

The effect of the mortality cycle in two competitive plants: Is Sasa really advantageous to competitor?

ササは本当に強いのか？

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Abstract

植物は季節や環境変動、寿命などによって様々な死亡サイクルを持つ。例えば、60年以上の寿命を持つといわれるササは、死期が近づくと一斉に開花結実して一斉に枯死する竹の一種である。ササは、生態系の遷移を著しく遅くし、環境を均一化させることで生物の多様性を大きく下げる。ササが優占になると、被覆により樹木の実生や草本植物の生育が妨げられる。このように、ササが競争に非常に強いのは、その一斉死の特徴が原因の一つであると言われている。ササだけではなく、植物の様々な死亡サイクルが生息地や栄養分、光などを巡り競争する植物の共存に大きな影響を与えるに違いない。ここでは、まず、死亡サイクルが競争する2つの植物に与える影響を同じ死亡周期をもつ場合とそうでない場合について議論する。また、ササ刈りと同時に競争種も一定に減らすことがササの持続的生存を助ける可能性とササの一斉死が必ずしも競争に有利ではないことを考える。

1 Introduction

In the forest community, the interactions of plants and canopy give an effect to the community structure and dynamics of forest. Plants coexist with competing to dominate over the open space for reproduction and seeding, and obtain water or nutrition. Such a coexistence with the competition is affected by environmental or hereditary elements such as seasonal variations, life span and so on.

The seasonal effect between two competitive plant species has been studied in many literatures ([5], [9], [10]), and has been considered to be important to study the dynamics and coexistence of plants. On the other hand, the life span of plants can be considered as the element determining the community structure of forest in a long-time scale. The life span of plants has much to do with the death rate of the plants. The death rate of population is affected by the life span of each individual as well as the environmental elements such as seasonal variations.

For example, the dominance and simultaneous death of Sasa, the dwarf bamboo, has a great influence on the regeneration of beech in Japan ([7], [8]). Sasa is a monocarpic plant and a sort of bamboo distributed widely in Japan. It flowers then die simultaneously in a wide area after rhizomatous vegetative reproduction during a long period. It is reported that the life span of Sasa is greater than 60 years ([1], [15]). Sasa maintains low death rate for a long time and has one peak of high death rate by simultaneous death.

In this paper, we consider the effect of the mortality cycle for two competitive plants. Climatic changes or simultaneous withering can vary the death rates of plants. What effect is given by the mortality cycle to competitive plants? Which mortality cycle is the most advantageous to competition? Through mathematical analysis and numerical simulations, we propose the answer about the questions above.

Finally, we discuss the effect for humans to mow Sasa. Sasa is usually known as a very strong plant for competition because other plants almost cannot invade an area where Sasa has already spread out. People of the past in Japan often mows Sasa in order to keep the woods for livelihood. We show the effect that humans mow Sasa, which can make Sasa be stronger when it competes against the canopy tree of long periodic death rate or the weeds of short periodic death rate.

2 Model

The model that we consider here is given as follows.

$$\begin{aligned}\frac{d}{dt}S &= e_1S - d_1(t)S - a_1S^2 - b_1WS, \\ \frac{d}{dt}W &= e_2W - d_2(t)W - a_2W^2 - b_2SW\end{aligned}\tag{1}$$

where

$$d_1(t) = \gamma_1 \left[\frac{1 + \sin(2\pi t/T_1)}{2} \right]^{\beta_1}, \quad d_2(t) = \gamma_2 \left[\frac{1 + \sin(2\pi t/T_2)}{2} \right]^{\beta_2}.$$

