

Forest Dynamics Models Based On Field Measurements

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<https://doi.org/10.11501/3134901>

出版情報：九州大学，1997，博士（理学），課程博士
バージョン：
権利関係：



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Dissertation

submitted in partial fulfillment of the requirements

for the degree of

DOCTOR OF SCIENCE

in Biology

Division of Science,

Graduate School of Kyushu University

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I. Preface

In order to construct a mathematical model aiming to explain some ecological dynamics and patterns observed in the field, we should pay attention in two processes: explicit parameterization based on field measurements and choosing the correct procedure for calculating the model. The purpose of this study is to investigate how we develop a model of forest dynamics realizing both of these points.

I would like to focus on the forest dynamics in the range of 0.01 to several decades hectares. In such scale, forest ecologists can track the time change of the size of all trees in a research plot, hence they consider the relationship between the forest dynamics and its size structure (e.g. Nakashizuka *et al.*, 1992). Here we review four major models to answer the problems in such spatial scale: JABOWA-FORET models, density distribution models described by Fokker-Planck equation, SORTIE and lattice models of wave regeneration. All of them has two common features: considering the size structure in which the size of each tree is denoted by a real number and the localized interaction between individual trees. Let me briefly outline them in the following.

Forest simulators like JABOWA (Botkin *et al.*, 1972) and FORET (Shugart, 1984) are the most widely studied for the forest all over the world. Here we call them JABOWA-FORET models. One of the feature of this series is that whole forest dynamics is represented as an ensemble of the small stands (or, patches) in which the fate of every tree are tracked. This approach is called individual based modeling. Although all the parameter was determined based on field observation, the way of their parameterization is not always clear. For example, Shugart (1984) classify the shade tolerance of trees in three categories, but there are no the statistical justification for such modeling. In addition, Pacala *et al.* (1996) pointed out "the single greatest shortcoming" of JABOWA-FORET models was that they simply assign the same growth dependent mortality function to all species because of the lack of published data relating growth and mortality. These things might suggest the importance of explicit parameterization.

In the second approach, the density distribution of trees is directly calculated by a partial differential equation. The density distribution is the function of time and the size of trees. Kohyama (1989, 1991, 1992a and 1992b) applied this method to explain the coexistence of trees observed in a warm-temperate rain forest in southern Japan dominated by evergreen broad trees, and found the mechanism, called the architecture hypothesis, maintaining the species diversity of forest trees. Although such a new understanding was obtained and the method to estimate parameters are much more explicit than those of JABOWA-FORET models, it could be said that the assumption for calculation is not so realistic. The assumption, frequently called mean field approximation, is to set always the correlation between trees zero. Certainly, if there were no interaction between trees, the Fokker-Planck equation would work well. However, the "one-directional competition" (explained in chapter III) is significantly detected in the field (e.g. Kohyama, 1992a). Hence it is natural that such the local competition generates the forest with negative covariance structure, or in other terms, the forest becomes mosaic-like structure of two different kind of patches, one where a few large canopy trees suppress the newly settlement of small trees and the other called "canopy gap" with a large number of small trees and no canopy tree. It can be said that the mean field approximation encounters difficulties to calculate the forest dynamics with local interaction and local disturbance.

Recently, Kohyama (1993 and 1994) developed a improved model to avoid the problem by introducing a new dimension, "patch age" to separate the old mature patches from "young" (i.e. canopy gaps). This technique succeeded to generate the negative covariance structure in forest, however, the modification of the mean approximation would face a new difficulty: the age of a patch is defined as the passing time from the last disturbance destroying the patch, and it is very hard to measure the accurate value of such the "age" in the field.

One of the modern forest simulator, SORTIE (Pacala *et al.*, 1993 and 1996) has

realized an ideal synthesis of explicit parameterization (maximum likelihood method) and appropriate calculation (individual based modeling). The SORTIE is an empirically based model of forest dynamics derived from data in the research plot in Connecticut, USA. It tracks the position of each tree and determines tree performance based on the individual's local neighborhood. Pacala and his colleague revealed the importance of spatial structure in forest dynamics and the functional responses of forest against various disturbances. We have only one practical difficulty in SORTIE: it needs much more power of computer than JABOWA-FORET models.

Constructing more simple and abstract model than those in above, lattice structured models (Iwasa *et al.*, 1991; Sato and Iwasa, 1993) succeeded to generate the wave-like regeneration pattern observed on subalpine forests. In these models, whole forest consists of a large number of sites arrayed on one or two dimensional rectangular lattice. A site is assumed that a cohort of trees. The interaction between sites is always local and horizontally one-directional. Most of its parameters are estimated from field data, and a few unknown are determined such that the generated pattern of tree height becomes similar to that in the real forest.

In this thesis, I investigate two models for forest dynamics with considering the merits and demerits of the model in above. In chapter II, I develop a simple lattice model which has only two states (gap and nongap) for each site. This model was developed to predict the forest canopy dynamics with localized interaction between sites. The importance of local correlation is shown by comparing the results from the mean field approximation (in this case, mean field of horizontal space) and the pair approximation which calculates the approximated correlation between two neighbor sites. Because this study aims to understand how processes at local scale are translates into patterns at larger scale, the global statistics like mean local density or gap size distribution are examined by comparing to the indexes measured in Barro Colorado Island, Panama.

In chapter III, an individual based model is developed to evaluate the sustainability of an isolated beech stand with *Sasa* undergrowth which disappears and recovers reciprocally. The basic design of this model is similar to that of JABOWA-FORET models, while the submodel of growth is almost the same as that of Kohyama's model. The parameters used in the submodel are estimated by using maximum likelihood method like SORTIE. The sustainability of an isolated beech stand is evaluated by a statistical index calculated from several hundreds of replications of simulation.

In the following, I summarize the content of each chapter in more detail.

Chapter II. Forest Spatial Dynamics with Gap Expansion: Total Gap Area and Gap Size Distribution

Recent studies on forest dynamics in diverse forested ecosystems suggest that forest stands are disturbed more frequently if they are next to existing gaps, and that gaps once formed tend to expand their area in subsequent years. We examine total gap area and the size distribution of gaps at equilibrium in a lattice structured forest model. Each site undergoes transition between two states (gaps and nongaps), and the disturbance rate (transition from nongap to gap) increases with the number of gap sites in the neighborhood. Dynamics based on mean-field approximation (i.e. neglecting of spatial structure) failed to predict total gap area and the gap size distribution in the equilibrium forest. Pair approximation, which considers in a closed dynamical system of average and local gap density (the conditional gap density among neighbors of a randomly chosen gap site), can predict the total gap area, the correlation between neighbors, and the gap size distribution fairly accurately. If the recruitment rate increases in proportion to nongap area in the forest, the model may show bistability. We analyze data on forest spatial dynamics in the light of the model. We conclude that gap size distribution can

often be described using two statistics (global and local gap densities) and that these in turn can be predicted by the dynamics of gap formation, gap expansion, regeneration, and gap closure.

