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透過模型解析孟宗竹林產量周期及擴張機制

A modeling approach for understanding annual production  
cycles and expansion phenomenon of Moso bamboo

(*Phyllostachys pubescens*)

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## 中文摘要



孟宗竹 (*Phyllostachys pubescens*) 是東亞地區重要的經濟物種，可供食用或作為結構材料，並能固碳。近二十年發現孟宗竹有擴張並取代周圍植被的現象。透過生態模擬了解孟宗竹生產及擴張的影響因子，或有助於為野外研究及管理政策提供新的見解。

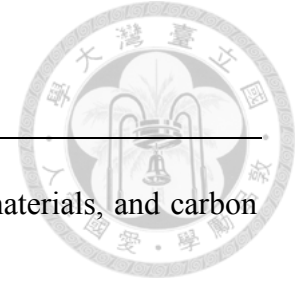
長期記錄顯示管理孟宗竹林的新筍產量有豐欠年循環。現有假說認為兩年換葉周期與林齡結構失衡是豐欠循環的維繫機制。然並非各地管理孟宗竹林都有豐欠年，或同一竹林僅部分時期有明顯豐欠年，而既有假說於此無法提供解釋。本研究第一部分即透過年齡結構族群成長模型(Age-structured population growth model)分析影響新筍產量周期的潛在因素。模型結果顯示(1)來自老葉、一年生新葉的碳水化合物與 (2)來自儲藏於竹根、地下莖的碳水化合物，皆會讓孟宗竹林的新筍產量趨向長期穩定，而非豐欠循環。

根據前人研究，地下莖長度、資源量與空間分布是影響孟宗竹擴張的潛在因子，本研究第二部分即透過個體基礎模型(Individual-Based Model)探討導致孟宗竹易於擴張的影響因子。結果顯示，在資源量適中、地下部低成本的情況下，延長地下莖可以增加孟宗竹擴張成功的機會，並且讓擴張面積更大；而在資源量豐富、地下部高成本的情況下，延長地下莖則對族群存續並無好處。此結果或能進一步提供線索，解釋何以單桿散生竹多分布於溫帶、合軸叢生竹分布於熱帶。

**關鍵詞：**竹、模擬、生產、豐欠年、葉片生理、竹林擴張、地下莖

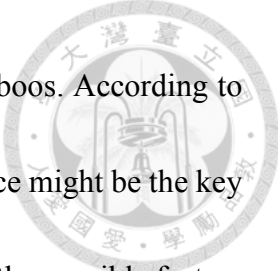
## Abstract

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Moso bamboo (*Phyllostachys pubescens*) is useful for food, materials, and carbon fixation. In East Asia countries, the Moso bamboo forest has expanded in these decades. The understanding of the factors that influence productivity and expansion phenomenon based on ecological modeling approaches might help to propose new insights for field measurements and development of management policy in the Moso bamboo forests.

Long-term records in managed Moso bamboo forests have shown the two-year cycles of new shoots production. One previous hypothesis said the two-year leaf lifespan and uneven composition of newer and older leaves every year is the causes of the two-year production cycles. However, why the cycles were not obvious in some cases if the leaf lifespan is the cue for the two-year cycles? The first part of this study aimed to understand the potential determinants of inter-annual cycles of new shoots production in Moso bamboo stand through an age-structured population growth model. The model analysis demonstrated that the two-year cycles could easily disappear due to the considerable contribution of carbohydrates originating from (1) photosynthesis of old leaves and first-year culms' leaves and (2) carbon storage of roots and rhizomes. The results suggested that only the two-year leaf lifespan could not be a complete explanation for the biennial production cycles, and further study about the allocation of carbon from photosynthesis of different-age leaves could contribute.



In the second part, this study explored expansion of Moso bamboos. According to previous studies, the rhizome length and spatial distribution of resource might be the key factors for expansion. The second part of this study aimed to find out the possible factors promising Moso bamboo expansion based on an individual-based model developed in this study. The results indicated the rhizome length changed success frequency of expansion and territory of bamboo population. In general, elongating rhizome could improve the frequency of expansion when the cost for elongations was low and the amount of resource was middle-level. On the contrary, bamboo received little benefit or even negative impacts from elongation in high-cost and high-level resource amount condition. The former and latter simulations might provide reasonable interpretations for difference in habitat of bamboos with monopodial and sympodial rhizome systems, respectively.

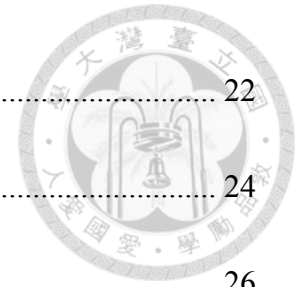
**Key words:** bamboo, modelling, production, biennial cycles, leaf phenology, expansion, rhizome



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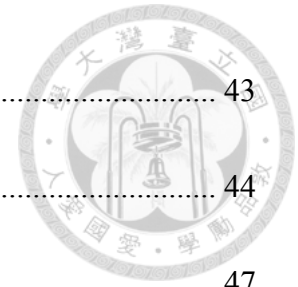
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# Chapter 1 General Introduction

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## 1.1 Bamboo Geographic Distribution and Uses

Bamboo is a unique group of evergreen perennial grass with woody jointed stems. It belongs to the subfamily *Bambusoideae* of the grass family *Poaceae*. The Bamboo distributes widely, growing naturally in the tropical, sub-tropical, and temperate regions on all continents except Europe and from sea level up to 4000m elevation (Clark *et al.*, 2015). Globally, the bamboos grow on at least 37 million hectares and on average make up 3% of the forest area of the countries which have bamboo, such as India, China, and Indonesia, etc. (Lobovikov *et al.*, 2007).

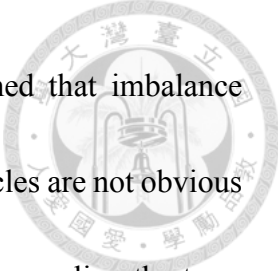
Bamboo is fast-growing species, which has been used for multipurpose. It has played a necessary part in daily life of many people in the tropical region for centuries. In the last decades, bamboo has been noticed as the renewable resource, the regenerative energy, and a substitute material for timber. Its shoots can be served as food. Its culms have excellent technological properties for construction, furniture, and handicraft products. It can be processed into bamboo flooring, bamboo charcoal products and so on. Its fibers are a valuable material for paper as a substitute for wood. Bamboo is also used to provide wind protection in farming and to stabilize riverbanks and hillsides (Clark *et al.*, 2015).

## 1.2 Annual Production Cycles of Moso bamboo



Moso bamboo (*Phyllostachys pubescens*) is one of the major forest types in East Asia. It is native to the southern part of China and was introduced in Japan, Korea, Vietnam, the USA and Europe (Rao *et al.*, 1998; Benton, 2015). Moso bamboo is useful for food, materials, and carbon fixation. Hence, the understanding of the factors that influence its productivity is important.

The two-year production cycles have been observed in managed Moso bamboo stands; A high number of new shoots is produced in a good year, and then a poor year follows with a low rate of productions (Li *et al.*, 1998b; Kleinhenz and Midmore, 2001; Song *et al.*, 2016). One hypothesis for explaining this production cycles has been widely accepted; telling that the leaf lifespan and the age structure of bamboo population are the causes. The leaf lifespan of Moso bamboo is mainly two years. New leaves have good photosynthesis capacity, but they are aging and have low photosynthesis capacity in the second year (Huang *et al.*, 1989). Except for the first-year culms, the “even” age culms have new leaves and “odd” age culms have old leaves. Since the production of new shoots highly depends on photoassimilates from mature bamboo, the number of new shoots can positively correlate with the proportion of culms with new leaves (that is “even” age culms). The hypothesis argues that the two-year production cycles occur because that imbalance between “even” and “odd” age structure once happened for some external



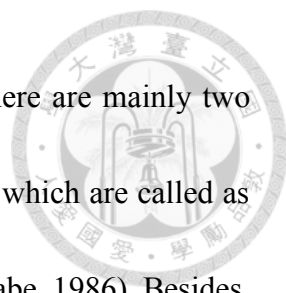
factors, subsequently, the two-year leaf lifespan precisely maintained that imbalance structure (Li *et al.*, 1998a; Li *et al.*, 1998b). However, the two-year cycles are not obvious in some cases. Further studies are needed to clarify possible factors canceling the two-year production cycles.

The long-term field study could provide us empirical evidence for the positive correlation between the number of new shoots and the proportion of culms with new leaves. However, there were so many factors in the field, thus the causality that leaf lifespan cause the two-year production cycles is still uncertain. To test the previous hypotheses without uncertainties, the ecological modeling approaches might be a suitable method.

### **1.3 Expansion of Moso bamboo**

The phenomenon of Moso bamboo expansion has been described for decades (Okutomi *et al.*, 1996; Yuji Isagi and Torii, 1997; Ding *et al.*, 2006). However, the mechanism behind the expansion is still unclear. From a viewpoint of population ecology, the expansion of bamboo is the consequence of competition between forest trees and Moso bamboo.

According to previous studies, the rhizome system plays an essential role in the production of bamboo (Tachiki *et al.*, 2015; Song *et al.*, 2016). Bamboo is a clonal plant. Its vegetative propagation is done through developed rhizomes system. Rhizome is



underground stem, sending out roots and shoots from its nodes. There are mainly two forms of bamboo rhizome system, monopodial and sympodial ones, which are called as running and clumping bamboos, respectively (McClure, 1966; Watanabe, 1986). Besides, the monopodial species mainly grow in the temperate region; the sympodial species usually grow in the tropical areas (Lobovikov *et al.*, 2007).

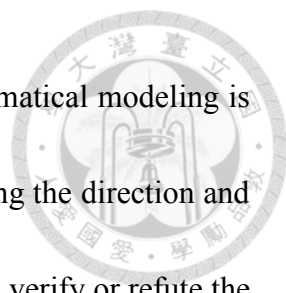
The Moso bamboo has the monopodial rhizome system. The rhizomes can maintain connection over tens of meters and keep alive for over ten years (Li *et al.*, 1998a). Therefore, the new shoots can emerge far away from the existing mature bamboo. This characteristic might enable Moso bamboo to invade to surroundings. With longer rhizome, the rapid expansion seems more likely to happen. However, there must be some cost for growing and maintaining this underground system (Lin, 2015).

Under the conditions of having both benefits and costs, a certain rhizome length should maximize the survival rate and/or expansion frequency of bamboo population. Besides, the appropriate rhizome length for survival under different environment might be different since the species with different types of rhizome grow in different climate zones (Lobovikov *et al.*, 2007).

## **1.4 Modeling Approach**

Many ecological studies rely on observation in natural environment. However, due to complexity of natural systems, long-time observation on many different components

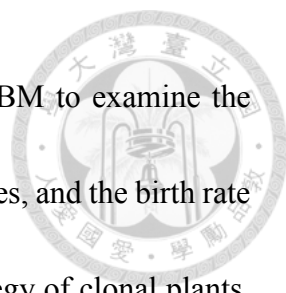




will not always bring us clear understanding of ecology. The mathematical modeling is an alternative approach, which can act as simplified road maps, giving the direction and idea of exactly what things we should observe in nature. By trying to verify or refute the model predictions, we will make faster progress in understanding nature. It is worth noting that the models often tell us more about nature when their predictions do not match with our field observations. By comparing the predictions and observations, then carefully checking the assumptions of the model, researchers could find the missing link that might be important in the mechanism. In other words, the model predictions can provide new insights and interpretations in field observations (Gotelli, 2008).

For most plants and animals, birth and death rates depend on the age of an individual. Therefore, the age structure of a population has the potential to affect population growth (Gotelli, 2008). The production capability of a Moso bamboo population could be related to its age structure through specific leaf lifespan. By building and testing an age-structured model reproducing annual cycles of bamboo shoots production, this study might validate the previous hypotheses (Li et al. 1998) without a long-term field observation.

The expansion of Moso bamboo is a phenomenon that might relate to the local interaction and variability among individuals. Individual-based models (IBMs) allow researchers to study how system level properties emerge from the behavior of individuals



(Grimm *et al.*, 2006). For instance, Oborny *et al.* (2001) used an IBM to examine the efficiency of foraging by differential birth rate and death rate in patches, and the birth rate and death rate was related to patch quality and split/integration strategy of clonal plants.

The IBMs approaches might be suitable for reproducing the ability of bamboo to invade and expand in other forest types and enable to examine the effect of elongation rhizomes on the expansion in different environment conditions.

## 1.5 Objectives

This study used modeling approaches to understand the production and expansion of Moso bamboo. The chapter reviewed the previous study about production, leaf phenology and rhizome system. In chapter 3, this study aimed to understand the potential determinants of inter-annual cycles of new shoots production in Moso bamboo stand through an age-structured population growth model. Based on the modeling results, this study discussed the effect of leaves phenology and belowground carbon storage. In chapter 4, this study aimed to find out the possible factors promising Moso bamboo expansion. A one-dimensional IBM was built to observe the effect of rhizome length, the cost for elongation, and available resource on the survival and expansion of Moso bamboo. By this, this study summarized the conditions that enable the expansion of bamboo forest and provided a new insight for the geographic distribution of two types of rhizome system.

## Chapter 2 Literature Review

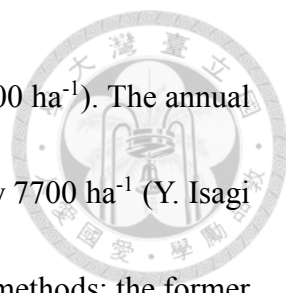
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### 2.1 Production of Moso bamboo

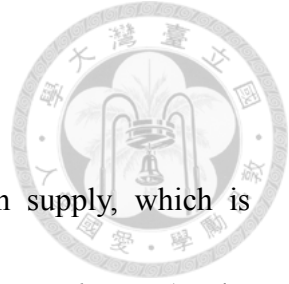
Bamboo is roughly classified into two groups based on different growth form: herbaceous bamboo and woody bamboo. The lignification makes the woody bamboo strong enough to grow as high as tree species. *Dendrocalamus giganteus*, one of the largest bamboo, can grow up to 40 meters or more. However, unlike tree species, the absence of secondary growth limits the bamboo size after it mature. All of these special characteristics let it be referred as “giant woody grass”.