Here, $S(t)$ and $W(t)$ denote the densities of competing plants. e_i and a_i ($i = 1, 2$) are the reproductive increase rates and intra-specific competition rates of each plant-species. b_1 and b_2 are inter-specific competition rates. $d_i(t)$ ($i = 1, 2$) are the death rates of the T_i -periodic functions of time. T_i ($i = 1, 2$) are the period of death rate which imply the longevity of S -species and W -species, respectively. γ_i ($i = 1, 2$) are the maximum values of death rates. The parameters β_i ($i = 1, 2$) determine the patterns of distributions of death rates. For example, if β_1 is sufficiently large, then the death of the plant S is considered to occur simultaneously. Figure 1 shows the graphs of the death rate depended on β_i with $\gamma_i = 1$ and $T_i = 10$ ($i = 1, 2$). Note here that all of parameters in the system (1) are positive values. In what follows, let

$$[d_i] = \frac{\gamma_i}{T_i} \int_0^{T_i} \left[\frac{1 + \sin(2\pi t/T_i)}{2} \right]^{\beta_i} dt$$

denotes the average of $d_i(t)$ ($i = 1, 2$).

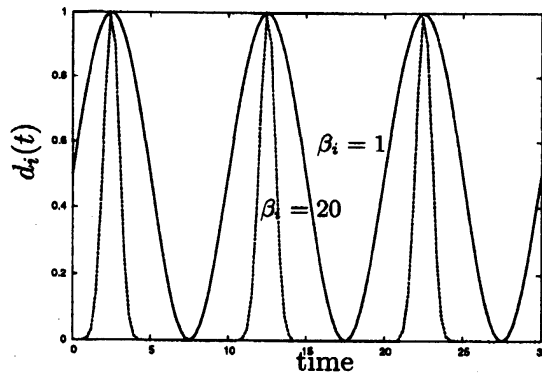


Figure 1: Dependence of death rate on β_i .

3 The effect of the mortality cycle in two competitive plants

In the system (1), we have the solutions $E_0 = (0, 0)$, $E_S = (\bar{S}, 0)$, and $E_W = (0, \bar{W})$. Here $\bar{S}$ is the T_1 -periodic solution of the periodic logistic equation;

$$\frac{d}{dt}S = (e_1 - d_1(t))S - a_1S^2,$$

provided $e_1 > [d_1]$, and $\bar{W}$ is the T_2 -periodic solution of the periodic logistic equation;

$$\frac{d}{dt}W = (e_2 - d_2(t))W - a_2W^2$$

provided $e_2 > [d_2]$ ([3]).

The system (1) has a positive periodic solution $E_* = (S_*, W_*)$ provided $e_1 > [d_1]$ and $e_2 > [d_2]$ ([2]). From Theorem 2 and Theorem 4 of [4], we have the following results.

Proposition 1 E_0 is stable if $e_1 < [d_1]$ and $e_2 < [d_2]$. E_0 is unstable if $e_1 > [d_1]$ or $e_2 > [d_2]$.

Proposition 2 Suppose that $e_1 > [d_1]$. The periodic solution E_S is locally asymptotically stable if and only if

$$[d_2] > e_2 - [b_2\bar{S}]. \quad (2)$$

and is unstable if $[d_2] < e_2 - [b_2\bar{S}]$

Proposition 3 Suppose that $e_2 > [d_2]$. The periodic solution E_W is locally asymptotically stable if and only if

$$[d_1] > e_1 - [b_1\bar{W}] \quad (3)$$

and is unstable if $[d_1] < e_1 - [b_1\bar{W}]$.

Proposition 4 Suppose that $e_1 > [d_1]$ and $e_2 > [d_2]$, the following conditions are satisfied.

$$a_1 > b_1 \quad \text{and} \quad a_2 > b_2.$$

Then the positive periodic solution E_* is locally uniformly stable.

Proposition 4 implies that the two species can coexist if the intra-specific competition of the species is severer than the inter-specific competition. W -species (S -species) cannot succeed in invading if the condition (2) (the condition (3)) is satisfied.

Proposition 2 and Proposition 3 show that the greater the average of death rate of the invasive species is, the more advantageous the resident species is. On the other hand, the lesser the average of death rate of the invasive species is, the easier the invasion is.

First, we verify the effect of the parameter β_i with numerical simulations where $T_1 = T_2 = 30$. The parameter values of the figures 2, 3, 4 are given by $e_1 = 3, e_2 = 2, a_1 = 2, a_2 = 1, \gamma_1 = 1.5, \gamma_2 = 1, b_1 = 1.5, b_2 = 1$ and $\beta_2 = 1$.