Chapter III. Sustainability of an Isolated Beech-Dwarf Bamboo Stand: Analysis of Forest Dynamics with Individual Based Model

The beech *Fagus crenata* forest on Mt. Jippo in southwestern Japan has been diminished in small fragments by past human activity. The forest floor is covered by dense dwarf bamboo, *Sasa*, which is an inhibitor of beech regeneration. One of the ecological feature of *Sasa* is that they wither synchronously over a large area once in several decades. An individual based model (IBM) was developed to evaluate the sustainability of such a fragmented beech stand with considering the dynamics of *Sasa*. The model has three submodels for beech individuals: growth, mortality and seed production. The parameters of these submodels are estimated from field measurements. By using this model together with *Sasa* dynamics, we can evaluate the adverse effect of *Sasa* on enhancing the risk of extinction of a single fragmented beech stand during 500 years. The results obtained by Monte Carlo simulations are: (1) *Sasa* has a strong impact on the sustainability of a isolated beech stand; (2) The effects of two parameters for *Sasa* life history, the longevity and the recovery time, can be statistically separated from each other; and (3) The probability of extinction of a beech stand depends much more strongly on the parameters of beech mortality than those of growth rate.

II. Forest Spatial Dynamics with Gap Expansion: Total Gap Area and Gap Size Distribution*

2.1. Introduction

Last two decades, many ecologists working on forest dynamics have focused their attention to "gaps", openings created in the forest canopy (Whitmore, 1975; Yamamoto, 1992). Gaps may range in area from the openings created by the death of a single branch to larger scale blowdown of a catastrophic disturbance, such as a storm, a fire or an aggregated insect outbreak. The size, the number and the spatial distribution of gaps and the processes of gap formation and canopy recovery have been studied extensively (e.g. Kanzaki *et al.*, 1994; Nakashizuka, 1987, 1991; Runkle, 1984; Yamamoto, 1992, 1993; Masaki *et al.*, 1992).

Many studies of forest gap dynamics have demonstrated that new gaps are more likely to occur adjacent to pre-existing gaps. Trees in the border of gaps tend to have a higher rate of disturbances.

For example, Foster and Reiners (1986) reported the ~~size~~ distribution and expansion of canopy gaps in a subalpine spruce-fir forest in the White Mountains, USA. The gap area distribution was a negative exponential in form. They observed that gap expansion occurs as the result of the fall of canopy trees at gap perimeters subsequent to initial gap formation. By the gap expansion process, the areas of gaps were increased from the initial value by factors of 1.4 to 13.7. Since wind was the major gap-forming disturbance agent, the increased exposure to wind of trees at gap edges suggested that wind-induced treefall were continuously eroding the margins of gaps. A similar expansion of gaps was also reported in a subalpine forest in Japan: Komiyama and Ohnishi (1981) analyzed aerial photographs in different years: 1948, 1959, 1969, and 1979. For example, a gap, which was absent on a photograph taken in 1948, appeared first in 1959 and expanded toward all the directions during subsequent 20

* This chapter was done in collaboration with Prof. Yoh Iwasa and Mr. Naoki Furumoto. The original paper was published in *Journal of theoretical Biology* (180: 229-246) in 1996.

years. Foresters have long been aware of the increased incidence of windthrow at the downwind edges of logging-created forest openings in spruce-fir forest (Alexander, 1964).

In an old-growth deciduous forest, Runkle (1984) recensused canopy gaps 4 year following his initial census and found that 11% of the gaps had enlarged by the blowdown on peripheral canopy trees, and that 31% of the gaps had enlarged via the death standing of surrounding trees, but the mortality of gap-edge trees was the same as for overstory trees in general.

In a wind-exposed tropical cloud forest in Costa Rica, Lawton and Putz (1988) found gaps spatially aggregated, with more gaps occurring within 17-20 m of one another than expected by chance. Kanzaki *et al.* (1994) observed in tropical seasonal evergreen forest in Thailand that all the gaps formed from 1985 to 1993 in their belt plot were in contact with older gaps or building-phase patches (low in height).

A very clear quantitative demonstration of new gap formation occurring near pre-existing gaps was given by Hubbell and Foster (1986) from their study of Panamanian neotropical forests. They observed that trees adjacent to gaps, or trees standing above the surrounding canopy, suffer a greater risk of falling than trees which are surrounded by plants as tall or taller than themselves. The analysis of spatial patterns of trees in 1983 and in 1984 showed that drops in canopy height are much more likely to occur on the edges of gaps. The data were arranged on a regular two-dimensional square lattice with each unit a 5x5 m plot (we call this a 'site' in the following). If the focal plot in the centre was taller than 30 m in 1983, and all neighboring plots were taller than 30 m as well, the probability of a fall in canopy height in the focal plot to lower class in a year was only 0.039. In contrast, focal plots surrounded by all 8 neighboring plots less than 20 m height had an annual rate of fall of 50% (0.515).

Another very clear example of enhanced disturbance rate by the surrounding neighbors with lower height is given by wave regeneration, fir-wave, or Shimagare in Japanese (Sprugel, 1976; Kohyama, 1988; Kohyama and Fujita, 1981): In subalpine forests dominated by *Abies*

species in Japan and Northeast USA, forests show a large scaled regeneration pattern with many stripes of stand-level dieback perpendicular to the direction of prevailing wind, spaced regularly with the distance between adjacent dieback zones of about 100-150 m, with the whole pattern moving slowly (1-1.5 m per year) downwind.

In a lattice structured model in which each site is a forest stand occupied by a cohort of trees, it has been shown that simple rules of mortality and growth are capable of generating regular wave-regenerating pattern from random initial patterns if the trees much taller than windward neighboring sites die after some number of years (Iwasa *et al.*, 1991; Sato and Iwasa, 1993). Comparing the model with the observed data of canopy height, growth rate, and the speed of waves, we can predict parameters difficult to measure directly, such as the time required for newly exposed cohort of trees to show stand level dieback and the spatial range of wind-shielding effect (Iwasa *et al.*, 1991).

A very useful method of modelling when the interaction between neighbors is important is lattice structured models, or cellular automata models, which consider the nearest neighbor interaction explicitly. Models for wave regeneration (Iwasa *et al.*, 1991; Sato and Iwasa, 1993) are examples of the use of lattice models in forest dynamics. Other examples of lattice structured models in population biology include not only forest dynamics (Green, 1989; Smith and Urban, 1988; Nakashizuka, 1991; Kawanô and Iwasa, 1993), but also population dynamics with perennials capable of vegetative propagation (Crawley and May, 1987; Silvertown, 1992; Harada and Iwasa, 1994), marine invertebrate community (Caswell and Etter, 1992; Etter and Caswell, 1994), predator-prey (Tainaka, 1988; de Roos *et al.*, 1991; Wilson *et al.*, 1993), host-pathogen (Ohtsuki and Keyes, 1986; Sato *et al.*, 1994), and host-parasitoid (Hassell *et al.*, 1991, 1994) dynamics with spatial structure.

In this paper, we examine the effect of gap expansion on total gap area and the size distribution of gaps in lattice structured population models. The forest is assumed to be composed of many sites arranged on a regular square lattice, each corresponding to a forest stand of about 10x10 m. Each site is either a gap or a nongap, and changes its state between

the two stochastically. The rate of disturbance, causing a transition from a nongap site to a gap site would increase with the number of neighbors which are currently in gap state, indicating gap expansion. We analyze the model by three methods: (1) mean-field approximation (ignoring spatial structure), (2) pair-approximation (tracing both the average gap density and the correlation between neighbors), and (3) computer simulation.