Nath *et al.* (2015) suggests that woody bamboo offers tremendous opportunity for carbon farming and carbon trading because of its rapid biomass accumulation. Moso bamboo (*Phyllostachys pubescensin*), a monopodial woody bamboo, is one dominant species in East Asia. Although Moso bamboo belongs to the grass family, it builds up a landscape that may be called as a forest rather than a grassland. The biomass carbon storage of Moso bamboo is about 46 t ha<sup>-1</sup> (Yuen *et al.*, 2017) with the carbon concentration of about 46 % (Y. Isagi *et al.*, 1997). The biomass accumulation comes from photosynthesis. Photosynthesis rate and leaf area determine the total photosynthesis of a bamboo stand (Kleinhenz and Midmore, 2001). The photosynthesis rate of new leaves was 6.0 - 9.5  $\mu\text{molm}^{-2}\text{s}^{-1}$  (Shi *et al.*, 2005; Gratani *et al.*, 2008). The annual CO<sub>2</sub> sequestration was estimated as about 14 kg per culm (Gratani *et al.*, 2008), which can be



equivalent to 29.4 t C ha<sup>-1</sup> (when I assume stand culm density of 7700 ha<sup>-1</sup>). The annual gross production was about 32.8 t C ha<sup>-1</sup> in a stand with culm density 7700 ha<sup>-1</sup> (Y. Isagi *et al.*, 1997). These production values were measured with different methods; the former was directly measured on leaf photosynthesis and the latter summarized the outflow of carbon (that is respiration) and increment in biomass. Even though, the two values nearly corresponded to each other, showing large annual gross production, which were equivalent to annual gross production in tropical forests (Isagi *et al.* 1997).

The photosynthesis rate of a leaf depends on its age, the age of culm that it is growing on, position in the canopy, nutritional status, and climate condition. The lifespan of leaves of Moso bamboo is mainly two years. That is, the lifespan of leaves on culms of  $\leq 1$ -year-old is only one year, while the lifespan of all leaves on culms of  $>1$ -year-old is two years. Furthermore, the leaf age on the culms of a specific age is very similar (Li *et al.*, 1998b). That is because about 70% of old leaves falling together during the new shoots growing period. Following the defoliation, the new leaves develop in June, reaching the maximum expansion in the middle of July (Gratani *et al.*, 2008). The photosynthesis rate of new leaves is nearly 3 times higher than old leaves (Huang *et al.*, 1989). Since the carbohydrates for growth and production all comes from photosynthesis, the leaf phenology might play an essential role in the production of Moso bamboo.




## 2.2 Rhizome

New shoots emergence and growth owe the external carbon supply, which is transported from the mature bamboos through rhizome system (Song *et al.*, 2016). The root:shoot ratio of Moso bamboo is 0.55 (Yuen *et al.*, 2017), it is relatively high compared with root:shoot ratio 0.2-0.4 of natural forest (Mokany *et al.*, 2006). Moso bamboo allocates a considerable amount of carbon to underground tissue.

Bamboos have developed rhizomes system. Rhizome is specific underground stem, sending out roots and shoots from its nodes. The rhizome system can be categorized into two groups: sympodial and monopodial. The bamboo species with sympodial rhizome clump together. Their rhizomes are generally short and thick, spreading in short distances each year, so the new shoots emerge just beside the existing mature bamboos. In contrast, the bamboo species with monopodial rhizomes spread fast, so called as running bamboos. They extend their rhizomes for a long distance, so the new shoots can emerge far away from the existing one. This characteristic enables them to invade surrounding ecosystems. Interestingly, the rhizomes systems are related to climate zone. The sympodial (short rhizomes) species usually grow in the tropical areas and the monopodial (long rhizomes) species usually grow in the temperate regions (Lobovikov *et al.*, 2007).

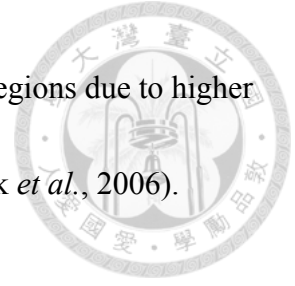
Moso bamboo has monopodial rhizomes. Contrary to tree seedlings, which are independent of mother tree, the Moso bamboo shoots connect to surrounding mature



bamboos through the rhizome system. Thus, bamboo shoots can receive materials for growth from mature bamboos. Song *et al.* (2016) reported that the Moso bamboo shoots reach an average height of 13.26m and biomass 3.89kg within 38 days after shoots emerging. In this fast growing period, all the carbon contents needed for structural growth and metabolism are transferred from surrounding mature bamboo to new shoots via underground rhizomes. The transportation continued until the leaves of young bamboos can provide enough carbohydrates to satisfy its own demands.

The Moso bamboo with the monopodial rhizome might enable it to invade surrounding ecosystems. The elongation of rhizome may benefit to expansion. However, there must be some cost for growing and maintaining this underground system. There is a tradeoff to allocate biomass to aboveground and belowground. To grow long rhizomes means that proportionately less new shoot production. In addition, the metabolism of rhizomes system also consumes the resource. The annual underground autotrophic respiration of Moso bamboo stand was about 5.0 t C ha<sup>-1</sup>, which was higher than temperate forest (Lin, 2015). In addition, the temperature sensitivity (Q10 value, it is the coefficient for the exponential relationship between root respiration and temperature) of Moso bamboo was significantly higher than that of surrounding forest such as *Cryptomeria japonica* (Lin, 2015), suggesting the cost for growing underground system would obviously increase if the temperature is higher. The cost for rhizosphere biomass

developments in tropical regions might be higher than in temperate regions due to higher temperature in tropical regions than that of temperate regions (Kottek *et al.*, 2006).







# Chapter 3 The Potential Determinants of Inter-annual Production Cycles of Moso bamboo

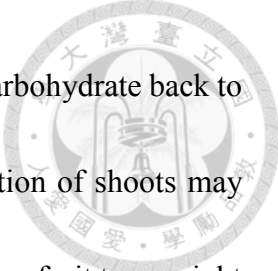
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## 3.1 Introduction

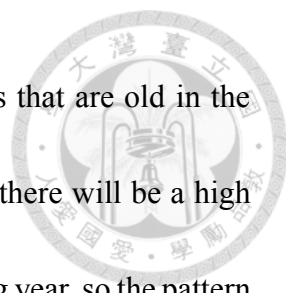
Moso bamboo is one of the major forest types in East Asia. It has a long period of vegetative propagation in lifespan, reproducing new shoots from nodes on rhizomes. Normally, new shoots sprout in early spring and complete their growth within two months. After that, no stem growth is found (Song *et al.*, 2016). Thus, the new shoots emergence in the spring can determine the annual productivity in Moso bamboo forests. Hence, the understanding of the new shoots productivity is important to consider management practices in the bamboo forests.

The two-year cycles have been observed in managed Moso bamboo stands; A high number of new shoots is produced in a good year, and then a poor year follows with a low production (Li *et al.*, 1998b; Kleinhenz and Midmore, 2001; Song *et al.*, 2016). Similar two-year cycles of production have also been found in species of fruit trees such as apples and pears. The studies suggested that: at the individual level, a fruit tree takes time to recover from depletion of carbohydrate reserves after a good year; at the stand level, abnormal weather conditions act as triggers that can synchronize fruiting cycles of trees (Silvertown and Charlesworth, 2009). Yet the bamboo is well known for fast vegetative growth. Unlike the fruits just take out carbohydrate from their mother trees, the new



bamboo shoots elongate fast then start photosynthesis, contributing carbohydrate back to the bamboo stand. The consumption of carbohydrate for the production of shoots may recover fast, probably within one year. Thus, different mechanisms from fruit trees might cause the periodic population dynamic of Moso bamboo.

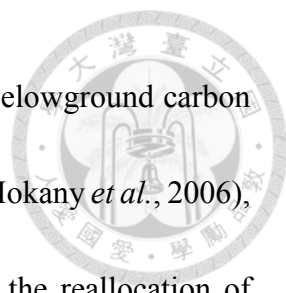
Long-term records in East Asian countries tell us distinctive two-year cycles of new shoots production, and one hypothesis has been widely accepted. The two-year leaf lifespan combined with the imbalance between “even” and “odd” age structure leads to the two-year production cycles (Li *et al.*, 1998b). Moso bamboo leaves show a particular lifespan. The lifespan of leaves is mainly two years, that is, the lifespan of leaves on culms  $\leq 1$ -year-old is only one year, while the lifespan of all leaves on culms  $>1$ -year-old is two years. Furthermore, all leaves in an individual are at the identical age. All culms with a specific age have similar leaf age. If so, the leaves of first-year culms and even age culms are both new leaves. Contrary, the leaves of other odd age culms are old leaves (Li *et al.*, 1998b). Photosynthesis rate of new leaves is much higher than old leaves (Huang *et al.*, 1989), leading to more significant contribution of carbohydrate assimilation by new leaves than old leaves to new shoots production. Thus, the number of new shoots can positively correlate with the proportion of bamboo with new leaves in a stand. If for any reason (e.g., disturbances or management practices), the ratio between number of adult bamboos with new leaves and those with old leaves deviates from 1:1, the bamboo



stand will have more leaves that are new in the year and more leaves that are old in the next year. When there are more leaves that are new in a given year, there will be a high production of new shoots. Then new leaves getting old in the following year, so the pattern is reversed and leading to low production. This mechanism was proposed by Li *et al.* (1998b) and it has been widely accepted for explaining the marked biennial alternations in production of shoots.

Although there are widespread observations of the two-year cycles of new shoots production in managed forests, the two-decade observation on the productivity of Moso in Sichuan (Li *et al.*, 1998b), located in the southern part of mainland of China, also revealed that the cycles of new shoots production were not obvious in some period.

Why the two-year cycles of new shoots production are not obvious in some periods if the two-year leaf lifespan can cause the biennial production cycles in Moso bamboo forests? There might be two types of possible reasons. First is about the leaves. The contributions of the old leaves with lower photosynthesis rate to total carbon assimilation might not be negligible at the population scale and then suppress the year-to-year variations in new shoots productions. In addition, leaf lifespan of first-year culms is an exception, they renew their leaves in one year (Kleinhenz and Midmore, 2001). Since their leaves are new and productive, the carbohydrate assimilated by this age class is supposed to be high in every year, leading continuous good years, and then eliminating



the two-year cycles. Second is about the carbon storage. The large belowground carbon storage, probably supported by high root:shoot ratio (Li *et al.*, 1999; Mokany *et al.*, 2006), would acts as a buffer to stabilize the production. The storage let the reallocation of resource in time scale possible. The photoassimilates produce in this year can supply the production of new shoot in the years to come by the mechanism of storage.

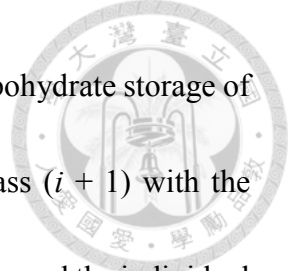
This study aimed to understand the potential determinants of inter-annual cycles of new shoots production in Moso bamboo stand through an age-structured population growth model. To start with, this study established an age-structured population growth model considering the specific leaf phenology and belowground carbon allocation in Moso bamboo forests. Then the effect of carbon assimilation and specific lifespan of leaf on the production at the population scale was examined through systematically changing the parameters related to photosynthesis rate of three-type leaves (first-year culms' leaves, new leaves, and old leaves) in the model. Subsequently, this study examined the impact of carbon storage by changing the allocation of carbohydrate from now to future use.

## **3.2 Materials and Methods**

### **3.2.1 Model Description**

#### **3.2.1.1 Major Assumptions**

This study considered the age structure of the bamboo population (Figure 1). The density of bamboo at age  $i$  ( $i = 0, 1, 2, \dots, 6$ ) at a stand  $N_i$  changes year by year. The density



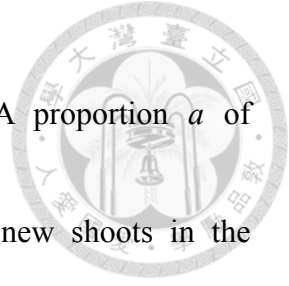
of new shoots depends on the leaf photosynthesis production and carbohydrate storage of the whole stand. The individual at the age  $i$  enters the next age class ( $i + 1$ ) with the constant survival rate  $s_i$  before age 7 ( $s_i=0.95$  for  $i = 0, 1, 2, \dots, 5$ ). I assumed the individual which grows up to age 7 is harvested and moved out from the stand, so its survival rate is zero ( $s_6=0.0$ ). To simulate the two-year leaf lifespan, I distinguished three types of leaves, new shoots ( $i = 0$ ) has first-year culms' leaves; age one, three and five have new leaves; age two, four and six have old leaves. The carbohydrate from leaf photosynthesis  $PH$  contributes to new shoots growth and/or carbon storage. The carbon storage  $ST$  contributes to current and/or following year new shoots growth. The model also considered carbon loss ( $L$ ) due to below-ground autotrophic respiration including fine, coarse roots, and rhizomes (Hsieh *et al.*, 2016).

### 3.2.1.2 Model equations

Density of bamboos at age  $i$  ( $i = 0, 1, 2, \dots, 6$ ) at a stand  $N_i$  changes with year  $t$  through following the age-structured model:

$$\begin{aligned}
 N_0(t+1) &= a \cdot PH(t) + (1-b) \cdot ST(t) \cdot (1-L), \\
 N_i(t+1) &= s_{i-1} \cdot N_{i-1}(t), \quad i = 1, 2, 3, \dots, 6 \\
 ST(t+1) &= (1-a) \cdot PH(t) + b \cdot ST(t) \cdot (1-L), \\
 PH(t) &= \left[ N_0(t) \cdot P_{first} + (N_1(t) + N_3(t) + N_5(t)) \cdot P_{new} \right. \\
 &\quad \left. + (N_2(t) + N_4(t) + N_6(t)) \cdot P_{old} \right] \cdot \exp\left(-d \sum_{i=0}^6 N_i(t)\right),
 \end{aligned}$$

Where  $N_i(t)$  is evaluated at spring of year  $t$ , and the total amount of photosynthetic carbohydrate product  $PH(t)$  from leaf photosynthesis is decreased by the total population



density (  $\sum_{i=0}^6 N_i(t)$  ) with the density dependence strength  $d$ . A proportion  $a$  of carbohydrate from leaf photosynthesis contributes to generating new shoots in the following year, the other  $(1-a)$  is transferred to the carbon storage. A proportion  $L$  of the storage  $ST(t)$  is lost until the following year spring due to belowground autotrophic respiration. The remaining carbohydrate storage at the beginning of the year  $t + 1$  (i.e.,  $(1 - L) ST(t)$ ) contributes to generating new shoots  $N_0(t+1)$  while the other fraction  $b$  remains as the storage at the year  $t + 1$ .