The figures 2, 3, 4 show that S -species cannot invade the habitat of W -species with $\beta_1 = 1$, but S -species can coexist with W -species when β_1 becomes large. However, if β_1 is sufficiently large, the two species cannot coexist at the same time. S -species always can persist but W -species appears only periodically.

Remark 1 In Figure 2, W -species is advantageous to compete against S -species when $\beta_1 = \beta_2$. However, S -species becomes more advantageous than W -species when β_2 is large enough. The death rate of *Sasa* has the value of β_i large enough. Thus, a plant of small β_i which has the same period with *Sasa* is difficult to invade an area where *Sasa* has already spread out. *Sasa* is advantageous to plants which has the same period with itself.

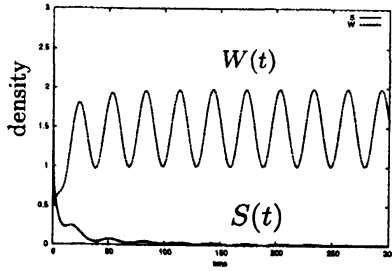


Figure 2: The case of $\beta_1 = 1$. The dotted line and the solid line denote the densities of S -species and W -species respectively. S -species vanishes as time goes by.

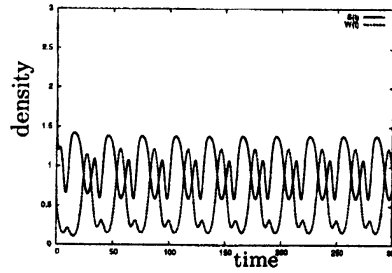


Figure 3: The case of $\beta_1 = 10$. The two species can coexist all the time.

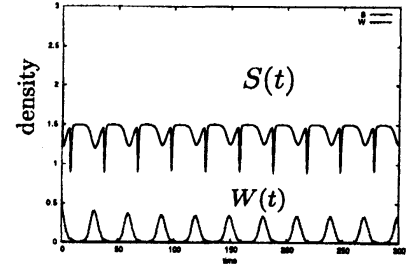


Figure 4: The case of $\beta_1 = 300$. The two species can coexist but not always. W -species appears only periodically.

In what follows, we consider the effect of the period of death rates, T_i with numerical simulations. We choose the parameter values as $e_1 = 3, e_2 = 2, a_1 = 2, a_2 = 1, \gamma_1 = 1.5, \gamma_2 = 1, b_1 = 1$ and $b_2 = 1$. We also choose $T_1 = 30, \beta_1 = 100$ in $d_1(t)$, and $\beta_2 = 1$ in $d_2(t)$. Let us consider the two cases; $T_2 = 10$ and $T_2 = 200$. Note here that

$$\frac{1}{mT_i} \int_0^{mT_i} d_i(t) dt = \frac{1}{T_i} \int_0^{T_i} d_i(t) dt, \quad m : \text{natural number}.$$

Thus, we have the same average of death rates $d_2(t)$, $[d_2] = 0.5$, for $T_2 = 10$ and $T_2 = 200$. The average of death rates $d_1(t)$ is given by $[d_1] = 0.085$.

First, let us consider the corresponding averaged system of the system (1) as follows:

$$\begin{aligned} \frac{d}{dt} S(t) &= (e_1 - [d_1])S - a_1 S^2 - b_1 W S, \\ \frac{d}{dt} W(t) &= (e_2 - [d_2])W - a_2 W^2 - b_2 S W. \end{aligned} \quad (4)$$

The system (4) is the well-known Lotka-Volterra system ([13]), and the two species can coexist, and the equilibrium of the coexistence is globally asymptotically stable when $a_2(e_1 - [d_1]) - b_1(e_2 - [d_2]) > 0$ and $a_1(e_2 - [d_2]) - b_2(e_1 - [d_1]) > 0$. This condition holds when $a_1 > b_1$ and $a_2 > b_2$, that is, the intra-specific competition is stronger than the inter-specific competition.