Pair approximation is a technique which constructs the simultaneous dynamics of the average density and the neighbor-conditional local density by neglecting correlation beyond nearest neighbors. It has been shown to be very powerful for analyzing the population dynamics with spatial structure although it is not exact (Matsuda *et al.*, 1992; Sato *et al.*, 1994; Harada and Iwasa, 1994; Harada *et al.*, 1995). Because of gap expansion, spatial pattern of gap sites generated by the model is aggregated, forming more large gap clusters than expected by chance in a random spatial pattern. We construct a closed dynamical system for the global density of gap sites (total fraction of gap sites in the system) and the local density of gap sites (the fraction of gap sites among neighbors of gap sites), the latter being larger than the former due to spatial clumping. We conclude that gap size distribution can often be summarize by two statistics (global and local gap densities) and that these can be predicted from the processes of gap formation, gap expansion, regeneration and gap closure.

2.2. Model

We consider a habitat consisting of infinitely many sites arranged on a regular lattice. Each lattice site corresponds to a forest stand of area about 10×10 m and can be occupied by a large canopy tree.

After canopy trees fall due to disturbances of various sources, the site becomes a "gap" site. It takes some number of years until young trees from seedlings or seeds will grow and fill the gap. During this recovering period, the height of trees is still clearly lower than the height of surrounding mature canopy trees, and can be recognized as a gap. In general, we may classify the state of a site into a gap phase, a building phase and a mature phase (Whitmore,

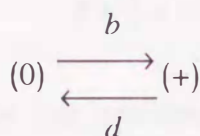
1975; Kanzaki *et al.*, 1994), or to several size categories (Hubbell and Foster, 1986). Here we simply consider two categories only: gaps and nongaps. An operational definition of gaps and nongaps is given by choosing a certain threshold height, say 20 m (Runkle, 1984; Hubbell and Foster, 1986), 10 m (Runkle, 1981; Yamamoto, 1993), or 3 m (Lawton and Putz, 1988), depending on the height of mature canopy trees, and regarding a site as a gap site if the height of trees is lower than that level.

Transition from a newly formed gap to a nongap may occur by canopy closure, instead of growth by new recruiting individuals. For a single individual seedling to reach the canopy layer, multiple gap episode may be needed (Runkle and Yetter, 1987). In this paper, we do not consider detailed mechanisms of canopy recovery, but we concentrate on the fraction and the spatial pattern of gaps in the forests.

We denote a gap or a nongap by two symbols, 0 and +, respectively and assume that each site experiences transition between the two states through time. Although real forests are 2-dimensional, we examine both 1-dimensional and 2-dimensional lattices in this paper. Applying the analysis to 1-dimensional system is useful in checking the accuracy of our method of analysis in different situations, and also useful in explaining method of analysis, e.g. calculating the frequency of gap cluster of a particular size. In addition, the effect of spatial structure to population dynamics is more pronounced in a 1-dimensional model than in a 2-dimensional model.

Before examining the case in which gaps expand to adjacent occupied sites, we first summarize the results for cases in which each site of the forest undergoes independent transition between gap and nongap states: A gap site becomes a nongap by the growth of trees in the site, and a nongap site becomes a gap due to the death of canopy trees by disturbances. Assume that the rate of transition from a gap to a nongap occurs at rate b per year, and transition from a nongap to a gap occurs at rate d . The inverse of recruitment rate, $1/b$, is the average length of time for sites to be gaps (recovery time), and the inverse of

disturbance rate, $1/d$, is the average length of time for sites to be nongaps (average tenure of canopy trees).

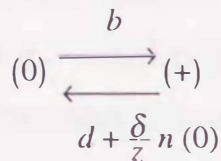


The fraction of gap sites in the equilibrium is $d/(b+d)$. Gaps are distributed randomly over the lattice because different sites are independent of each other (Fig. 2.1A).

2.2.1. Gaps causing more gaps

The enhanced disturbance rate per site in the periphery of gaps is reported in subalpine spruce-fir forest (Lawton and Putz, 1988), in deciduous old-growth forest (Runkle, 1984), and in tropical forest (Hubbell and Foster, 1986; Kanzaki *et al.*, 1994). Wave-regeneration of *Abies* forest (Kohyama, 1988; Sprugel, 1976) is an illuminating example of large scaled pattern formed by between-stands interaction, in which a cohort of trees in a site experience a stand-level dieback if its windward neighbors are clearly shorter than the site.

As the simplest modeling of gap expansion, we consider the case in which the transition rate from a nongap to a gap increases with the number of neighbors which are gaps. For example we assume that the transition rate is not a constant d but is an increasing function of the number of surrounding gap sites. Let $n(0)$ be the number of 0 sites among the nearest neighbors. It satisfies $0 \leq n(0) \leq z$, where z is the number of nearest neighbors: $z=2$ for a one-dimensional linear lattice, $z=4$ for a two-dimensional square lattice with Neumann neighborhood, and $z=8$ for two-dimensional system with Moore neighborhood (Durrett and Levin, 1994). z can be even larger if ecological interaction occurs between more distant neighbors, such as 2 step neighbors. We assume that an individual with $n(0)$ gap neighbors has the death rate $d + \frac{\delta}{z} n(0)$. The rate of transition from a nongap site to a gap site is the highest when all the surrounding nearest neighbors are gaps and is equal to $d + \delta$.



We assume that each transition event occurs instantaneously at rates given above. The model then gives a continuous-time Markov chain (Liggett, 1985). Starting from a random initial distribution, the spatial pattern would change with time, and becomes a clumped distribution, as shown in Fig. 2.1B. If spontaneous disturbance is absent, the model is called the basic contact process (Griffeath, 1979).

2.3. Total gap area

Now we consider the total gap area, or the fraction of gap sites in the equilibrium forests. Let ρ_+ be the fraction of nongap sites in the whole lattice, or the probability for a randomly chosen site to be occupied. Similarly let ρ_0 be the fraction of gap sites, or the probability for a randomly chosen site to be a gap. We may call these two quantities the global densities of states + and 0, respectively (Matsuda *et al.*, 1992; Harada and Iwasa, 1994). They are the average densities of nongap sites and gap sites, respectively.

The dynamics of the total fraction of gap sites, or the global density ρ_0 , are :

$$\frac{d\rho_0}{dt} = -b\rho_0 + (d + \delta q_{0/+})\rho_+ \quad (2.1)$$

The first term in the right hand side indicates the transition from a gap site to a nongap site ($0 \rightarrow +$) by the recruitment and growth of trees. We here assume that the transition occurs randomly at rate b . The second term of Eq. 2.1 indicates disturbances, causing transition from a nongap site to a gap site ($+ \rightarrow 0$). This term includes both random creation of novel gaps independent of nearest neighbors at a rate d , and the expansion of existing gaps towards their neighboring sites. To express this transition rate per nongap site, we need the

conditional probability that a randomly chosen neighbor of an occupied site (state +) is a gap (state 0). We denote this conditional probability by $q_{0/+}$, which is an example of local densities (Matsuda, 1987; Matsuda *et al.*, 1992). Local densities like this indicate the degree of crowding around each individual or site, and $q_{+/+}$ is closely related to the "mean crowding" index m^* (Lloyd, 1967) for clumping of spatial patterns (see Harada and Iwasa, 1994).