The photosynthesis rate of each type of leaves was controlled by parameter  $P_k$ , where  $P_{first}$  is the photosynthesis rate of first-year culms' leaves,  $P_{new}$  is the photosynthesis rate of new leaves, and  $P_{old}$  is the photosynthesis rate of old leaves. Note that  $N_0(t)$  has first-year culms' leaves,  $N_1(t), N_3(t)$ , and  $N_5(t)$  have new leaves,  $N_2(t), N_4(t)$ , and  $N_6(t)$  have old leaves in the model.

### 3.2.2 Model Analysis

This study focused on dynamics of production of new shoots ( $N_0$ ) as the indicator of bamboo forest productivity. I focused on the final state of the model bamboo population but not on the transient states that are highly dependent on the initial conditions. For this purpose, the model was run from year 0 to  $10^8$  ( $t = 0 - 10^8$ ) and the population size was recorded in the final five hundred years for further analyses, that represents the final state of the population dynamics. All of the numerical calculations was conducted by C

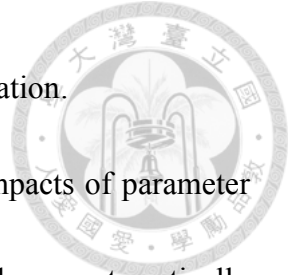


language.

To clarify the relationship between the number of new shoots and the leaf lifespan, this study observed the impacts of parameter  $P_{first}$ ,  $P_{new}$  and  $P_{old}$  on the production of new shoots. The first way to analyze and categorize the behavior of the population dynamics is to draw the bifurcation diagram. The bifurcation diagram is a visual summary of the succession produced as parameter increases (Jones *et al.*, 2009). For each value of  $P_k$ , the model was firstly run from year 0 to  $10^8$  ( $t = 0 - 10^8$ ) and then the successive values of  $N_0$  from the final five hundred years (i.e., five hundred values) were plotted. If the final state is a stable equilibrium (i.e., the population size approaches to a single value), the all 500 points will overlap and look like one point. Similarly, if the final state is the  $n$ -year (periodic) cycles, that is the  $N_0$  alternated between  $n$  values ( $n = 2, 3, 4 \dots$ ), the points will look like  $n$  points. Another possibility is that many different points in the diagram represent a pseudoperiodic cycle with very long period  $n$ , which implies a chaotic behavior of the population dynamics. As the second method, this study calculated the coefficient of variation (CV) base on the last five hundred data points. CV, which is defined as the ratio of the standard deviation to the mean, is a standardized measure of dispersion. When the final state is the equilibrium and a two-year cycle, CV will be equal

to 0 and  $\frac{N_{0\_max} - N_{0\_min}}{N_{0\_max} + N_{0\_min}}$  (if the number of new shoots in good and poor year is  $N_{0\_max}$

and  $N_{0\_min}$ ), respectively. When the final state shows more than two-year cycles, CV will



be larger than zero, the exact value depends on the dynamic of population.

In order to test the impact of leaf phenology, I observed the impacts of parameter  $P_{first}$ ,  $P_{new}$  and  $P_{old}$  on production of new shoots by fixing each one of them, systematically changing the other two from 0.0 to 10 with a step 0.05 and calculating coefficient of variation (CV) from the final state of the model. To test the impact of carbon storage, this study selected several parameter sets of  $P_{first}$ ,  $P_{new}$  and  $P_{old}$ , and changed parameter  $a$ ,  $b$  and  $L$  to observe the effect of the storage on final population state (Table 1).

### 3.3 Results

#### 3.3.1 Final States

The final states of this model were classified into three types: two-year cycles, stable equilibrium, and others (i.e., longer periodic cycles or chaotic fluctuations) (Figure 2).

For the case of two-year cycles, the population size (the number of annual new shoots) alternated regularly between two values in the final state, resulting in  $CV=$

$$\frac{N_{0\_max} - N_{0\_min}}{N_{0\_max} + N_{0\_min}} \quad (\text{if the number of new shoots in good and poor year is } N_{0\_max} \text{ and } N_{0\_min}).$$

For the equilibrium type, population sizes were constant in the final state ( $CV=0$ ). In the other type, population size alternated between more than two values or generated chaotic conditions, resulting in  $CV$  of  $> 0$  (Appendix S 1, S 2 dark blue region). Although the two-year and other cycles both show  $CV$  of  $> 0$ , I confirmed they appeared with different





range of the each parameter using bifurcation figures (Appendix S 3), the other type only appears when  $P_{first}$  was large.

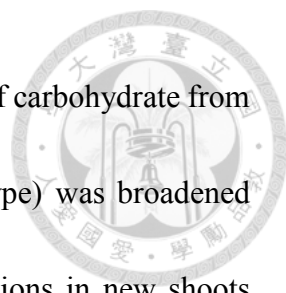
### 3.3.2 Impact of Leaf Phenology

The white region (i.e., stable type) was broadened with increases in  $P_{old}$ , indicating the contribution of carbohydrate assimilated by old leaves will weaken the two-year cycles (Figure 3). When  $P_{old}$  was relatively small (= 0.0), smaller and larger  $P_{first}$  produced 2-year cycles and stable condition, respectively, under the larger  $P_{new}$  ( $> 1$ ). On the other hand, under the smaller  $P_{new}$  ( $< 1$ ), smaller and larger  $P_{first}$  produced stable conditions and more than 2-year cycles, respectively (Figure 3a). In contrast, when  $P_{old}$  was relatively large (= 2.5), most of the parameter sets produced stable conditions (Figure 3c).

The white region (i.e., stable type) was also broadened with  $P_{first}$ , indicating the presence of the first-year culms' leaves will weaken the two-year cycles (Figure 4). When  $P_{first}$  was relatively small (= 0.0), all of  $P_{old}$  (=0.2-10) produced stable condition under smaller  $P_{new}$  ( $< 1$ ). On the other hand, smaller and larger  $P_{old}$  produced 2-year cycles and stable condition, respectively, under the larger  $P_{new}$  ( $> 1$ ) (Figure 4a). In contrast, when  $P_{first}$  was relatively large (= 10), most of the parameter sets produced stable conditions, except smaller  $P_{old}$  ( $< 1.5$ ) with small  $P_{new}$  ( $< 1.8$ ) produced more than 2-year cycles (Figure 4c).

### 3.3.3 Impact of Carbon Storage

As decreasing parameter  $a$  (decreasing proportion of carbohydrate from leaf




photosynthesis to generating new shoots means a higher proportion of carbohydrate from leaves became belowground storage), the white area (i.e., stable type) was broadened obviously, indicating the storage could stabilize year-to-year variations in new shoots production. When no carbohydrate became storage ( $a = 1.0$ ), the two-year cycles were found in the region with  $P_{new}$  of  $> 2$  and  $P_{first}$  of  $< 8$  (Figure 5a). When twenty percent of carbohydrate from leaf photosynthesis became storage ( $a = 0.8$ ), most of parameter sets ( $P_{new} = 2-10$ ,  $P_{first} = 0-10$ ) produced stable condition (Figure 5e).

On the other hand, final state conditions were insensitive to parameter  $b$  (proportion of carbohydrate from storage of roots and rhizomes to remain as storage). Slightly the white regions decreased with  $b$  (Figure 5bcd and efg), but the changes were not as large as those of parameter  $a$  (Figure 5abe). In addition, as increasing the loss ( $L$ ) of storage, the white area was decreased (Figure 6), indicating the loss of storage would promote year-to-year variations in new shoots production.

## 3.4 Discussion

### 3.4.1 Effect of Leaves Phenology and Belowground Carbon Storage

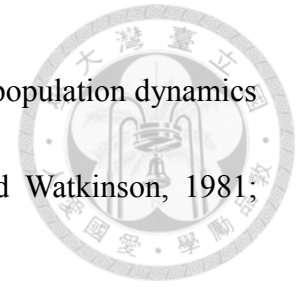
In this study, the increases in photosynthetic carbohydrate production from old leaves stabilized the production of new shoots (Figure 3). In addition, the increases in photosynthetic carbohydrate production from first-year culms' leaves led to stable state or  $>2$ yr periodic cycles (Figure 4). In contrast, the increases in photosynthetic



carbohydrate production from new leaves indeed brought about the two-year cycles of new shoots production (Figure 3abc, Figure 4ab, and Figure 5abcd). Whereas, only when the new leaf photosynthesis rate was much higher than that of old leaves and first-year culms' leaves, the two-year cycles appeared. In fact, even the old leaves are less active than new leaves; their photosynthesis rate still can be one-third of new leaves (Huang *et al.*, 1989). Moreover, photosynthesis rate of first-year culms' leaves is nearly same with new leaves. The parameter settings which satisfy the above conditions (ie,  $P_{old} = 1/3 P_{new}$  or  $P_{new} = P_{first}$ ) could not generate the two-year cycles of new shoots production in Moso bamboo forests (Figure 3abc, Figure 4abc, Figure 5abcdefg). The unneglectable impact of carbohydrates from photosynthesis of old leaves and first-year culms' leaves may cancel the two-year cycles of new shoots production. Therefore, this study would argue that only the two-year leaf lifespan could not be a cause of the two-year cycles of new shoots production.

In addition, increases belowground carbon allocation and storage in roots and rhizomes will stabilize the year-to-year variations in new shoots production (Figure 5). When new shoots production did not exhaust carbohydrate assimilated by leaves in the previous year, the carbohydrate could become carbon storage. As a result, a part of photosynthetic carbohydrate product from leaves could be supplied to new shoots production in following years, and the system would tend to be stable. The effect of

carbon storage is similar to the seed bank that could stabilize plant population dynamics by buffering against environmental perturbations (Macdonald and Watkinson, 1981; Eager *et al.*, 2014).



### 3.4.2 New Insight for Carbon Allocation

Although this study suggested that the two-year leaf lifespan could not be a complete explanation for the biennial production cycles, many bamboo forests showed two-year production cycles. If it were not a transition period after disturbances, we would need a more exhaustive explanation. New studies about carbon allocation of bamboo might help to bridge the gap between this study and previous observations. During the growing season, new shoots complete full height and diameter of growth within two months after emergence (Song *et al.*, 2016; Yen, 2016), this means the new shoots need massive resource in a short period. At the same time, culms with old leaves and first-year culms shatter and unfold new leaves during the period (Li *et al.*, 1998b). A previous study indicated that the surrounding mature bamboos attached to new shoots with rhizomes can transfer considerable amount of the non-structural carbohydrates (NSCs) in leaves, branches, trunks and rhizomes to new shoots (Song *et al.*, 2016). Thereby, it is possible that culms with new leaves could be responsible for the growth of new shoots and those culms with old leaves and first-year culms would use NSCs mainly for changing their own leaves. In this case, the photosynthesis of old leaves and first-year culms' leaves

could not contribute to new shoots production, while, only the number of individuals with new leaves could contribute to new shoots production. This is equivalent to  $P_{first}$  and  $P_{old}$  are both nearly zero, then the two-year cycles are more likely to occur.

The carbon allocation in different age culms and its temporal dynamics are still unclear. Further studies including an isotope labeling study conducted in different age culms are needed to clarify the possibility of mechanism maintain the biennial production cycles.



# Chapter 4 The Possible Factors Promising Moso bamboo Expansion

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## 4.1 Introduction

Moso bamboo forests expansion has been described and studied for decades. In Japan, the local bamboo industry was replaced by the import of bamboo products, thus some of the managed bamboo forests were abandoned due to lack of profits. The abandoned bamboo forests spread into or even replace surrounding vegetation (Yuji Isagi and Torii, 1997; Suzuki and Nakagoshi, 2008). In China, the Moso bamboo encroach surrounding primary broadleaved forest in the nature reserve. In Taiwan, Moso bamboo has been invading surrounding ecosystems such as *Cryptomeria* plantation in an experimental forest (private note). Researchers speculated that the rapid expansion of Moso was caused by few human interventions and difficult rejuvenation of other vegetation (Ding *et al.*, 2006).

The mechanism behind the expansion is unclear. The expansion happened without anthropogenic interferences (Okutomi *et al.*, 1996; Yuji Isagi and Torii, 1997; Ding *et al.*, 2006; Suzuki and Nakagoshi, 2008). From a viewpoint of population ecology, the expansion of bamboo is a competition between coniferous forests\temperate broadleaf forests and the Moso bamboo. Competition is a complex process containing both biotic and environmental factors. The Moso bamboo needs to survive in the competition, and




then it can have the chance to expand its territory.

There are some clues from previous studies to understand the mechanism behind expansion. Bamboo is a clonal plant, which produces new shoots through rhizome system. The shoots can grow to their full height within two months after their emergence. To implement this, the mature bamboos transfer considerable amount of NSCs to the growth of new shoots via rhizomes (Song *et al.*, 2016). The rhizome system can be an essential physiological factor in the production of bamboo (Tachiki *et al.*, 2015).

The Moso bamboo with the monopodial rhizome system can extend rhizomes for a long distance. Its new shoots can emerge far away from the existing mature bamboo. This characteristic might enable it to invade surrounding ecosystems. The elongation of rhizome may be beneficial to expansion, but there must be some cost for growing and maintaining the underground system. In addition, the amount of cost might be influenced by temperature, as rhizosphere autotrophic respiration increased with temperature with high temperature sensitivity (Lin, 2015).

Besides physiological factors, environment conditions, such as topography and latitude, can change the distribution and/or amount of resource. The available resource control the survival of species (Tilman, 1988; Tatenno and Takeda, 2003). The distribution of resource might be affected by the terrain (Giambelluca, 2014). The uneven distribution of resource might affect the expansion of moso bamboo. In global scale, species with





different type of rhizomes grow in different climate zone. The monopodial species mainly grow in the temperate region; the sympodial species usually grow in the tropical areas (Lobovikov *et al.*, 2007). This implies the bamboos may have appropriate rhizome length for survival under different environment.