Now, the numerical simulation results are given by the following figures 5,6,7.

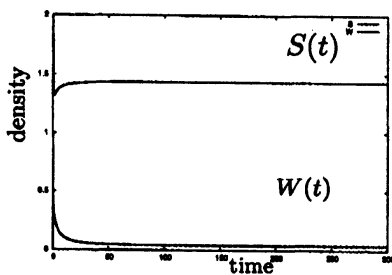


Figure 5: The case of average death rate system. The two species coexist, but W -species maintains very small density as time goes to.

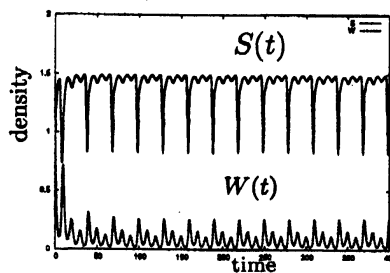


Figure 6: The case of the periodic system (1). $T_1 = 30, \beta_1 = 100, T_2 = 10$ and $\beta_2 = 1$. Two species can coexist.

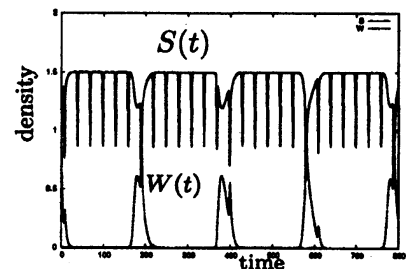


Figure 7: The case of the periodic system (1). $T_1 = 30, \beta_1 = 100, T_2 = 200$ and $\beta_2 = 1$. W -species has the period that it goes to extinction.

In Figure 5, the two species coexist, but W -species almost dies out and remains only slightly as time goes to infinity when we choose the death rate as the average of it. In Figure 6, however, the periodic death rate makes W -species coexist with S -species and have greater density than

that of Figure 5. We give the greater period T_2 of W -species in Figure 7 than that of Figure 6. Then, Figure 7 shows that two species can coexist but not always. W -species has a period where it goes to extinct.

Remark 2 When the two species have the same periods of death rates, the smaller β_i is advantageous to compete because the average of death rate becomes smaller (Figure 1 and Figure 2). However, Figure 6 shows that W -species can have the higher density than that of the case of the average death rate when it has a proper period T_2 (here $T_2 = 30$) when β_2 is greater than β_1 . If T_2 is large enough, then W -species is more disadvantageous to competition than that of the case of $T_2 = 30$ because it has a extinct period. Even though W -species has the same average death rate in Figure 6 and Figure 7, the longer period gives the disadvantage for competition.

Remark 3 For the averaged system (4), we have the following properties ([13]):

(i) Either the equilibrium $(0, (e_2 - [d_2])/a_2)$ or the equilibrium $((e_1 - [d_1])/a_1, 0)$ is globally asymptotically stable if $\{a_2(e_1 - [d_1]) - b_1(e_2 - [d_2])\}\{a_1(e_2 - [d_2]) - b_2(e_1 - [d_1])\} < 0$,

(ii) A positive interior equilibrium exists if $\{a_2(e_1 - [d_1]) - b_1(e_2 - [d_2])\}\{a_1(e_2 - [d_2]) - b_2(e_1 - [d_1])\} > 0$, and it is unstable if $a_2(e_1 - [d_1]) - b_1(e_2 - [d_2]) < 0$ and $a_1(e_2 - [d_2]) - b_2(e_1 - [d_1]) < 0$.

However, we should notice that a nontrivial positive periodic solution can exist in the system (1) even if $\{a_2(e_1 - [d_1]) - b_1(e_2 - [d_2])\}\{a_1(e_2 - [d_2]) - b_2(e_1 - [d_1])\} < 0$ is satisfied. Moreover, a nontrivial positive periodic solution can exist in the case of either $a_2(e_1 - [d_1]) - b_1(e_2 - [d_2]) < 0$ or $a_1(e_2 - [d_2]) - b_2(e_1 - [d_1]) < 0$ ([12]). That is, the periodic death rate may cause the two species to coexist even if the corresponding averaged system would force either of the two species to extinction.