In the following, we discuss two ways to derive the dynamics for gap density: one is a traditional way of neglecting spatial structure, and the other is pair approximation.

2.3.1. Mean-field approximation

A common way to simplify population dynamics, such as Eq. 2.1, is just to neglect spatial structure. This can be done by neglecting the correlation between neighbors, i.e. by assuming that the local density is the same as the global density: $q_{0/0} = q_{0/+} = \rho_0$. If we adopt this simplification, the dynamics of the global density ρ_0 given by Eq. 2.1 are:

$$\frac{d\rho_0}{dt} = d - \{b + d - \delta(1 - \rho_0)\} \rho_0, \quad (2.2)$$

where we used relation $\rho_+ = 1 - \rho_0$. Eq. 2.2 gives an autonomous differential equation for the global gap density ρ_0 . Standard analysis shows that Eq. 2.2 has a single globally stable equilibrium between 0 and 1, which is derived from $d\rho_0/dt = 0$. The equilibrium fraction of gap area is:

$$\rho_0^M = \frac{-(b + d - \delta) + \sqrt{(b + d - \delta)^2 + 4d\delta}}{2\delta}, \quad (2.3)$$

where superfix M indicates mean-field approximation. When $\delta = 0$, this equilibrium becomes $\hat{\rho}_0^M = \frac{d}{b+d}$, the fraction of occupied sites in the case without interaction.

2.3.2. Pair approximation and clumped distribution

Instead of neglecting the difference between global and local density, we may distinguish them and derive a closed dynamical system for both variables. Pair approximation is a method of constructing a system of ordinary differential equations for the global density and the local density (Harada and Iwasa, 1994).

First we note that $q_{0/+} = (1 - q_{0/0})\rho_0/(1 - \rho_0)$ holds from the definition of conditional probability. Using this relation, Eq. 2.1 is rewritten as

$$\frac{d\rho_0}{dt} = d - \{b + d - \delta(1 - q_{0/0})\}\rho_0, \quad (2.4)$$

which gives the dynamics of global density ρ_0 in terms of local density $q_{0/0}$. Since the dynamics of global density ρ_0 , given by Eq. 2.4, is determined by ρ_0 and $q_{0/0}$, we must consider a differential equation for $q_{0/0}$. Let ρ_{00} be the density of (0,0) pairs, i.e. the probability for a randomly chosen nearest neighbors to be gap sites. According to the definition of conditional probability, the local density $q_{0/0}$ is equal to ratio ρ_{00}/ρ_0 , and hence the dynamics of local density are:

$$\frac{d q_{0/0}}{dt} = -\frac{\rho_{00}}{\rho_0^2} \frac{d\rho_0}{dt} + \frac{1}{\rho_0} \frac{d\rho_{00}}{dt}.$$

The time change of ρ_{00} is:

$$\frac{d\rho_{00}}{dt} = -2b\rho_{00} + 2\left\{d + \delta\left(\frac{1}{z} + \frac{z-1}{z}q_{0/+}\right)\right\}\rho_{+0}, \quad (2.5)$$

where the first term indicates a transition of a (0,0) pair to a (+,0) pair. Here we denote that ρ_{+0} is the probability that a randomly chosen nearest neighbor pairs is a (+,0) pair in this order, distinguishing the order of two sites. Factor 2 comes from the fact that the recruitment of

either of the two sites can turn + to make such a transition. The total fraction of pairs of + and 0, neglecting the order, is hence $2\rho_{+0}$. The second term of Eq. 2.5 indicates a transition from a (+,0) pair to a (0,0) pair. Here we note that the mortality depends on the fraction of 0 sites in nearest neighbors of a + site, where one of the nearest neighbor of the + site is known to be 0. In Eq. 2.5, we denote this higher order conditional probability by $q_{0/+0}$.

The conditional probability $q_{0/+0}$ can be expressed by using a still higher probability related to a triplet instead of a doublet, but the dynamics for triplet probabilities will include conditional probabilities of a still higher order. We here introduce a pair approximation, namely $q_{0/+0}$ is replaced by $q_{0/+} = (1 - q_{0/0}) \frac{\rho_0}{1 - \rho_0}$ (In general, $q_{\sigma\sigma'\sigma''}$ is replaced by $q_{\sigma\sigma'}$, Matsuda *et al.*, 1992), in which the correlation beyond nearest neighbors is neglected.

Using Eq. 2.4 and Eq. 2.5 with the pair approximation, the dynamics of local gap density $q_{0/0}$ can be rewritten as:

$$\frac{d q_{0/0}}{dt} = -q_{0/0} \left[\frac{d}{\rho_0} - \{b + d - \delta(1 - q_{0/0})\} \right] - 2b q_{0/0} + 2(1 - q_{0/0}) \left[d + \delta \left(\frac{1}{z} + \frac{z-1}{z} (1 - q_{0/0}) \frac{\rho_0}{1 - \rho_0} \right) \right] \quad (2.6)$$

Eqs. 2.4 and 2.6 constitute a closed dynamical system of two variables, ρ_0 and $q_{0/0}$. Now we apply standard analysis of nonlinear differential equations to these equations. The equilibrium of Eqs. 2.4 and 2.6 can be obtained from $\frac{d \rho_0}{dt} = 0$ and $\frac{d q_{0/0}}{dt} = 0$, as follows:

$$q_{0/0}^P = 1 - b \frac{(b + d + \delta \frac{z+1}{z}) - \sqrt{(b + d + \delta \frac{z+1}{z})^2 - 4\delta(b + \frac{d}{z} + \frac{\delta}{z})}}{2\delta(b + \frac{d}{z} + \frac{\delta}{z})} \quad (2.7a)$$

$$\rho_0^P = \frac{d}{b + d - \delta(1 - \hat{q}_{0/0}^P)} \quad (2.7b)$$

where superfix P indicates pair approximation.

In Appendix A, we can prove that in the limit when z increases infinitely large, $q_{0/0}^P$ and ρ_0^P in Eqs. 2.7a, 2.7b converge to $\rho_\bullet^M$ given by Eq. 2.3, the average gap density predicted by mean-field approximation. A similar result has been proved rigorously for $d = 0$, the basic contact process (Bramson *et al.*, 1989). This implies that when the range of ecological interactions is large and includes many sites, the dynamics become similar to the case of complete mixing.

In the absence of interaction between neighbors ($\delta = 0$), the equilibrium local density and the global density predicted by pair approximation are both equal to $\frac{d}{b+d}$.

In Appendix A, we prove that local gap density is greater than the global gap density ($q_{\bullet/0}^P > \rho_0^P$) if $\delta > 0$. We also prove that the density predicted by mean-field approximation is between these two densities predicted by pair approximation ($\rho_0^P < \rho_\bullet^M < q_{0/0}^P$). The global and local densities for nongap sites are calculated from ρ_0^P and $q_{0/0}^P$:

$$\begin{aligned}\rho_+^P &= 1 - \rho_0^P \\ q_{+/+}^P &= 1 - (1 - q_{\bullet/0}^P)\rho_0^P(1 - \rho_0^P)\end{aligned}$$

In this section, we first constructed the dynamics of ρ_0 and $q_{0/0}$, the global and the local densities of gap sites based on pair approximation, and then from the equilibrium, we predict ρ_+ and $q_{+/+}$, the global and the local densities of nongap sites. Alternatively, we may start with the dynamics of global and local densities of nongap sites ρ_+ and $q_{+/+}$, based on pair approximation, and then calculate ρ_0 and $q_{0/0}$ from these results. This is done in Appendix B. Calculation is a little easier than the one in this section, but the result is almost exactly the same.