This study aims to find out the possible factors promising Moso bamboo expansion through a one-dimensional individual-based model. Considering the rhizome length as physiological factor and resource distribution and amount as environmental factors, this study attempted to understand the impact of these factors on the survival and expansion of Moso bamboo. After that, this study summarized the conditions that enable the expansion of bamboo forest. In addition, the specific rhizome length with higher survival and expansion frequency under a certain environment might indicate appropriate rhizome length for survival in the certain environment. This might help to explain the distribution pattern of sympodial and monopodial along the latitude.

## **4.2 Materials and Methods**

### **4.2.1 Model Description**

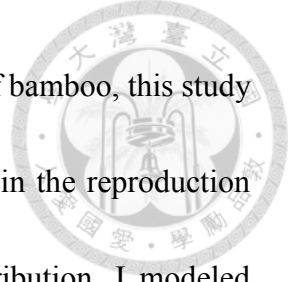
#### **4.2.1.1 Major Assumptions**

This study followed the invasion and expansion of Moso bamboo in a habitat with established forest. One bamboo individual was placed in the center of the habitat. Then let the bamboo clonally grow and compete with trees in the established forest. The spatial

variations in resource availability were also considered in this model (Figure 7).

Habitat space was represented by a series of square lattices, which consisted of  $1 \times 199$  grids, with fixed boundary. Each grid had one established tree and offered a potential habitat for the bamboos. Probabilities of survival and vegetative reproduction of the bamboos in one grid depended on the amount of the available resource, the size of the existed tree, and the number of the existed bamboos in that grid. The trees in established forest grew their size through time but do not produced seedlings; similarly, their probabilities of survival depended on the amount of the available resource, the size of itself, and the number of the bamboos. Thus, competition for space was directly implemented in the model at the unit spatial scale.

In the beginning of one simulation, I put one bamboo in the center grid (the 100th grid); and generated a series of tree size to represent the established forest and a series of resource amount (Figure 7bc). There were three actions for each time step, 1) reproduction for the bamboos with rhizome elongation, 2) growth for the trees, and 3) death for both of them. The simulation ran for 100 time steps (i.e., 100 years). One possible result was that the bamboo population disappeared; in other words, all bamboos died. In other results, the bamboos expanded their territory. For each combination of a set of parameters, 10,000 repetitions were made (i.e., 100-year simulation repeated 10,000 times).



To observe the impact of the rhizome length on the expansion of bamboo, this study varied the potential distance from the shoot to the mother bamboo in the reproduction stage (Figure 7d). To understand the impact of the resource distribution, I modeled resource as different degree of concentration in the center of the habitats as shown in section 4.2.2 (Figure 7c dashed line). To know the impact of the resource amount, I varied the mean amount of the resource (Figure 7c dotted line).

#### 4.2.1.2 Model equations

This study built three layers to record the number of bamboos, tree size in established forest, and the available resource. The initial condition of Moso bamboo layer was:

$$B_{100} = 1,$$

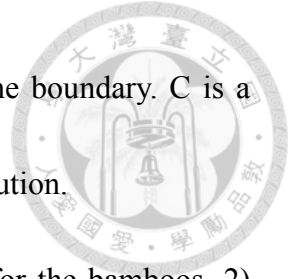
$$B_i = 0, \quad i = 1, 2, 3, \dots, 99, 101, \dots, 199$$

$B_i$  is the  $i^{\text{th}}$  grid of the Moso bamboo layer. There was only one bamboo in 100<sup>th</sup> grid. The initial sizes of trees in established forest were generated with spatial autocorrelation, using the libraries `gstat` in software R. The mean of trees size was nearly 1. The resource distribution was a quadratic equation:

$$R_i = R_{mean} + t \cdot \left( \frac{\sqrt{k}}{99} \cdot (i - 100) \right)^2 - C, \quad t = \pm 1, \quad i = 1, 2, 3, \dots, 199, \quad k \geq 0,$$

$$C = \sum_{i=1}^{199} t \cdot \left( \frac{\sqrt{k}}{99} \cdot (i - 100) \right)^2 \div 199$$

$R_i$  is the  $i^{\text{th}}$  grid of the resource layer. When  $t = 1$ , the distribution curve is concave, the minimum resource is at the center and the maximum is at the boundary. On the contrary, when  $t = -1$ , the distribution curve is convex, the maximum resource is at the center. I



used  $k$  to control the absolute difference between the center and the boundary.  $C$  is a constant to let the mean amount of resource keep same in any distribution.

There were three actions for each time step, 1) reproduction for the bamboos, 2) growth for the trees, and 3) death for both of them. Each bamboo had the opportunity to produce one new shoot in a time step. The location of shoot was randomly chosen from grids in a certain distance from mother bamboo. The rhizome length determined the certain distance. The survival probability for a new shoot in located grid was:

$$s_i(t) = \exp\left(-\frac{1}{R_i}(B_i(t) + T_i(t))\right) \cdot (1 - c \cdot |i - i_m|)$$

$s_i(t)$  is the survival probability of the new shoot when it located in  $i^{\text{th}}$  grid.  $R_i$  is the amount of available resource.  $B_i(t)$  is the number of the existed bamboos.  $T_i(t)$  is the size of the existed tree.  $i_m$  is the location of mother bamboo.  $c$  is the unit cost for reproducing a shoot away from mother bamboo. The longer distance from the mother bamboo caused higher cost than that of shorter distance.

The new shoot had probability  $s_i(t)$  to survive. If the shoot survives in that  $i^{\text{th}}$  grid:

$$B_i(t+1) = B_i(t) + 1$$

On the other hand, the existed trees grow through time:

$$T_i(t+1) = T_i(t) \cdot \left(1 + \frac{R_i}{2500}\right) \quad i = 1, 2, 3, \dots, 199$$

The growth rate of trees depended on resource amount.

The death probability for the bamboos and trees was:

$$d_{B_i}(t) = 1 - \exp\left(-\frac{1}{R_i} \cdot (B_i(t) + T_i(t))\right) \quad i = 1, 2, 3, \dots, 199$$

$$d_{T_i}(t) = 1 - \exp\left(-\frac{1}{T_i(t) \cdot R_i} \cdot B_i(t)\right) \quad i = 1, 2, 3, \dots, 199$$



The more resource caused the lower death probability. Due to density-dependent effect, the more existed bamboo in the same grid caused higher death probability for both. The size of the tree was conducive to survival for itself (Harcombe, 1987), and it was a disadvantage to bamboo. The bamboo and tree have probability  $d_{B_i}(t)$  and  $d_{T_i}(t)$  to die respectively. If the bamboo and/or tree die in  $i^{\text{th}}$  grid:

$$B_i(t+1) = B_i(t) - 1$$

$$T_i(t+1) = 0$$

#### 4.2.2 Model Analysis

This study used R as a platform of programming. During the 100 time steps simulation, the bamboo population expanded their territory or disappeared in the end. I recorded the spatial distribution of the Moso bamboos and trees in a column of grids in each time step. The history of one simulation could be shown as a gradient map (as Figure 8). For each combination of a set of parameters, 10,000 repetitions were made. I calculated expansion frequency of bamboo in the 10,000 repeats. In addition, this study averaged final territory of bamboo when they had expanded. That is, the results of a set of parameters were presented as two orientations, the expansion frequency, and the final



territory.

This study first examined the impact of the rhizome elongation and its cost on frequency of expansion and width of territory of bamboo. A rhizome length was set in each simulation. For example, there is a bamboo located in  $i^{\text{th}}$  grid. With a rhizome length equal to one, it can produce shoots at  $i-1^{\text{th}}$ ,  $i^{\text{th}}$ , and  $i+1^{\text{th}}$ . With a rhizome length equal to three, it can produce shoots in the range from  $i-3^{\text{th}}$  to  $i+3^{\text{th}}$  (Figure 7d). I tested the rhizome length from one to six. At the same time, I tested three levels of the unit cost ( $c=0.01$ ,  $0.05$ ,  $0.1$ ) for reproducing a shoot away from mother bamboo.

Secondly, this study focused on the effects of spatial distribution of resource on Moso bamboo expansion. Under the conditions of constant resource amount, I changed the distribution of resource using the quadratic equation (See 4.2.1.2). The distribution curve could be either concave, flat or convex. I also changed the absolute difference between the center and the boundary.

Thirdly, I observed the complex impact of physiological factor and environment factor. In low-cost ( $c=0.01$ ) and high-cost ( $c=0.1$ ) condition, I altered the mean resource amount respectively. Then the best strategies for Moso bamboo expansion under the different conditions were discussed.



## 4.3 Results

### 4.3.1 Time Series

The bamboo population expanded their territory or disappeared at the end of each simulation (Figure 8ab).

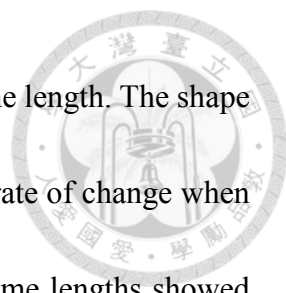
### 4.3.2 Impact of Rhizome Length

Mostly, elongating rhizome was beneficial for bamboo expansion. When the cost for elongating rhizome were low ( $c=0.01$ ), medium ( $c=0.05$ ), and high ( $c=0.1$ ), bamboos with rhizome length of six, four, and three had highest frequency of expansion respectively. The most significant increase of the frequency expansion appeared when the rhizome length changed from one to two. The negative impact of the cost was magnified with increases in the rhizome length (Figure 9).

When the cost for elongating rhizome were low ( $c=0.01$ ) and medium ( $c=0.05$ ), longer rhizome length could lead to broader territory. However, when the cost was high ( $c=0.1$ ), increasing rhizome length ( $> four$ ) did not change the final territory of the expansion (Figure 10).

### 4.3.3 Impact of the Distribution and Amount of Resource

The x-axis in Figure 11 presents resource distribution, the value means the difference of resource amount between middle and boundary ( $= R_{100} - R_1$ ). The negative values indicate concave curves; the zero is flat; the positive values are convex curves. All lines increased with the values in the x-axis, meaning that resource concentration in the middle




of the bamboo population was beneficial for expansion for all rhizome length. The shape of rhizome length of one showed a sigmoid curve. It had the fastest rate of change when resource distribution ranging from -2 to 2. The shape of other rhizome lengths showed power curve. They had the fastest rate of change when resource distribution from -4 to 0 (Figure 11). In the condition of concave resource distribution (i.e.,  $R_{100} - R_l < 0$ ), the benefit from elongate rhizome was obvious. Whereas, in the condition of convex resource distribution (i.e.,  $R_{100} - R_l > 0$ ), only elongate rhizome from one to two was beneficial. Focusing on rhizome length from one to two, the fastest rate of change appeared when the resource was evenly distributed, and the rate of change was relatively slow no matter resource concentrate in the middle or boundary (Figure 12).

The concentration of resource was beneficial for expanding bamboo's territory, except when the bamboo population was getting closer to the boundary (rhizome length=5,6). Increasing rhizome length was beneficial for expanding bamboo's territory in all resource condition (Figure 13).

Mean resource amount ( $R_{mean}$ ) and cost for elongate ( $c$ ) affected the benefit for elongate rhizome at the same time. Considering an evenly distributed resource, as the mean resource amount increased, the frequency of expansion increased (Figure 14ab). In low-cost condition ( $c=0.01$ ), bamboo improved the frequency of expansion by elongating rhizome (Figure 14a). However, the effect of improving would be different in different





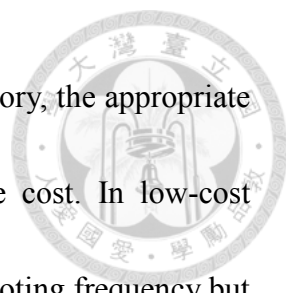
amount of resource. The degree of improving was highest in the middle-level amount of resource ( $R_{mean}=5$ ); it was not obvious in high-level ( $R_{mean}=6.5, 8.0$ ) or low-level ( $R_{mean}=3.5$ ) amount of resource (Figure 14a). On the contrary, in high-cost condition ( $c=0.1$ ), there was no help for elongating rhizome in low-level resource amount ( $R_{mean}=3.5$ ). In middle-level resource amount ( $R_{mean}=5.0$ ), the rhizome length elongating from one to three increased frequency of expansion, but elongating from three to six did not. In high-level resource amount ( $R_{mean}=8.0$ ), shorter rhizome (rhizome length = 1–3) showed higher frequency of expansion than that of longer rhizome (rhizome length = 6) (Figure 14b).

In all condition, increasing mean resource amount and/or increasing rhizome length were both beneficial for expanding bamboo's territory (Figure 15). Comparing the low-cost and high-cost condition, the territory was almost same in the case of rhizome length of one. However, the territory became narrow with increases in the cost when the case of the rhizome length of three or six. Especially, the decreased final territory was obvious in the middle-level amount of resource ( $R_{mean}=5$ ).

## 4.4 Discussion

### 4.4.1 Rhizome Length

Elongating rhizome was beneficial for bamboo expansion. However, there were diminishing returns, especially when the cost for elongating the rhizome increased




(Figure 9). Summarizing the expansion frequency and the final territory, the appropriate rhizome length for survival was different in accordance with the cost. In low-cost condition, rhizome length more than three was unnecessary for promoting frequency but it was still beneficial for broadening territory. In high-cost condition, rhizome length more than three caused negative impact on frequency of expansion and final territory (Figure 9 and 10).

#### **4.4.2 Resource Amount and Distribution**

The concentration of resource in the middle of the bamboo population (i.e., the convex distribution) is beneficial for bamboo to expand (Figure 11). However, a convex distribution means that the available resource will decrease when population expand away from the center. Thus, the bamboos on the edge of the population could gradually face to an unfitness environment. Therefore, the expansion slowed down and eventually stoped (Figure 13 rhizome length=5,6). This kind of resource distribution might be derived from topography, such as aspect and slope (ex., lower/upper slopes) (McCune and Keon, 2002).