4 Sasa is really advantageous to competitor ?

Sasa flowers then die simultaneously after rhizomatous vegetative reproduction during greater than 60 years. It is reported that understory bamboo abundance influence long-term stand structure and development of canopy tree by suppressing three recruitment ([14]). Thus Sasa is usually considered to be very strong to compete.

The dynamics of Sasa have been studied in many papers ([6], [7], [8], [11], [14]), especially as a lattice-structured model ([6]) and an individual based model ([7]). In Japan, Sasa produces a inhibiting effect on the regeneration of beech and has a very harmful effect on the sustainability of beech stand, which depends on the longevity of Sasa ([6], [8]). In this section, we discuss the dynamics of Sasa with a deterministic model of ordinary differential equations by numerical simulations.

First, let us note that $[d_i]$ is a non-increasing function for β_i because $(1/2) + (1/2) \sin(2\pi t/T_i) \leq 1$. Thus, $[d_i]$ becomes small when β_i becomes large. In Section 3, we also have known that stability results depend on the average death rates of the two species. A plant which dies simultaneously such as Sasa has a sufficiently large β_i , and thus we can consider Sasa to be advantageous to compete. However, we show that the simultaneous death of Sasa is not decisive cause for the advantage of Sasa by numerical simulations.

In what follows, $S(t)$ denotes the density of Sasa in the system (1). Note that Sasa maintains low death rate for a long time and has one peak of high death rate by simultaneous death. Let us choose a proper the parameter values which implies the life pattern of Sasa as follows:

$$e_1 = 3, \quad \gamma_1 = 3, \quad a_1 = 1, \quad \beta_1 = 50. \quad (5)$$

Here, we set the life span of Sasa at 60 years, that is, $T_1 = 60$. We also consider the two kinds of competitive plants against Sasa; A canopy tree of a long longevity and a weed of a short longevity, which are denoted by $W(t)$ in the system (1). A canopy tree which are forested in

a similar time can have a high death rate in the end of the time of longevity. Thus, we set $T_2 = 300$ years and $\beta_2 = 15$ in the case of canopy tree. In the case of some weeds of short longevity, we choose $T_2 = 1$ year and $\beta_1 = 1$. The other parameter values are given by

$$e_2 = 3, \quad \gamma_2 = 1, \quad a_2 = 1.5, \quad b_1(\text{canopy}) = 1.44, \quad b_1(\text{weed}) = 1.67, \quad b_2 = 0.5. \quad (6)$$

The time variations of the densities of the three species without a competitor are given by Figure 8.

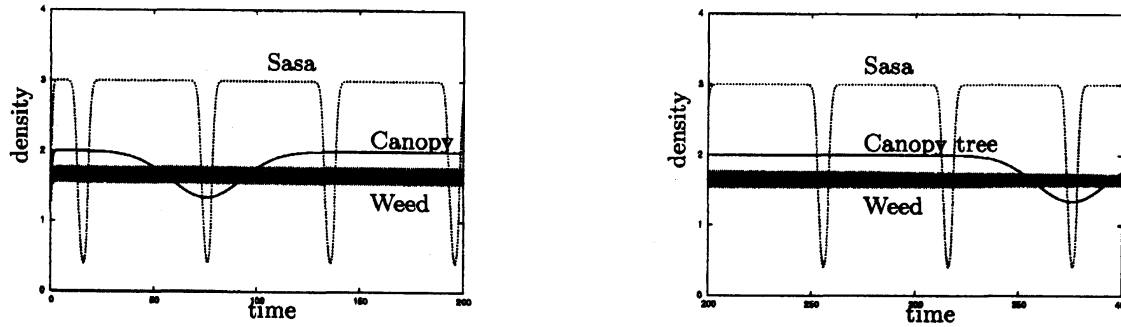


Figure 8: Dynamics of Sasa, Canopy tree and Weed without a competitor. The left and right figures describe the density's variation of each species from 0 year to 200 years and from 200 years to 400 years, respectively. The weeds have very small perturbations.