2.4. Computer simulation

In order to know the accuracy of the two methods of constructing approximated population dynamics (mean-field approximation and pair approximation), we compare the predictions of these dynamics with the direct computer simulation. We examine both one-dimensional and two-dimensional systems. Since the results of one-dimensional system are more pronounced than those of two-dimensional system, we first explain the former.

2.4.1. One-dimensional system

Stands are arranged on a circular lattice including about 1000 sites. To remove the effect of edges, we assume periodic boundary condition. In the initial pattern, each site is a gap or a nongap independently with a constant probability. After 1000 time units, the spatial pattern reaches to the equilibrium and the fraction of gap sites ρ_0 and the conditional fraction of gap sites among neighbors of gaps $q_{0/0}$ are stabilized, and then they fluctuate with small amplitude around their means due to the finiteness of the total number of sites. To remove these small fluctuation, we calculate the average density of gaps over many generations after the equilibrium is reached.

Figure 2.2A illustrates the equilibrium global density ρ_0 and local density $q_{0/0}$ for different δ , the neighbor-dependent mortality. We used $b = 0.20$, implying that the average gap age is 5 time units. The death rate caused by neighbor-independent component of disturbance is $d = 0.01$, which indicates the average tenure for canopy trees in the middle of continuous canopy is 100 time units. Symbols in this figure are the results of computer simulation: Solid circles are for global gap density ρ_0 , and triangles are for local gap density $q_{0/0}$. The local density of gaps is significantly higher than the global density, indicating a clumped spatial distribution of gap sites.

Mean field approximation does not distinguish these two densities, and its prediction ρ_0^M is shown by a broken line. In the mean-field approximation, the equilibrium of local density, $q_{0/0}^M$, is the same as the global density ρ_0^M , which is not the case for computer simulation.

The solid curve is for ρ_0^P , and the gray one is for $q_{0/0}^P$, given by Eq. 2.7a and 2.7b, respectively with $z = 2$. Prediction by pair approximation is clearly more accurate than that by mean-field approximation, and pair approximation correctly predicts that $q_{0/0}$ is larger than ρ_0 . We can see that the gap density given by mean-field approximation is larger than the global density given by pair approximation but smaller than the local density given by the pair approximation.

In Fig. 2.2A, we also indicated the global density ρ_+ by open circles and the local density $q_{+/+}$ of nongap sites by squares. The local density is clearly higher than the global density, implying that the spatial pattern of nongap sites is also clumped. Predictions based on pair approximation are given by solid curves, which are quite accurate.

2.4.2. Two-dimensional system

We also conducted the simulation in a two-dimensional system on a 100×100 lattice with periodic boundary condition (a torus type). Fig. 2.2B illustrates the results. Parameters are the same as in Fig. 2.2A.

Solid lines are the average fractions of gap sites ρ_0^P and the fractions of gap sites among neighbors of randomly chosen gap sites $q_{0/0}^P$, given by Eqs. 2.7a and 2.7b with $z = 4$, derived based on pair approximation. These lines fit very well the results of computer simulation shown by solid circles. A broken line is the prediction by mean-field approximation Eq. 2.3 with $z = 4$. It overestimates the fraction of gap sites.

These results are qualitatively the same as in one-dimensional system, but the difference between different methods of approximation is less pronounced in two-dimensional case than in one-dimensional case (Fig. 2.2A).

2.5. Supply-dependent recruitment and bistability

So far, we have assumed that seeds or seedlings needed for recruitment are always available and the rate of transition from newly formed gaps to nongaps is independent of the

number of parent trees that supply seeds. We may consider the case in which the supply of recruitment is strongly limiting the recovery process.

To simplify the situation, we here examine two cases: [1] recovery rate of a gap is proportional to the number of nongap sites in the forest, and [2] it is proportional to the number of nongap sites in the neighbors.

2.5.1. Recovery proportional to global density of nongap sites

First, we consider the case in which the recovery rate of a gap site is proportional to the fraction of nongap sites in the whole forest, so that b is replaced by $\alpha\rho_+$, where α is a positive constant. The equilibria of the dynamics based on the mean-field approximation and of those based on the pair approximation are shown in Appendix C. We see that there is a parameter region in which there are two simultaneously stable equilibria: one is for the positive equilibrium with a sufficiently high density and the other with $\rho_0 = 1$, implying the absence of trees.

Figure 2.3A illustrates the equilibrium global density ρ_0 and local density $q_{0/0}$ for different neighbor-dependent mortality δ for one-dimensional system. We fixed other parameters ($\alpha = 0.20$, $d = 0.01$). Circles are the results from computer simulation. Solid circles are for the global density ρ_0 , and triangles are for local density $q_{0/0}$. The result from mean field approximation is shown by a broken line. Solid curve is global gap density ρ_0^p , and gray one is local gap density $q_{0/0}^p$, Eq. C3 with $z = 2$. Prediction by pair approximation is more accurate than by mean field approximation, and pair approximation correctly predicts that $q_{0/0}$ is larger than ρ_0 .

We also conducted the simulation of a two-dimensional system on a 100×100 lattice with periodic boundary condition (torus type). Fig. 2.3B illustrates the case of two-dimensional system with theoretical curves, Eq. C3 with $z = 4$. We observe the same tendency as for one-dimensional circular lattice model, but the differences between curves are less pronounced than in one-dimensional system.

2.5.2. Recovery proportional to local density of nongap sites

Next we consider the case in which recovery rate is proportional to the fraction of nongap sites in the neighborhood ($\beta q_{+|0}$). This may be the case in which the supply of the seeds or seedlings is possible only within a short distance, i.e. only to the nearest neighbors, implying relatively heavy seeds (e.g. acorn) with limited dispersal or vegetative propagation. Analyses similar to the last section apply to this case, as shown in Appendix C. The results are illustrated in Fig. 2.3C, where bistability is not predicted by the pair approximation, nor is observed in computer simulation. The mean-field approximation gives ρ_0^M that happens to be the same as $q_{0|0}^P$ (gray line).

Even if the recovery rate may depend on the global and local densities, it may not be directly proportional. In general, we need to examine a nonlinear function of these densities. A simplest generalization would be a sum of three terms: a term independent of the parents, a term proportional to the fraction of nongap sites over the forests, and a term proportional to the number of nongap sites in the neighbors, as we will discuss later in the data analysis.

2.6. Gap size distribution

Now we consider the size distribution of gaps. The total gap area is the same between in Figs. 1A and 1B, but the spatial pattern of the gap sites is more clumped in Fig. 2.1B than in Fig. 2.1A. Fig. 2.1B includes fewer and larger gaps than in Fig. 2.1A. Here and in the rest of the paper, we regard a cluster of adjacent gap sites as a single large gap, and we call the number of sites included in a cluster of gap sites "the size of a gap" (Fig. 2.4).