Mean resource amount ( $R$ ) and cost for elongate ( $c$ ) affected the benefit for elongate rhizome at the same time. In low-cost condition, elongating rhizome could improve the frequency of expansion the most when the amount of resource was in middle-level (Figure 14a). On the contrary, in high-cost condition, bamboo had little benefit or even negative impact from elongation. Especially in high-level resource amount, no elongation would



be better strategy (Figure 14b). The high-cost and high-level resource amount condition might be similar to the climate in tropical rainforest since the high temperature might result in high autotrophic respiration of rhizosphere (Lin, 2015), and there are sufficient solar radiation and rainfall all year in tropical regions. On the other hand, the low-cost and middle-level resource amount condition might be similar to the climate in temperate monsoon regions since the relatively low temperature in temperate regions might result in low autotrophic respiration of rhizosphere, and the solar radiation and rainfall in temperate regions can be not plenty as those in the tropical rainforest. This simulation might provide reasonable interpretations for difference in habitat of bamboos with sympodial and monopodial rhizome systems in tropical and temperate regions, respectively.



## Chapter 5 General Conclusion

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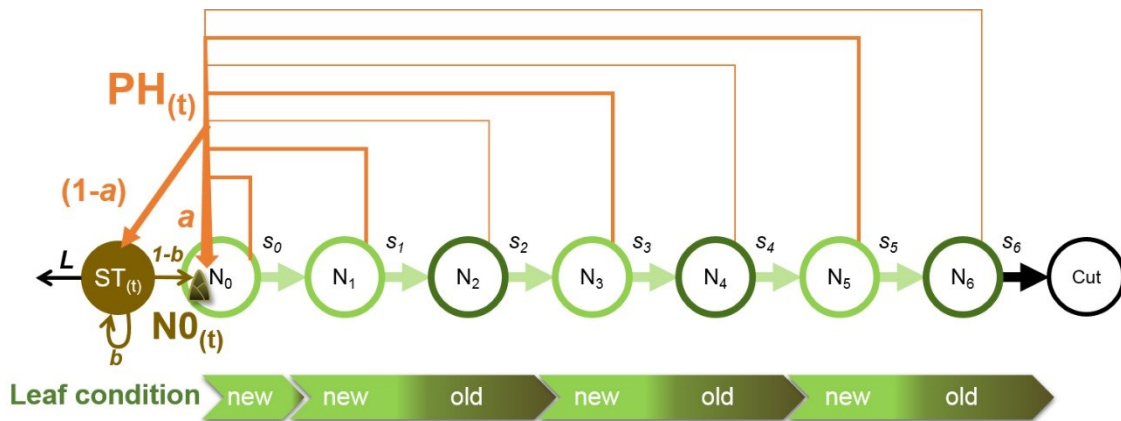
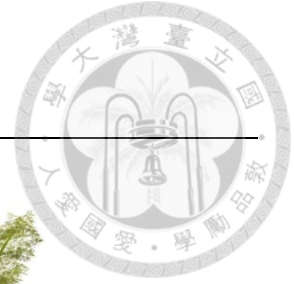
This study aimed to understand the potential determinants of inter-annual cycles of new shoots production in Moso bamboo stand and the factors promising Moso bamboo expansion based on ecological models developed in this study. The results from the age-structured population growth model suggested that photosynthesis contribution from the old leaves, first-year culms' leaves, and/or belowground carbon storage could cancel the 2yr-cycle. The production of Moso bamboo is stable in long-term in spite of the 2yr cycle of leaf phenology and the imbalance of initial culm age structure. Based on this fact, this study considered production without the influence of leaf phenology nor culm age in next part, the expansion model. The results from individual-based model indicated the rhizome length was important factors for expansion. The Moso bamboo population could easily invade to the surrounding forest and expand its territory with long rhizome when the cost for rhizome construction was low and the resource amount was middle-level.

Previous studies mostly focused on new leaves and productive culms of Moso bamboo. Whereas, further study of the physiology of old leaves, first-year culms' leaves is valuable for evaluating stand level production. In addition, the empirical study of the allocation of carbon from photosynthesis of different-age leaves is still needed for giving an evidence for the mechanism of production. In summary, the belowground carbon dynamic plays an important role in both production and expansion process of Moso

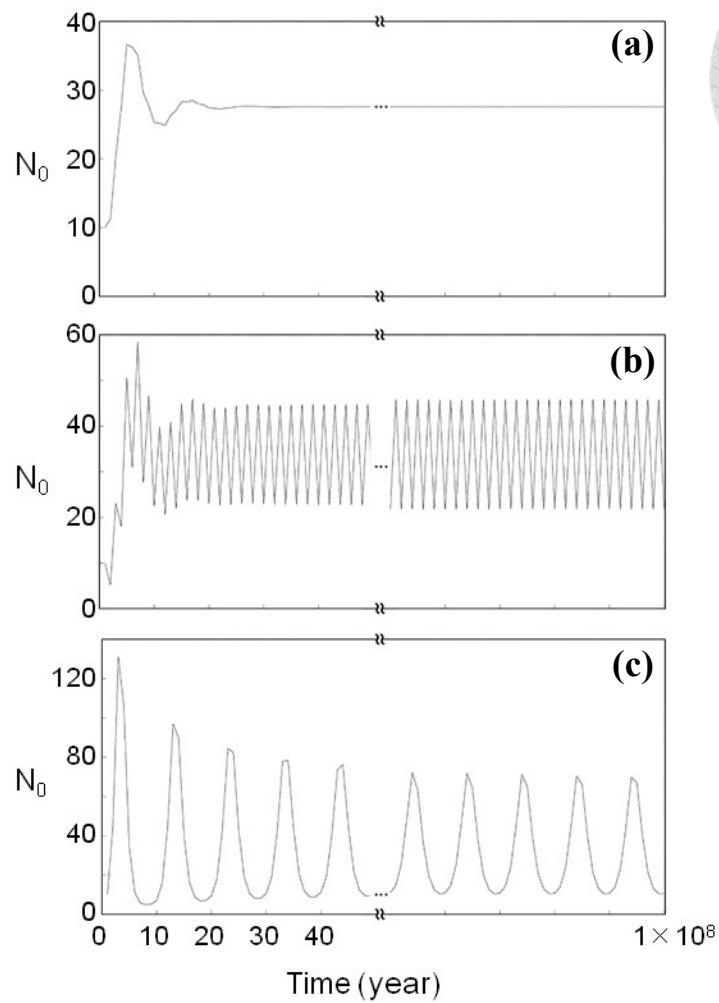
bamboo. Thus, the understanding of belowground carbon dynamic is important in future works.



# Figures and Tables

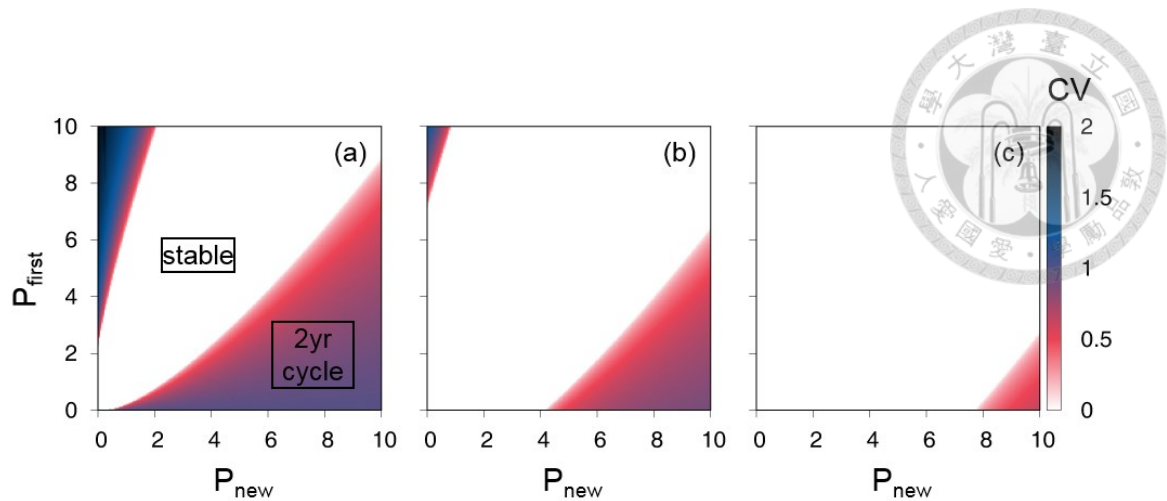


**Figure 1** Moso bamboos' age-structured model. The upper figure demonstrates the bamboos are connected through rhizomes and the shoots can get supply from surrounding bamboos. The lower figure is the framework of model.

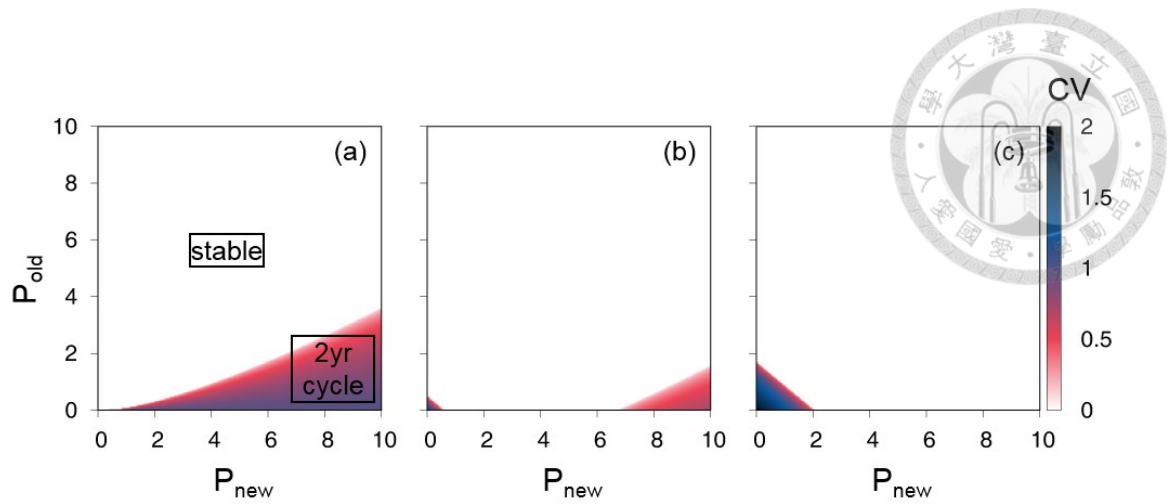


**Figure 2** Example of the three type final states of the Moso bamboos' age-structured model. (a) Stable type with parameter sets of  $P_{first}=1.2$ ,  $P_{new}=1.2$ ,  $P_{old}=0.4$ , (b) Two-year cycles type with parameter set of  $P_{first}=0.5$ ,  $P_{new}=2.5$ ,  $P_{old}=0.2$ , (c)  $>$ Two-year cycles with parameter set of  $P_{first}=5.0$ ,  $P_{new}=0.2$ ,  $P_{old}=0.2$ .

