higher and higher the BNF is. Especially, on 30 m canopy, it is remarkable that it gains explosively because of the Switching effect. This is the reason why the stand-level BNF on 30 m canopy is about three times as much as in forest floor per . For example, DeLuca suggests that some activity recover a little in October, and, if the time series' data are given in each week, then it is realized qualitatively [2]. This is because of the essential oscillation of the system. In winter season, the activity is disappearing rapidly.

The Poisson process simulations mean a kind of structural robustness of this function. In actual field of boreal forest, a lot of disturbance factors affect the system, and in such a noisy environment it is important that the function works stably. The structural stability of this function is ensured by the stochastic simulation, because the structural character is maintained even in a few populations per unit area.

By this fact, we can presume that it is also significant in view of evolutional ecology. If structural stability has robustness under a certain magnitude of environmental variation, then the property can be easy to be inherited and adaptively radiated. In Bay et al., they elucidate that the feather mosses secrete chemical signals to gain nitrogen from *Nostoc spp*. in the mutual symbiosis without any special room created for the cyanobacteria at all [6]. This way may be low-costed relatively, although this relationship can be fragile. This weak point may be compensated by that structural stability, and this is a very superior symbiosis creating system. Generally speaking [9,10], benefit acquired from mutual symbiosis system must be bigger than cost from creating and maintaining the system in order to inherit it.

In the future works, we continue to consider about it, and for instance, we make simulations to reveal the evolutional ecological meaning directly by making the bigger model system including the frequency model used this time in this paper and such a structural character and its resulting function is created, maintained and inherited stably. Eventually, environment of boreal forest does not only affect positively for productivity of BNF, but also structural reinforcement of memory contributes for it basically, and the mutual symbiosis becomes robust and fruitful, and moreover, it has advantage to be radiated adaptively in this boreal biome.

Acknowledgement

The most of calculations of this article is based on collaboration with Professor Tatsuo Shibata, who was in the same department as the author in 2007-2008. He is now in Laboratory for Physical Biology RIKEN Quantitative Biology Center/RIKEN Center for Developmental Biology. Especially, he has suggested the idea of making a binary digit of memory of the organisms from bistable equilibrium of the frequency model with scale effect. I must appreciate him at the point. During writing of this article, we have been informed of the news of Professor Sho Asakura's decease in age at 90 year-old. His insightful paper has inspired us deeply. We would like this article to be dedicated to him, and we extend our sincere condolence to him and his family.

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