2.6.1. One-dimensional system

We begin with one-dimensional habitat in which each site has just two neighbors. Let k be the cluster size (or gap size), or the number of sites included a single cluster (or a gap). Let n_k be the number of clusters (gaps) of size k within a large area including lattice sites L .

Now the number of gap sites included in a cluster of size k is kn_k and the probability that a randomly chosen site is a member of cluster of size k is kn_k/L .

First, consider the simplest case in which the spatial pattern is random. Those sites are either gap or nongap independently with probability ρ_0 and $1 - \rho_0$, respectively. Then the size of gaps follows a geometric distribution. To be specific, the probability that a particular site is included in a gap of size k is $k \rho_0^k (1 - \rho_0)^2$.

In the population with clumped distribution, the (unconditional) probability of a site to be a gap site is different from the conditional probability that a nearest neighbor of a gap site is also a gap site. The latter is $q_{0/0}$, which is larger than ρ_0 . Pair approximation considers this difference but neglecting the correlation beyond nearest neighbors. Using this approximation, we can express the probability of a randomly chosen site is included in a cluster of size k as follows:

$$\frac{kn_k}{L} = \rho_0 (q_{0/0})^{k-1} k (1 - q_{0/0})^2 \quad (2.8)$$

This was derived by the following consideration: First a randomly chosen site is a gap site with probability ρ_0 . Second, the probability that x consecutive sites in the left and the $k-1-x$ consecutive sites in the right of it are also a gap site and that the two surrounding sites for these k consecutive sites are nongaps is $(q_{0/0})^{k-1} (1 - q_{0/0})^2$. Finally, there are k possible values for x . The total fraction of gap sites is given by the sum of Eq. 2.8 over $k \geq 1$, and is equal to ρ_0 . The number of gaps of size k in the whole lattice is:

$$n_k = \rho_0 (q_{0/0})^{k-1} (1 - q_{0/0})^2 L \quad (2.9)$$

We may compare the prediction of Eq. 2.9 with the gap size distribution obtained from computer simulation. The equation has two parameters: the average fraction of gap site (ρ_0) and the fraction of gap sites among nearest neighbors of gaps ($q_{0/0}$), which can be obtained

from the spatial pattern. Solid circles in Fig. 2.5 indicate the gap size distribution for the spatial pattern generated by computer simulations. Solid lines indicate the prediction given by Eq. 2.9 using two parameters (ρ_0 , $q_{0/0}$) estimated from the observed spatial pattern. They are quite accurate in predicting the result of computer simulations. This indicates the usefulness of the approximation based on the neglect of higher order correlation beyond pairs.

In Fig. 2.5, we also illustrated a gray line indicating the equation in which $q_{0/0}$ replaced by ρ_0 . This gray line is the gap-cluster distribution for the pattern generated by a random spatial pattern of the same total gap area. When interaction term is absent ($\delta = 0$), the spatial pattern is random, and the broken and solid lines are the same. But for the cases with nearest neighbor interaction ($\delta > 0$), we have fewer small clusters and more large clusters than predicted by random spatial pattern (gray curves) due to a clumped spatial distribution of gap sites.

The broken line in Fig. 2.5 is the prediction using two parameters, $q_{0/0}$ and ρ_0 , from the pair approximation, Eqs. 2.7a and 2.7b. Here $q_{0/0}$ and ρ_0 are not from fitting to the data, but are calculated directly from basic parameters b , d , and δ using the dynamics analyzed in a previous section. We can see that the prediction is fairly accurate, and that pair approximation can explain the gap size distribution very well without relying on the fitting procedures.

2.6.2. Two-dimensional system

Similarly, we can calculate the gap size distribution on regular two-dimensional square lattice for Neumann neighborhood, but computation is more complicated than the case for one-dimensional system. For example, consider the probability that a randomly chosen site is an isolated gap site, i.e. it is itself a single cluster of size 1. According to the spirit of pair approximation, it is simply $\rho_0(1 - q_{0/0})^4$, where the site is a gap with probability ρ_0 and all of its four neighbors are nongaps with conditional probability $(1 - q_{0/0})^4$ (considering nearest neighbor correlation only). A similar probability for cluster of size 2 is $4\rho_0q_{0/0}(1 - q_{0/0})^6$,

where factor 4 comes from the number of configurations, and power 6 indicates the number of neighbors surrounding a (0,0)-pair.

Similar consideration applies to a larger cluster size. Consider a gap site that belongs to a cluster of size k . Let c_k be the total number of configurations of clusters of size k . We indicate the i th configuration among c_k possibilities by (i, k) . Let $P(i, k)$ be the number of sites in the perimeter of the configuration (i, k) . Then, based on the approximation neglecting higher order correlation beyond nearest neighbor pairs, the probability that a single site is included in a cluster of k -gaps is:

$$\frac{kn_k}{L} = \rho_0 q_{0/0}^{k-1} \sum_{i=1}^{c_k} (1 - q_{0/0})^{P(i,k)} \quad (2.10)$$

For one-dimensional case, Eq. 2.10 becomes Eq. 2.8 by using $c_k = k$ and $P(i, k) = 2$.

Table 2.1 shows the perimeter polynomials of the two-dimensional site problem, $f[x]$, which is defined as $f[x] = \frac{1}{k} \sum_{i=1}^{c_k} (1 - x)^{P(i,k)}$. We can rewrite Eq. 2.10 as follows:

$$n_k = \rho_0 q_{0/0}^{k-1} f[1 - q_{0/0}] L$$

which gives the number of gaps of size k in a large area including L sites. These polynomials have been derived in physics, because the current model becomes site percolation process if sites are independent ($\rho_0 = q_{0/0}$) (Stauffer, 1985; Sykes and Glen, 1983).

Fig. 2.6 illustrates gap size distribution from the simulation model and the prediction by the equations above. Solid circles indicate the results from computer simulations. A solid line indicates the prediction given by Eq. 2.10 using two parameters estimated from the spatial pattern generated by computer simulation. They are quite accurate, again confirming the usefulness of the approximation of neglecting higher order correlation beyond pairs. Gray lines in Fig. 2.6 illustrate the equation given by Eq. 2.10 with $q_{0/0}$ replaced by ρ_0 . The

broken lines in Fig. 2.6 are the prediction using two parameters, q_0/p_0 and p_0 , from the dynamics based on pair approximation (Eqs. 2.7a and 2.7b). They are very close to the solid lines and are able to predict simulation results (solid circles).

In short, Eq. 2.10 with Eq. 2.7, based on pair approximation predict the cluster size (or gap size) distribution very accurately, both in one-dimensional and two-dimensional systems.

2.7. Discussion

Many successful computer models of forest dynamics assume that the forest is an ensemble of independent patches or stands (e.g. Botkin *et al.*, 1972; Shugart, 1984; Leemans and Prentice, 1987; Kienast and Kuhn, 1989; Keane *et al.*, 1990; Prentice and Leemans, 1990; Mohren and Kienast, 1991). In addition, an analysis of forest dynamics most frequently adopted is the use of a transition matrix, in which the state of forest stands is classified into several categories, according to canopy height (e.g. Hubbell and Foster, 1986) or to species composition (Horn, 1974, 1975), and from the transition between one census to the next, the fractions of sites that undergo transition from one category to another are estimated and summarized as a table (e.g. Caswell, 1989). Using this table of transition probability, assuming Markovian property (neglect of past history), we can predict the temporal change and the equilibrium composition of the forests.