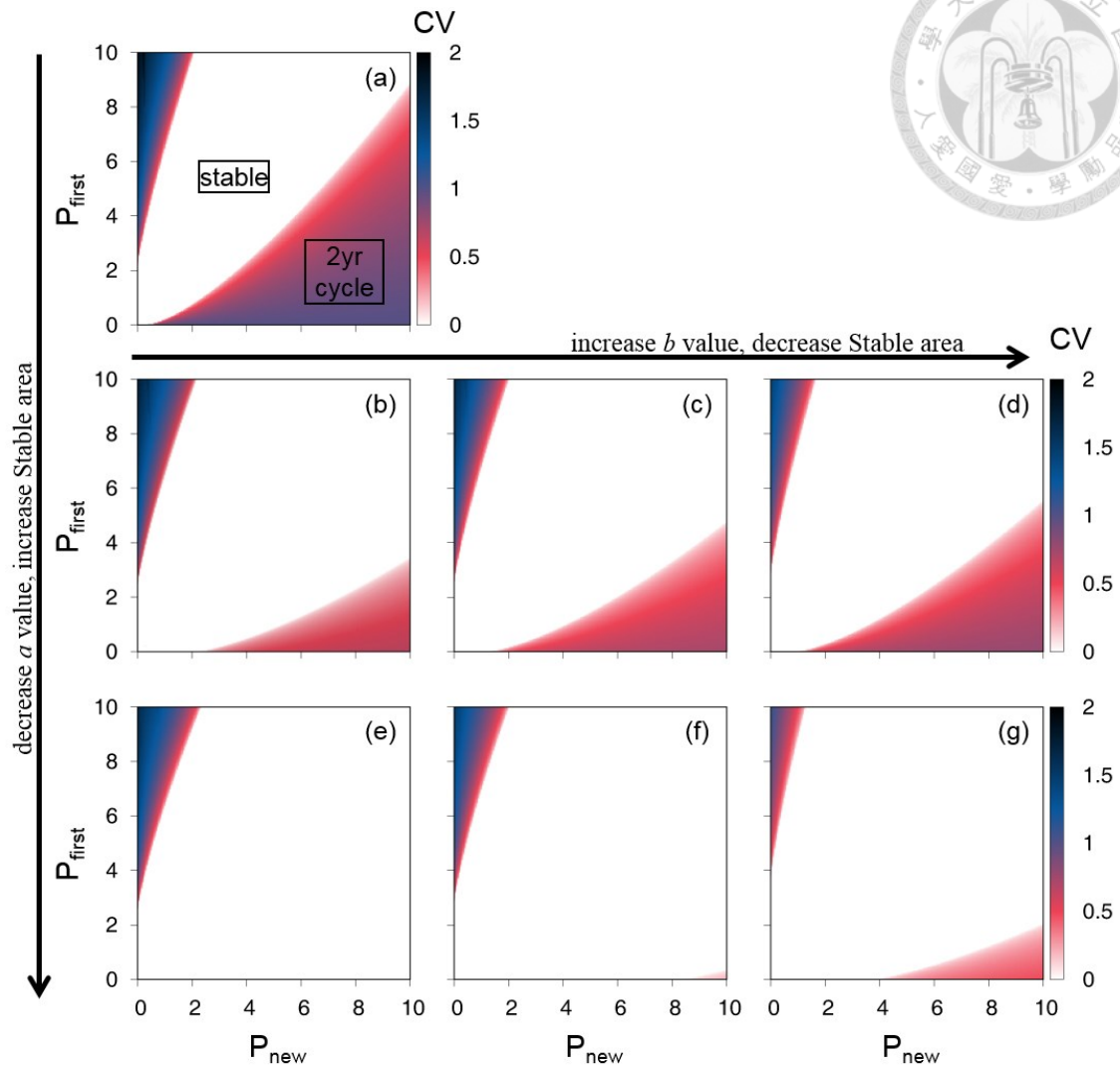




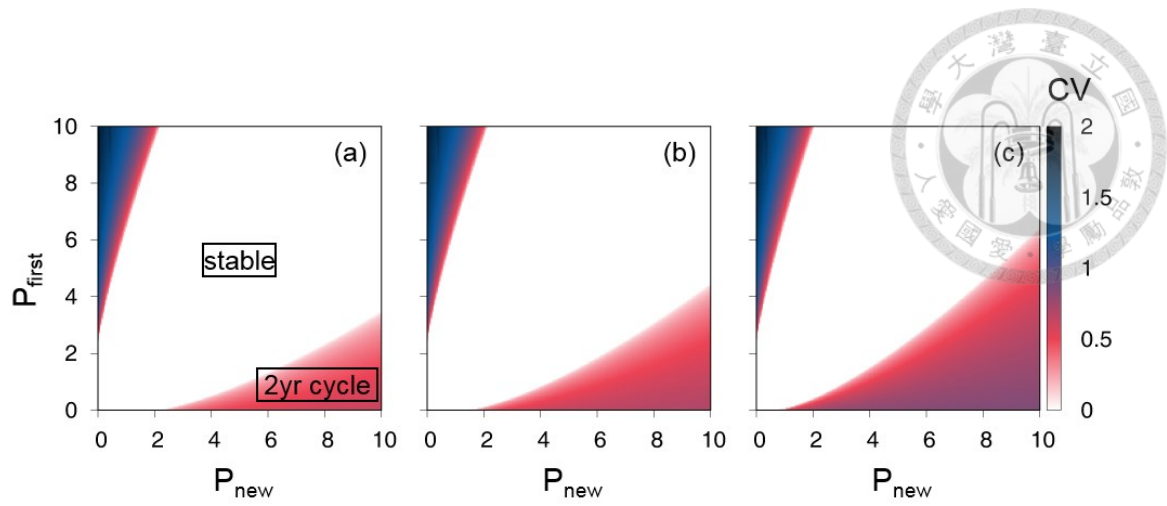
**Figure 3** The effect of old leaves carbohydrate capacity on new shoots production: The figures show the final state CV value from a series of  $P_{old}$  values of (a) 0.0, (b) 1.0, (c) 2.5. The color gradation bars represent the coefficient of variation (CV). Parameter settings of the upper left gray region generate the > two-year cycles or chaotic condition of production. Parameter settings of the center white region generate stable production. Parameter settings of the lower right gray region generate the two-year cycles.



**Figure 4** The effect of the first-year culms' leaves carbohydrate capacity on new shoots production: The figures show the final state CV value from a series of  $P_{first}$  values of (a) 0.0, (b) 5.0, (c) 10.0. The color gradation bars represent the coefficient of variation (CV). Parameter settings of the lower right gray region generate the two-year cycles of production. Parameter settings of the center white region generate stable production. Parameter settings of the lower left gray region generate  $>2$ yr cycles or chaotic conditions.



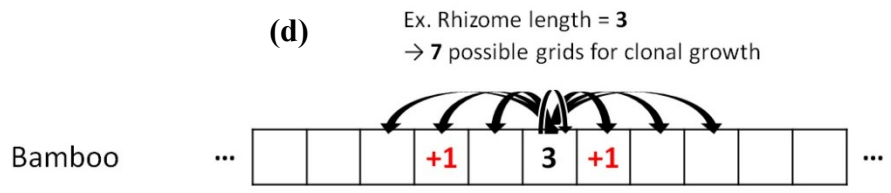
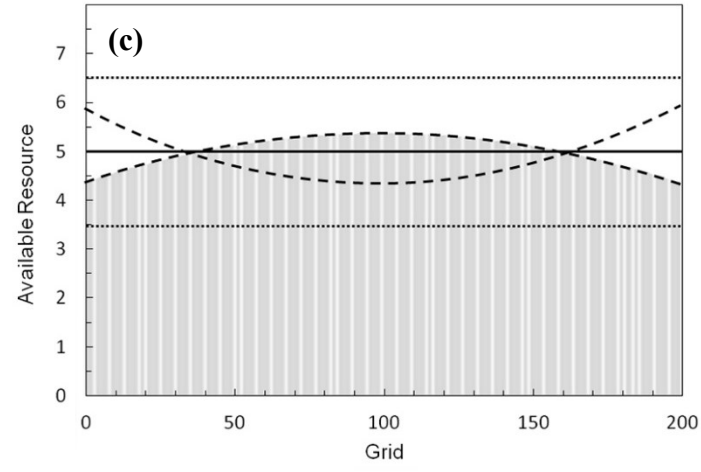
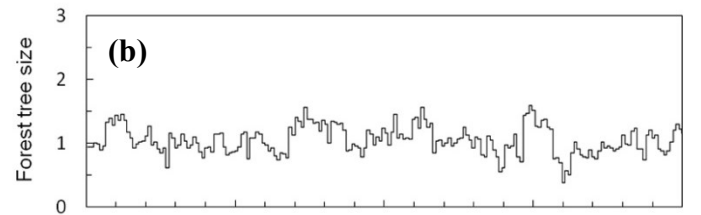
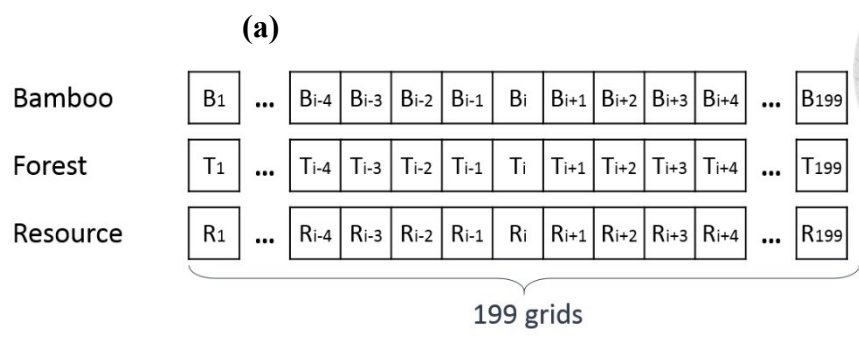
**Figure 5** The effect of belowground carbon storage on new shoots production. The figures show the final state CV value. The Parameter settings of left top (a) are same as those of Fig.3a. The other pictures showed the final state CV value from six sets of parameter  $a$  and  $b$ . The parameter  $a$  ranged from 1.0 (upper panel; a), 0.9 (middle panels; bcd), to 0.8 (lower panels; efg). The parameter  $b$  ranged from 0.0 (left column; abe), 0.3 (center column; cf) to 0.6 (right columns; dg). The color gradation bars represent the coefficient of variation (CV).



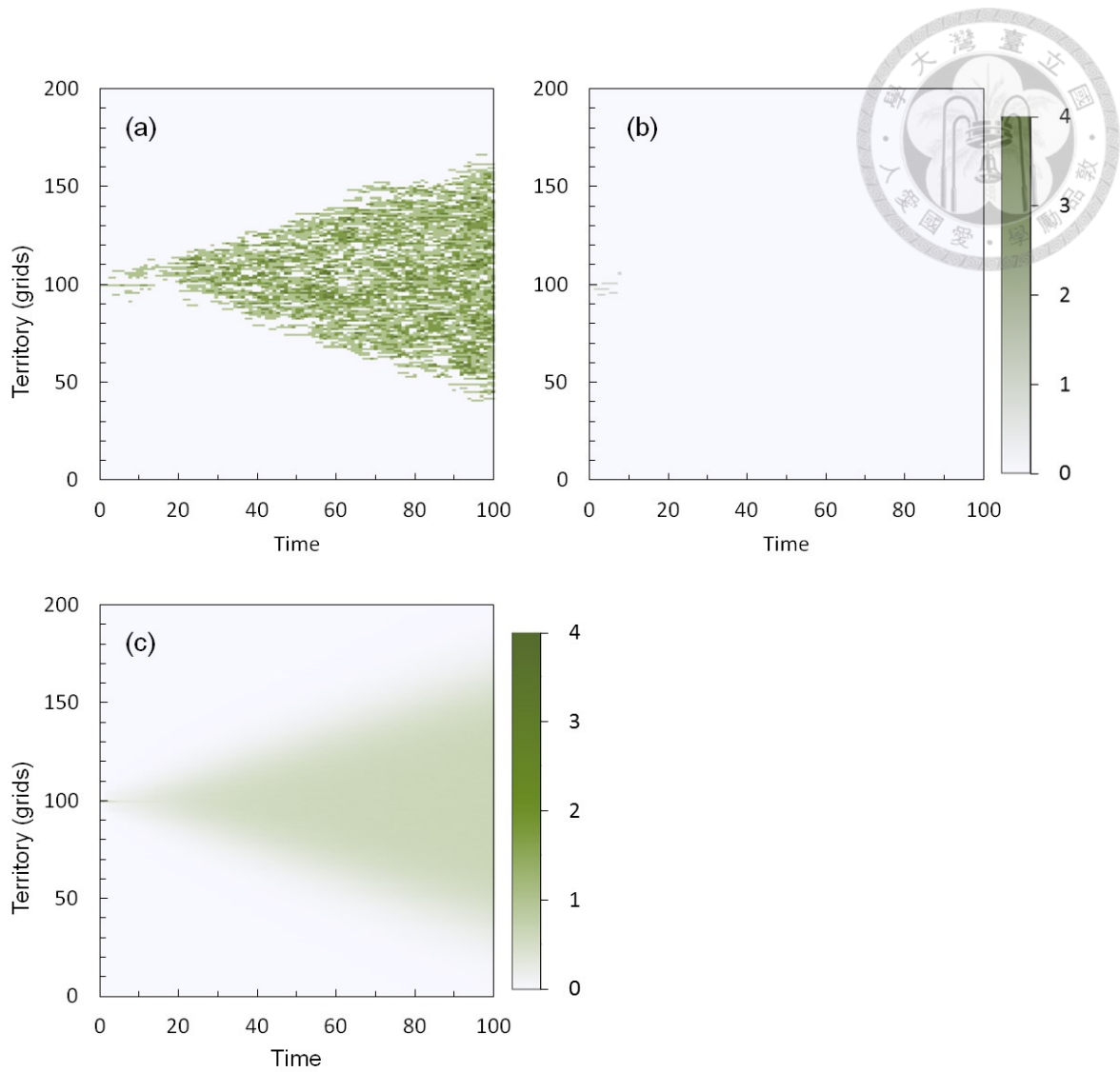
**Figure 6** The effect of the loss of belowground carbon storage on new shoots production:

The figures show the final state CV value from a series of  $L$  values of (a) 0.0, (b) 0.2, (c)

0.6. The color gradation bars represent the coefficient of variation (CV).

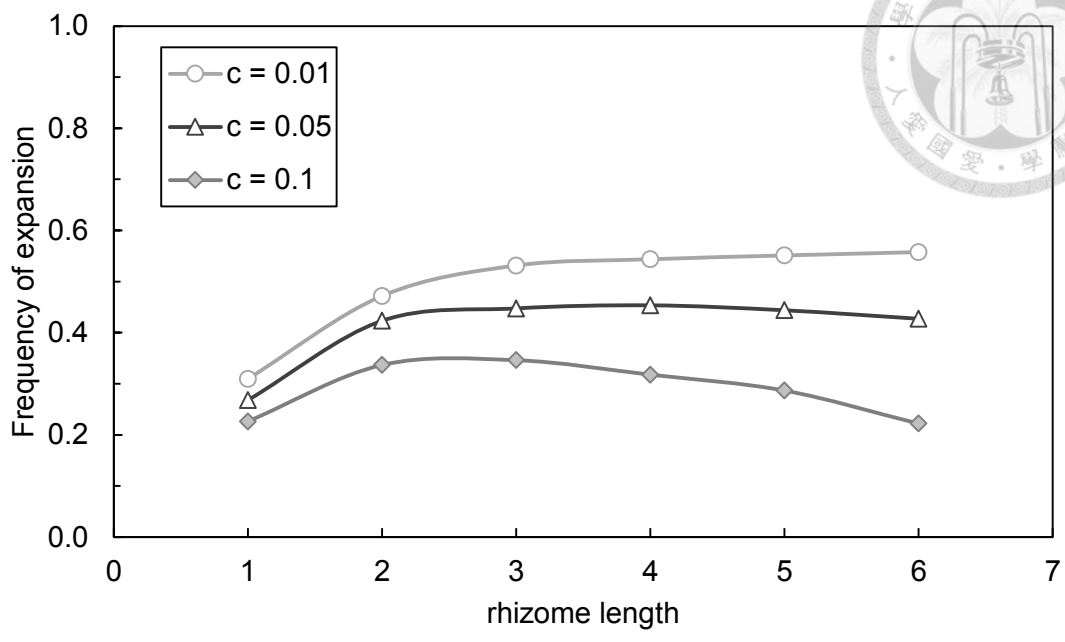


**Figure 7** The one-dimensional individual-based model. (a) is the three layers structure. (b),(c) is an example for distribution of trees and resource. (d) is an example for rhizome length.

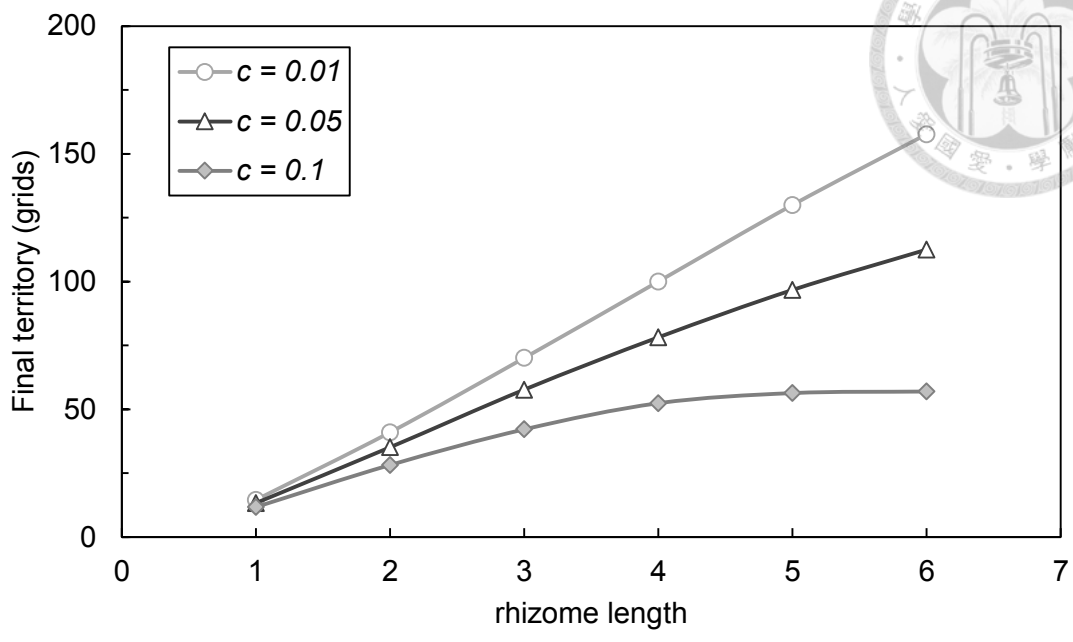


**Figure 8** Example of the history of bamboo numbers during the 100-time steps simulation.

The color gradation bars represent the number of bamboo in a grid. (a) The bamboo population expand their territory, (b) The bamboo population disappear, (c) Mean of 10,000 repetitions.