Now, we consider the effect that humans mow Sasa as well as the competitive plants of it. We suppose that the mowing by humans is done constantly, and thus the decreasing rates by mowing of Sasa and the competitive plant are given by constants. The model discussed here is as follows:

$$\begin{aligned} \frac{d}{dt}S(t) &= (e_1 - d_1(t) - a_1S - b_1W)S - c_1S, \\ \frac{d}{dt}W(t) &= (e_2 - d_2(t) - a_2W - b_2S)W - c_2W, \end{aligned} \quad (7)$$

where $c_i (i = 1, 2)$ are the decreasing rates for humans to mow Sasa and W -species.

Let us choose the values of c_1 and c_2 as 0.7 and 1.2, respectively. Then, the simulation results, Figure 9 and Figure 10, show that Sasa can still exist if humans mow the competitors as well as Sasa, and it is advantageous to the competitors because the densities' variations of the competitors are determined by the period of Sasa.

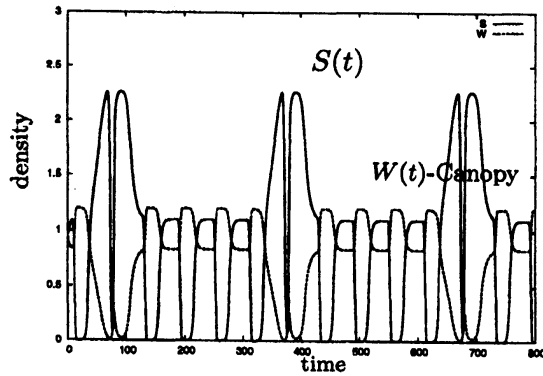


Figure 9: The case that Sasa competes to canopy tree when humans mow Sasa.

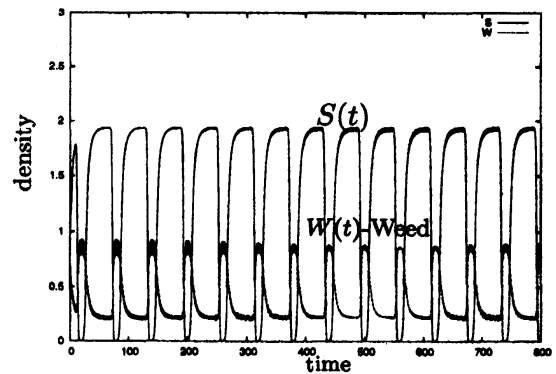


Figure 10: The case that Sasa competes to weeds when humans mow Sasa.

Now, let us remove the effect by mowing in the system (7). We choose the same parameter values above, (5) and (6). And we choose $c_i = 0 (i = 1, 2)$. Then the numerical results are given by the figures 11, 12.

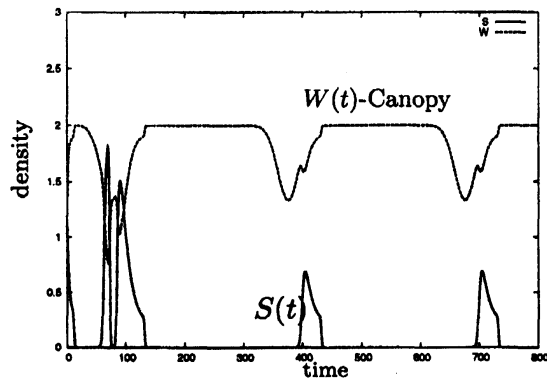


Figure 11: The case that Sasa competes to Canopy three without mowing.