However, we must note that this method is valid only when we can neglect the interaction between nearest neighboring sites. As we have shown in this paper, interaction between neighboring sites, in a form of gap expansion, has profound effects on the spatial pattern, and subsequently on the forest dynamics.

In this paper we studied the total gap area and gap size distribution in a lattice structured model in which disturbance occurs at a higher rate in nongap stands next to existing gaps than those surrounded by continuous canopy. Due to the neighbor-dependent mortality ($\delta > 0$), spatial distribution of gap sites becomes clumped (Fig. 2.1B). The fraction of gap sites among neighbors of gap sites is significantly higher than the average fraction of gap sites

($q_{0|0} > \rho_0$). This clumped spatial distribution affects the equilibrium level of total gap area. The dynamics based on mean-field approximation (neglecting nearest neighbor correlation) overestimate the equilibrium gap area, as shown by broken lines of Figs. 2A, 2B and 3. This is because the same total gap area would disturb the forest more extensively if it would be scattered over the forest with many more gap clusters. Spatial clumping of gap sites reduces the number of sites next to existing gap and the average rate of disturbance, and thus lowers a gap area level than predicted by the computation assuming random spatial distribution with the same total gap area (mean-field approximation).

In the case of supply-dependent recruitment illustrated in Fig. 2.3, the model may have simultaneously a locally stable positive equilibrium and a trivial equilibrium when trees are absent. This bistable situation can be predicted accurately by pair approximation but not by the mean-field approximation.

The pair approximation method constructs a closed dynamical system using average fraction of gap sites and the conditional fraction of gap sites among nearest neighbors of gaps, called global density and local density of gap sites, respectively. In a spatially structured model for herbaceous plants with vegetative reproduction and seed production, Harada and Iwasa (1994) showed that the local density is the same as the mean crowding by Lloyd (1967) if a sampling quadrat includes only a neighboring pair of sites. Mean crowding is defined as the average density experienced by individuals and has been developed as a very useful method of statistical analysis of spatial distribution (Iwao, 1968; Iwao and Kuno, 1971; Taylor, 1984; Iwasa and Teramoto, 1977, 1984). In the present mode, therefore, ρ_0 is the average gap density and $q_{0|0}$ the mean crowding of gap sites, and the dynamics of Eqs. 2.4 and 2.6 give closed autonomous equations for average density and mean crowding. The ratio of mean crowding to average density (denoted by m^*/m) is called as patchiness index (Iwao, 1968). The ratio $q_{0|0}/\rho_0$ corresponds to the patchiness (the ratio of mean crowding to the mean density, denoted by m^*/m) (Iwao, 1968).

In this paper, we also examined the size distribution of clusters of gap sites, or the size distribution of gaps if we regard a cluster of gap sites as a single large gap. The pair approximation in spite of simple assumptions again gives an accurate prediction of the gap size distribution for a highly clumped spatial distribution including a much higher fraction of large clusters than expected by chance (see Fig. 2.5 and 6).

2.7.1. Application to data from a tropical forest

To illustrate the use the present results to forest data, we here attempt to analyze the data in Hubbell and Foster (1986) from a neotropical forest in Barro Colorado Island, Panama. They chose 5x5 m as the size of each lattice site, and showed the spatial pattern of these sites as a map (Hubbell and Foster, p. 88, Fig. 2.3.4). On this map, [1] the sites lower than 20 m in height in 1983 census, [2] the sites higher than 20 m in 1983 but became lower than 20 m in height in the 1984 census, and [3] those that remain higher both in 1983 and 1984 census times, are displayed in different colors (the figure 2. caption included a typographical mistake known from comparing Table 3.1 of Hubbell and Foster, 1986). By reading the data from the map (except for unreadable leftmost column and bottom row), we can calculate various statistics needed for the analysis. The data we used for our analysis is in Fig. 2.7. By choosing 20 m as the threshold vegetation height separating gaps from nongaps, the global gap density is $\rho_0 = 0.331$ and local gap density is $q_{0/0} = 0.580$, and others are: $q_{+/+} = 0.801$, $q_{0/+} = 0.199$, and $q_{+/0} = 0.420$, from the census in 1983. The spatial pattern is clumped, as $q_{0/0} > \rho_0$.

The transition rate of a nongap (taller than 20 m) to a gap (shorter than 20 m) increases with the number of gap surrounding it in 1983 (Fig. 2.7). We attempted both Neumann neighborhood ($z = 4$) and Moore neighborhood ($z = 8$), and both gave very good fits to straight lines (Fig. 2.8). Since Neumann neighborhood gave a better fitting according to the likelihood function explained in Appendix D, we use Neumann neighborhood for the analysis below.

A transition matrix (Table 3.1, p. 87, in Hubbell and Foster, 1986) shows that the one-year transition of trees less than 20 m to taller than 20 m in the following year was $b = 0.177$ ($= 1173/6631$). In the model, the average transition rate from a nongap to a gap (disturbance rate) is $d + \delta q_{0/0}$, the parameters of which are known from the regression line ($z = 1$) in Fig. 2.8, as $d = 0.024$ and $\delta = 0.276$.

We examine three models differing in the assumption of recovery process:

[Case 1] Constant recovery rate:

Using the parameter $b = 0.177$, we can apply the model and the mean field approximation predicts the equilibrium fraction of gap sites $\rho_0^M = 0.461$, which does not explain the observed difference between global and local densities. Pair approximation gives the global density $\rho_0^P = 0.408$ and the local density $q_{0/0}^P = 0.485$ at the equilibrium. These overestimate observed values: $\rho_0 = 0.331$ and $q_{0/0} = 0.580$. In addition, their ratio $q_{0/0}^P/\rho_0^P = 1.189$ is smaller than the observed $q_{0/0}/\rho_0 = 1.752$, implying this model underestimates the patchiness of the spatial patterns.

[Case 2] Recovery rate proportional to global density of nongap sites:

By setting $0.177 = \alpha \rho_+$, we can estimate $\alpha = 0.243$. We may use the same parameters for d and δ as in the last section. In this case, the dynamics based on pair approximation (Appendix C) predict the extinction of the whole population at the equilibrium: $\rho_0^P = 1$. This does not fit to the observation.

[Case 3] Recovery rate proportional to local density of nongap sites:

By setting $0.177 = \beta q_{+/0}$, we can estimate $\beta = 0.423$. Pair approximation in Appendix C predicts: $\rho_0^P = 0.216$ and $q_{0/0}^P = 0.402$. These underestimate the observed values for gap fractions. Their ratio is $q_{0/0}^P/\rho_0^P = 1.861$, implying a more clumped spatial distribution than the observed pattern.

In short, the observed values of global and local densities of gaps are in between the equilibrium in Case 1 (constant recovery rate) and that in Case 2 (recovery rate directly proportional to the local density of nongap sites). A simplest modelling in such a situation

would be a linear combination of these two cases, with the recovery rate $b + \beta q_{+10}$. We have $0.177 = b + \beta q_{+10}$ as a constraint from the total rate of recovery in Table of Hubbell and Foster. Since the locations of recovered sites (those lower than 20 m but became taller than 20 m) were not shown in a map, we cannot estimate b or β directly. However we can confirm that by choosing $b = 0.135$ and $\beta = 0.100$, the dynamics based on pair approximation give the equilibrium population with $\rho_0 = 0.331$ and $q_{0/0} = 0.580$.