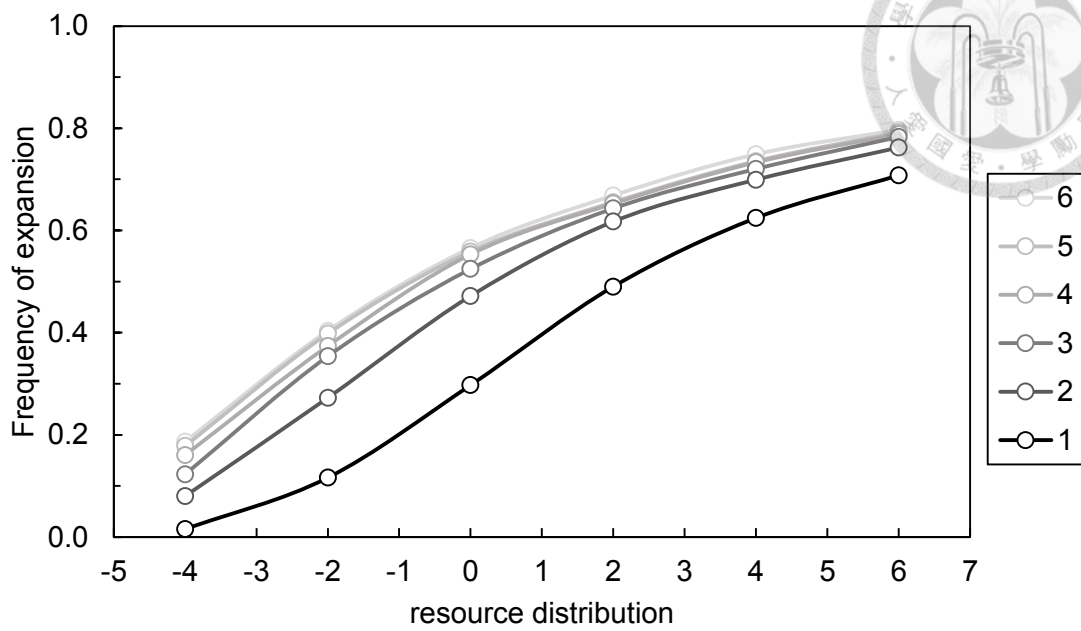


**Figure 9** Relationship between rhizome length and frequency of expansion under three levels of the unit cost for reproducing a shoot away from mother bamboo ( $c = 0.01, 0.05, 0.1$ ).

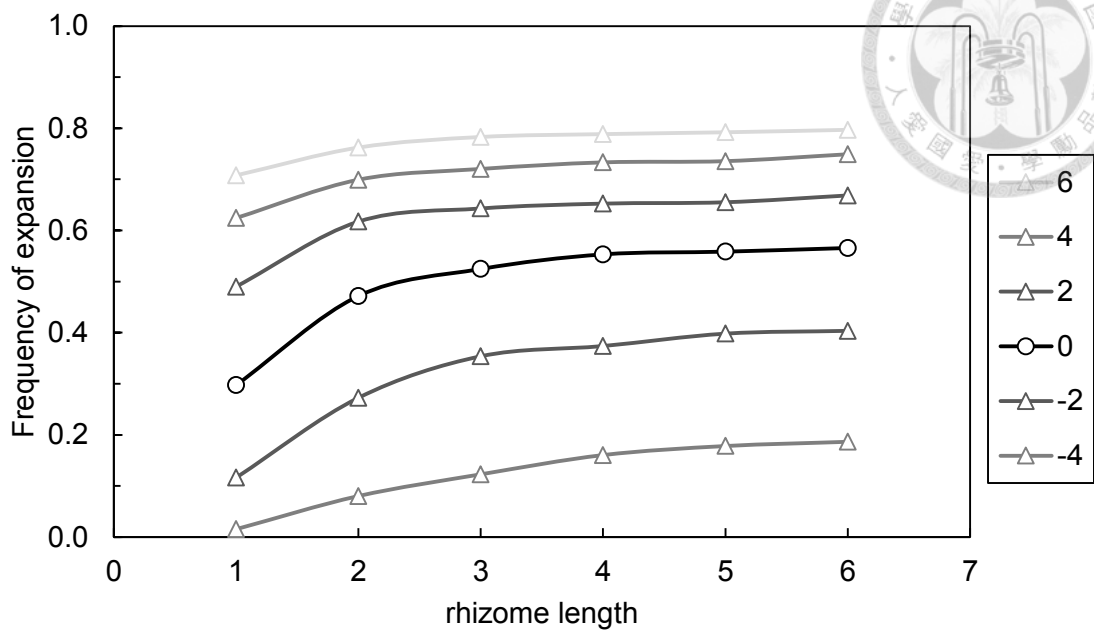


**Figure 10** Relationship between rhizome length and final territory under three levels of the unit cost for reproducing a shoot away from mother bamboo ( $c = 0.01, 0.05, 0.1$ ).

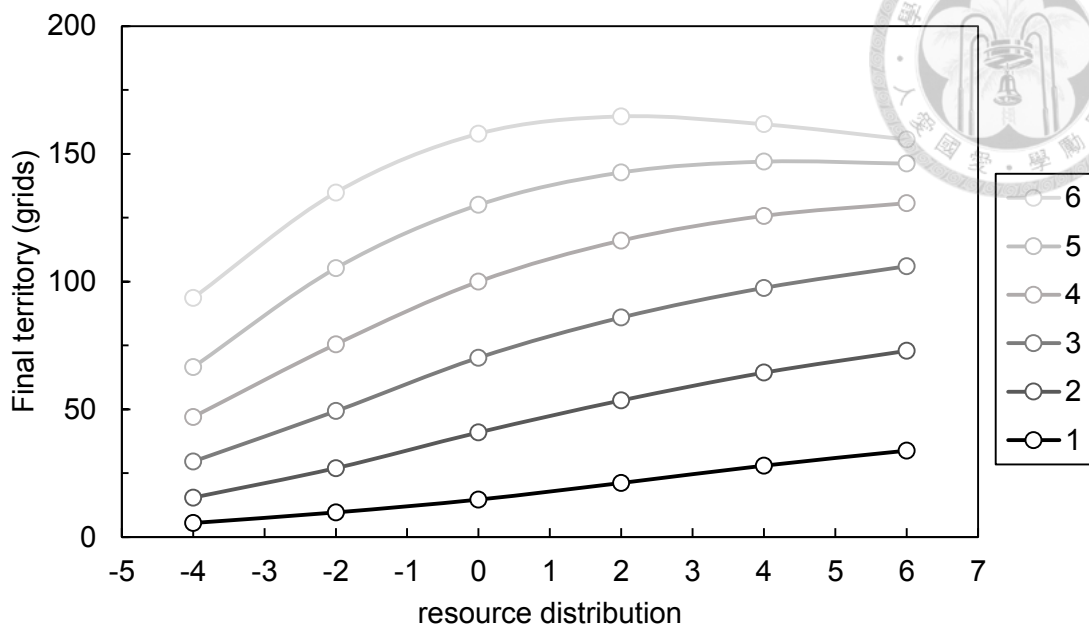




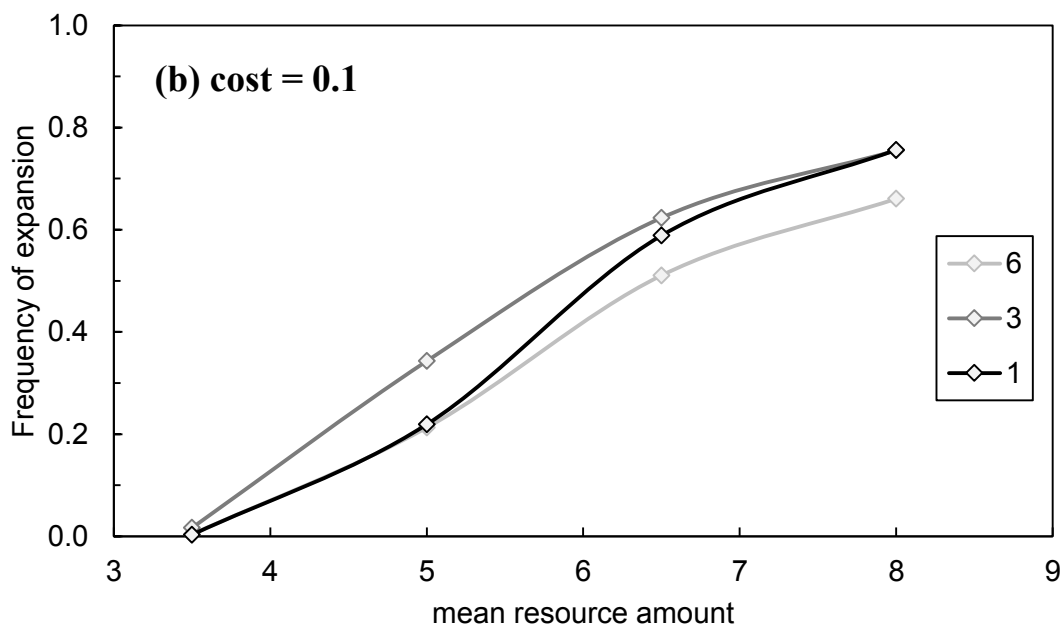
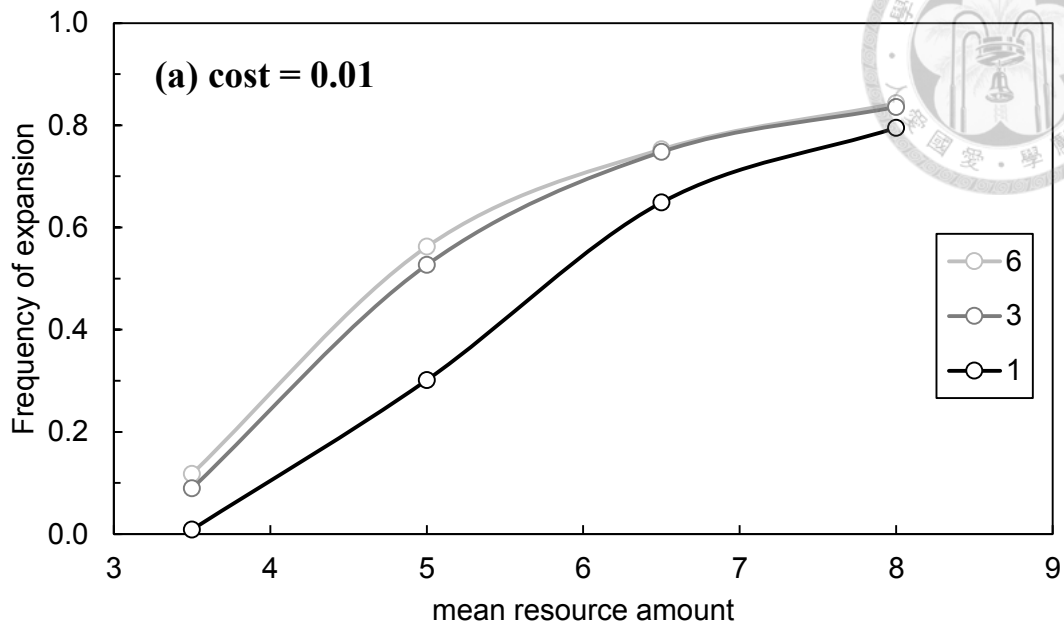
**Figure 11** Relationship between resource distribution and frequency of expansion with different rhizome lengths. The label of lines is the rhizome length. The value of resource distribution (x-axis) is the difference between the center and the boundary. The distribution curve is concave, flat, and convex when the value  $<0$ ,  $=0$ , and  $>0$  respectively.