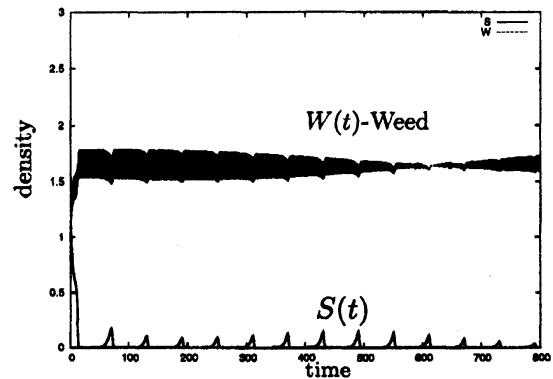


Figure 12: The case that Sasa competes to Weed with mowing.

Figure 11 and Figure 12 show that Sasa is disadvantageous to the two competitor, canopy three and weed. As a results, the effect that humans mow Sasa can make Sasa to be stronger to compete against the canopy three of long periodic death rate and the weed of short periodic death rate.

Remark 4 The average death rates of Sasa, canopy three and weed are given by $[d_{sasa}] = 0.239$, $[d_{canopy}] = 0.145$ and $[d_{weed}] = 0.5$, respectively. When Sasa competes with canopy three, the property (i) of Remark 3 is satisfied for the parameter values chosen in Figure 11. In the case that Sasa competes with weed, the property (ii) of Remark 3 is satisfied for the parameter values chosen in Figure 12. The simulation results of Figure 11 and Figure 12 show that a nontrivial positive periodic solution exists in the system (1) even if the corresponding averaged system would force either of the two species to extinction.

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References

- [1] J. J. N. Campbell, *Bamboo flowering pattern: A global view with special reference to East Asia*, J. Am. Bamboo Soc., **6** (1985) 17–35.
- [2] J. M. Cushing, *Stable limit cycles of time dependent multispecies interactions*, Math. Bioscience, **31** (1976) 259–273.
- [3] J. M. Cushing, *Stable positive periodic solutions of the time-dependent logistic equation under possible hereditary influences*, J. Anal. Appl., **60** No. 3 (1977) 747–754.
- [4] J. M. Cushing, *Two species competition in a periodic environment*, J. Math. Bio., **10** (1980) 385–400.
- [5] J. M. Cushing, *Periodic Lotka–Volterra competition equations*, J. Math. Bio., **24** (1986) 381–403.
- [6] K. Kawano and Y. Iwasa, *A lattice-structured model for beech forest dynamics: the effect of understory dwarf bamboo*, Ecological Modeling, **66** (1993) 261–275.
- [7] T. Kubo and H. Ida, *Sustainability of an isolated beech–dwarf bamboo stand: analysis of forest dynamics with individual based model*, Ecological Modeling, **111** (1998) 223–235.
- [8] T. Nakashizuka, *Regeneration of Beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*)* Ecol. Res, **3** (1988) 21–35.
- [9] T. Namba, *Competitive co-existence in a seasonally fluctuating environment* J.theor. Biol, **111** (1984) 369–386.
- [10] T. Namba and S. Takahashi, *Competitive coexistence in a seasonally fluctuating environment II. Multiple stable states and invasion success*, Theoretical Population Biology, **44** (1993) 374–402.
- [11] A. Makita, Y. Konno, N. Fujita, K. Takada and E. Hmabata, *Recovery of a *Sasa tsuboiana* population after mass flowering and death* Ecol. Research, **8** (1993) 215–224.
- [12] P. de Mottoni and A. Schiaffino, *Competition system with periodic coefficients: A geometric approach* J. Math. Bio, **11** (1981) 319–335.
- [13] N. Shigesada and K. Kawasaki, “Biological Invasions: Theory and Practice,” Oxford university press, 1997.
- [14] A. H. Taylor, H. Jinyan and Z. ShiQiang, *Canopy three development and undergrowth bamboo dynamics in old-growth *Abies–Betula* forests in southwestern China: a 12-year study*, Forest Ecology and Management, **200** (2004) 347–360.
- [15] K. Ueda, *On the flowering and death of bamboos and the proper treatment. (II) Relation between the flowering bamboo and a rhizome system in the bamboo grove with non flowering bamboo*, Bull. Kyoto Univ. For., **33** (1961) 1–26.