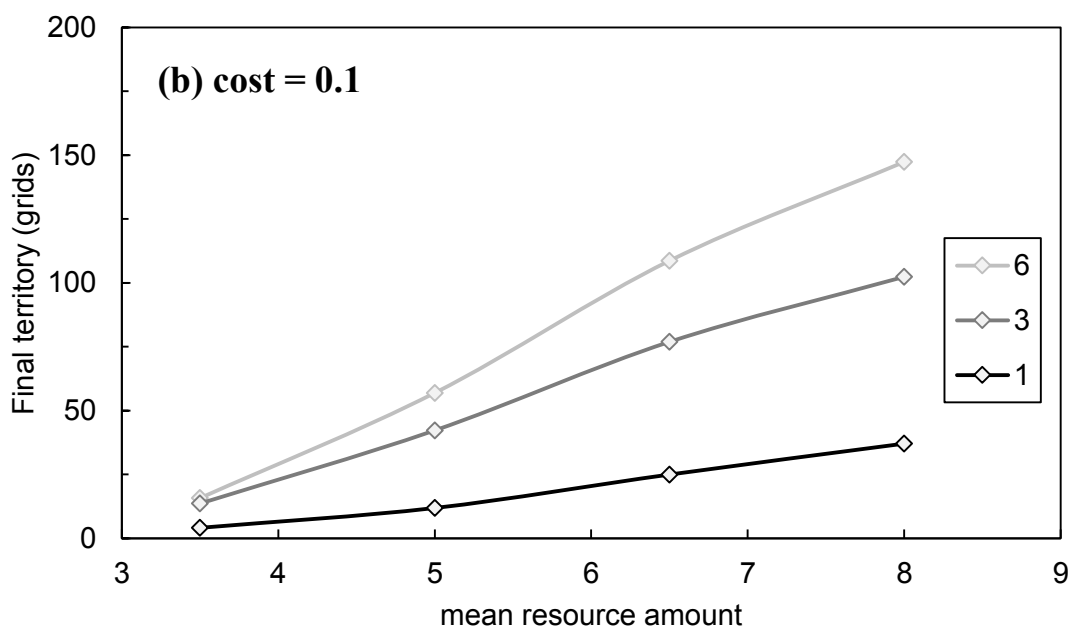
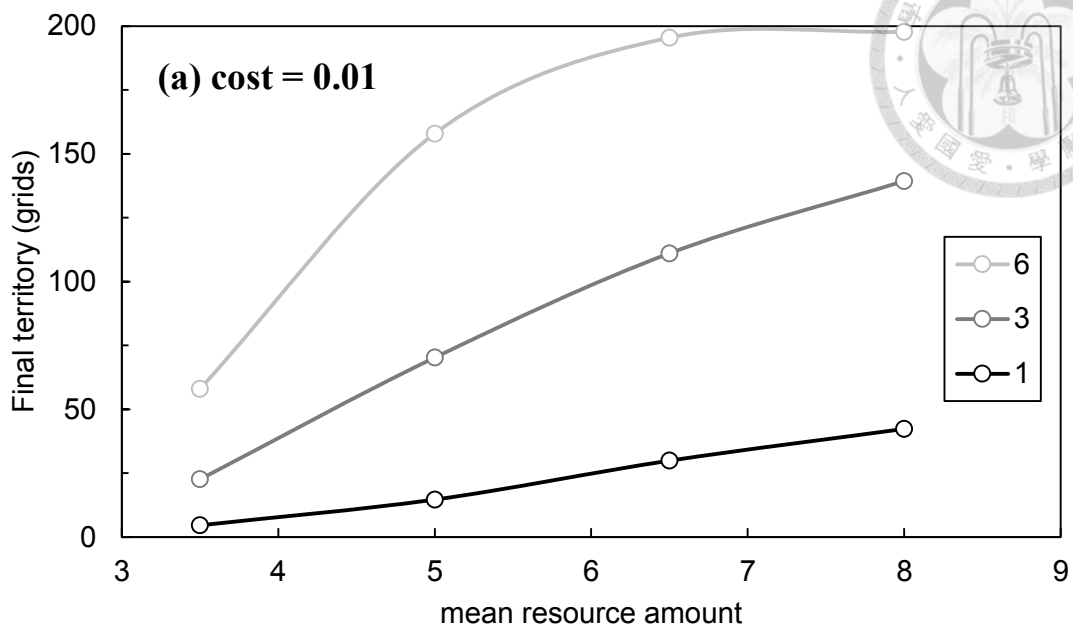
**Figure 12** Relationship between rhizome length and frequency of expansion under different resource distribution. The label of lines is the resource distribution. The value of resource distribution is the difference between the center and the boundary. The distribution curve is concave, flat, and convex when the value  $<0$ ,  $=0$ , and  $>0$  respectively.



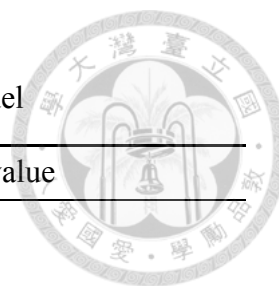
**Figure 13** Relationship between resource distribution and final territory with different rhizome lengths. The label of lines is the rhizome length. The value of resource distribution (x-axis) is the difference between the center and the boundary. The distribution curve is concave, flat, and convex when the value  $<0$ ,  $=0$ , and  $>0$  respectively.



**Figure 14** Relationship between mean resource amount ( $R_{mean}$ ) and frequency of expansion with different rhizome lengths in (a) low-cost condition ( $c = 0.01$ ). (b) high-cost condition ( $c = 0.1$ ). The label of lines is the rhizome length.



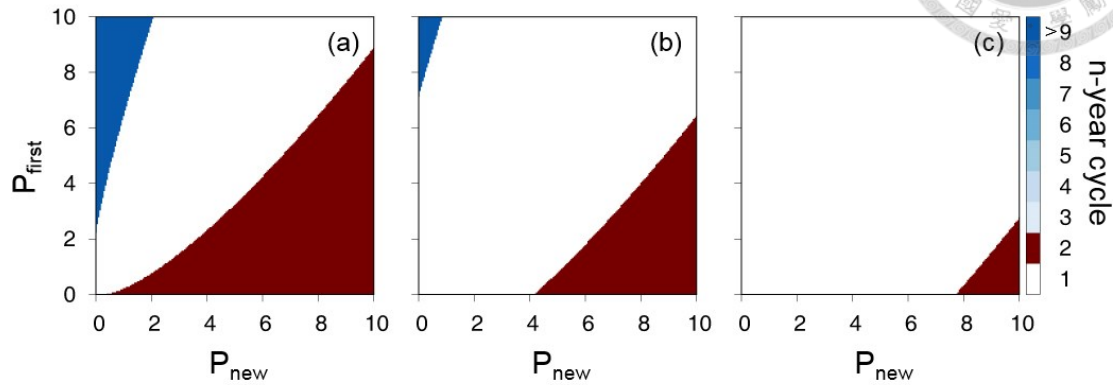
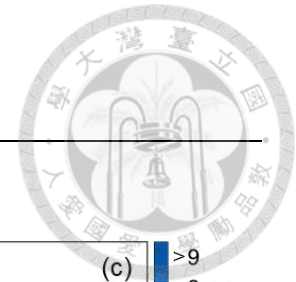
**Figure 15** Relationship between mean resource amount ( $R_{mean}$ ) and final territory with different rhizome lengths in (a) low-cost condition ( $c = 0.01$ ). (b) high-cost condition ( $c = 0.1$ ). The label of lines is the rhizome length.



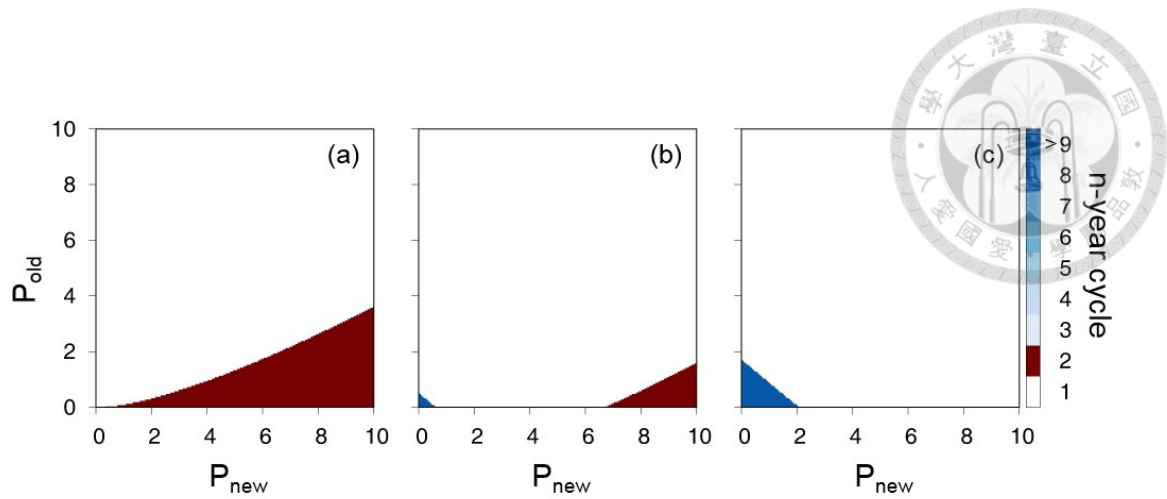
**Table 1** List of parameters for age-structured population growth model

Parameter	Definition	Default value
$P_{first}$	photosynthesis rate of first-year culms' leaves	0-10
$P_{new}$	photosynthesis rate of new leaves	0-10
$P_{old}$	photosynthesis rate of old leaves	0-10
$a$	Proportion of carbohydrate from leaf photosynthesis contributes to generating new shoots in the following year	0.8-1
$b$	Proportion of carbohydrate remains as the storage in the following year	0-0.6
$L$	lost until the following year spring due to belowground autotrophic respiration	0-0.6
$s$	The survival rate for individual at the age $i$ to enters the next age class ( $i + 1$ )	$s_i=0.95$ for $i = 0,1, 2, \dots, 5$ $s_6=0.0$
$d$	density dependence strength	0.01

## Appendix

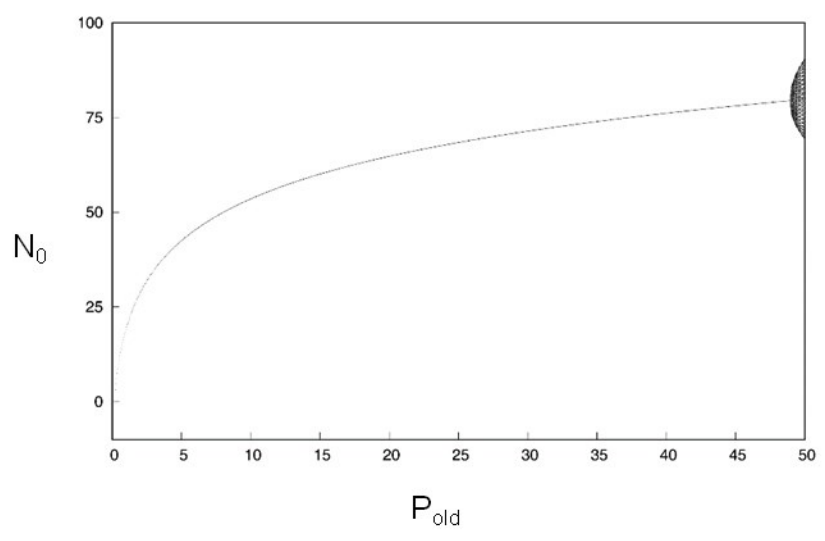
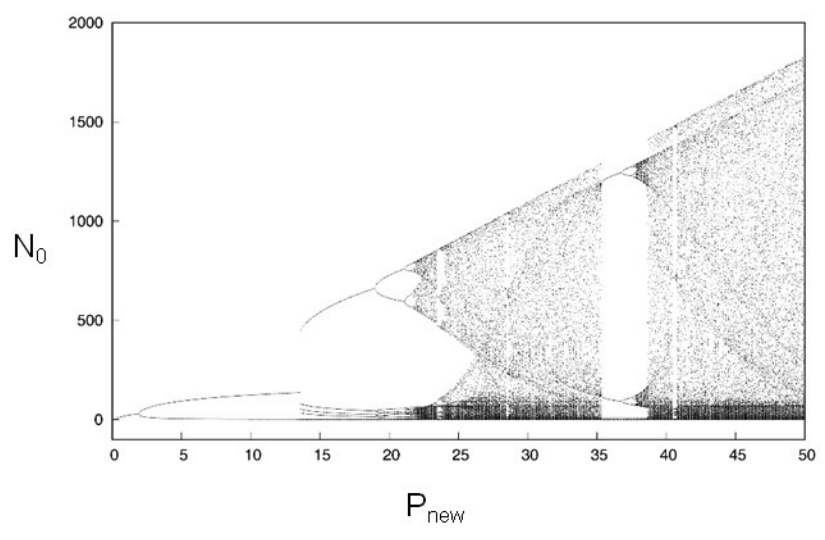
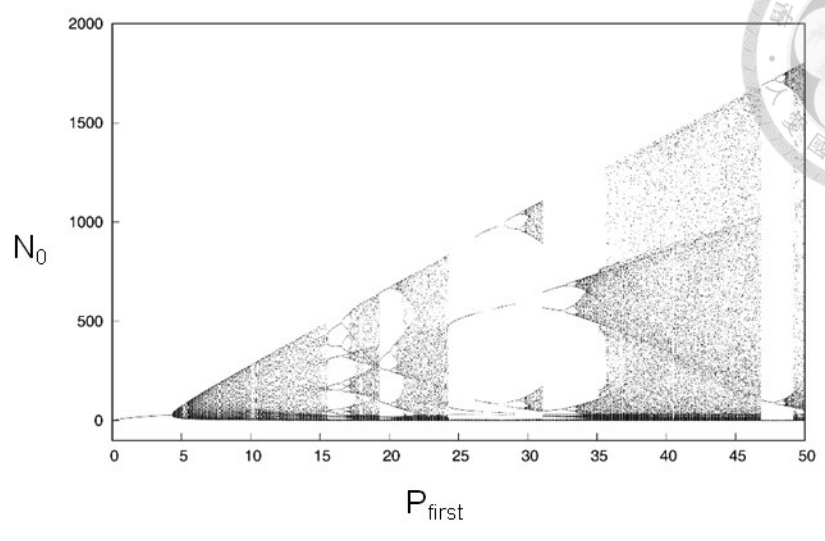
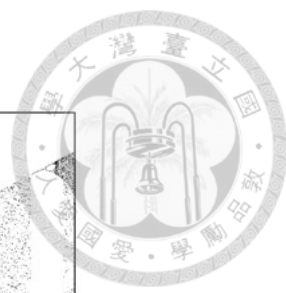


**S 1** The effect of old leaves carbohydrate capacity on new shoots production: The figures show the  $n$ -year cycles from a series of  $P_{old}$  values of (a) 0.0, (b) 1.0, (c) 2.5. Parameter settings of the upper left dark blue region generate the  $>$  two-year cycles or chaotic condition of production. Parameter settings of the center white region generate stable production. Parameter settings of the lower right red region generate the two-year cycles.



**S 2** The effect of the first-year culms' leaves carbohydrate capacity on new shoots production: The figures show the n-year cycles from a series of  $P_{first}$  values of (a) 0.0, (b) 5.0, (c) 10.0. Parameter settings of the lower right red region generate the two-year cycles of production. Parameter settings of the center white region generate stable production. Parameter settings of the lower left dark blue region generate >2yr cycles or chaotic conditions.





S 3 Bifurcation figures of parameter  $P_{\text{first}}$ ,  $P_{\text{new}}$ , and  $P_{\text{old}}$ .

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