When we observe deviation between the predicted equilibrium composition of the forest and the observed pattern, we may conclude that the current spatial pattern is not at equilibrium. It is also very likely however that the environment may not be perfectly constant and the transition of just one year period may not be enough to average out the fluctuations of growth and disturbance rates. This is quite likely to be important as many disturbances events in forests are episodic (as discussed later)

2.7.2. Percolation probability

As the fraction of gap sites increases, the average size of clusters of gap sites increases. Gaps merge with each other and form large gaps. When the fraction of gap sites exceeds a certain critical level for two-dimensional system, there appears a gap that stretches through the whole lattice. In the extreme case, most gap sites are connected with each other, in which "gaps" are no longer recognized as such, and instead there are patches of nongap sites scattered over the lattice that are mostly gap sites. This phenomenon is the same as site percolation process if each site is gap or nongap independently, which has been studied extensively in physics (Broadbent and Hammersley, 1957; Stauffer, 1985). For one-dimensional lattice, clusters of gap sites are always of a finite size except for the case that the fraction of gap sites is exactly 1 and percolation (appearance of cluster that stretches through the whole lattice) is not possible. In contrast, for a two-dimensional lattice with an infinite size, an infinitely large cluster of gap sites appears with a positive probability if the fraction of gaps exceeds a critical level, 0.59.

Open circles in Fig. 2.9 illustrate percolation probabilities in computer simulation of a two-dimensional finite lattice, i.e. the fraction of simulation runs in which there is at least one cluster of gap sites (or one large gap) that stretches either from the leftmost column to the rightmost column or from the top row to the bottom row. The horizontal axis is the average fraction of gap sites.

Solid squares in Fig. 2.9 show the percolation probability for the spatial pattern generated by the gap expansion model with constant recovery rate, in which the spatial distribution of gap sites is clumped. Squares indicate the results generated by various δ gap-dependent mortality (other parameters are fixed: $b = 0.20$, $d = 0.01$). Note that the relationship between the percolation probability (vertical axis) and the fraction of gap sites (horizontal axis) is not very different from the simple percolation model with random spatial pattern (open circles). Clumped distribution of gap sites tends to reduce the number of sites that are isolated, favoring the percolation phenomena. On the other hand, clumped distribution makes cluster more compact, and clusters are more difficult to stretch, discouraging percolation. These two tendencies seem to cancel with each other and the net result of percolation probability we examine was rather insensitive to the spatial structure.

The spatial pattern generated by the dynamics Eq. 2.1 is the same as the percolation model when $\delta = 0$, in which sites are independent of each other. In contrast, we may consider another extreme: all the new gap sites can be produced by the expansion of existing gaps ($d = 0$ and $\delta > 0$), the model is the same as the basic contact process in which gap sites are regarded as entity to reproduce (Liggett, 1985; Bezuidenhout and Grimmet, 1990; Matsuda *et al.*, 1992; Sato *et al.*, 1994; Durrett and Levin, 1994).

2.7.3. Future extension

The model analyzed in this paper includes many simplifying assumptions, some of which may be relaxed in future studies. First, we studied the case with only two states (gap and nongap). The extension of the method to the case in which sites are classified onto more

than two states would be useful, so that we can deal with the case including several or more states of transition. The pair approximation method must deal with all kinds of pair of states and there are $n(n-1)/2$ kind of pairs if there are n states. Extension of the method to multiple states would also allow the analysis of photographs from airplane or satellite that are increasingly available in near future. In the current state, these data tend to be analyzed by a transition matrix, in which the spatial correlation is completely neglected. Preliminary analysis of gap dynamics in a single example (Hubbell and Foster, 1986) suggests that if the data is available on the pattern of gap formation, expanding and closure, we will be able to answer several empirical questions based on the lattice structured model.

In this paper, we discuss disturbances that occurs at a constant rate and independently between sites. However, a global or regional scaled fluctuation of weather, such as El Niño, would create synchronization of different patches that are located distantly from each other. In addition, many processes causing disturbance, such as forest fire, land slides and insect outbreaks tend to create large gaps resulting in spatially clumped regeneration of trees (e.g. Lorimer, 1985; Iwasa and Kubo, 1995). Further, the variability of disturbance with very different spatial and temporal scales is of much importance (Levin, 1988). How to incorporate these aspects of disturbances with spatially structured forest dynamics is an important future theoretical problem.

Appendix A: Proof of the inequalities for local and global densities

Let $w = \rho_0^M$, the equilibrium density of gap sites predicted by mean-field approximation. We here introduce abbreviation: $x = q_{0/0}^P$, the local density of gap sites, and $y = \rho_0^P$, the global density of gap sites predicted by pair approximation. We first assume that parameters b , d and δ are positive, that variables w , x and y are between 0 and 1, and that z is an integer greater than 1. From setting Eq. 2.2 equal zero, we have:

$$b + d - \frac{d}{w} = \delta (1 - w) \quad (A1)$$

Eq. 2.7b becomes

$$b + d - \frac{d}{y} = \delta (1 - x) \quad (A2)$$

Eq. 2.7a together with Eq. A2, becomes

$$b + d - \frac{d}{x} = \delta (1 - x) \left[\frac{1}{z x} + \frac{(z-1)(1-x)y}{z x (1-y)} \right] \quad (A3)$$

The difference between Eq. A1 and Eq. A2 leads to:

$$d \frac{w-y}{w y} = \delta (x - w) \quad (A4)$$

Examining Eq. A4, we can conclude that either $x > w > y$, or $x = w = y$, or $x < w < y$ must hold.

Second, the difference between Eq. A3 and Eq. A2 is:

$$d \frac{x-y}{x y} = \delta (1 - x) \left[\frac{1}{z x} + \frac{(z-1)(1-x)y}{z x (1-y)} - 1 \right] \quad (A5)$$

Suppose $y \geq x$. Then, the right hand side of Eq. A6 is:

$$\begin{aligned} & \delta(1-x) \left[\frac{1}{z x} + \frac{(z-1)(1-x)y}{z x (1-y)} - 1 \right] \\ & \geq \delta(1-x) \left[\frac{1}{z x} + \frac{z-1}{z} - 1 \right] \\ & = \frac{\delta(1-x)^2}{z x} > 0 \end{aligned} \quad , \quad (A6)$$

which leads to $x > y$ from Eq. A6, which is the contradiction. Hence $x > y$ holds.

Combined this with the pervious result, we can conclude $x > w > y$. Hence $q_{0/0}^P > \rho_{\bullet}^M > \rho_0^P$, as shown in Figs. 2A and 2B.

If δ is zero, Eqs. A1, A2 and A3 show $x = w = y$.

Consider the case when z is infinitely large, corresponding to compete mixing with spatial structure negligible. Eq. A5 with $z \rightarrow \infty$ can be rewritten as

$$(x-y) \frac{d(1-y) + \delta(1-x)}{x y (1-y)} = 0 \quad , \quad (A7)$$

implying that $x = y$. Hence we conclude $x = w = y$.

Appendix B: Analytical solutions from pair approximation (1)

We can carry out similar analysis using the global and local densities of nongap sites (ρ_+ and $q_{+/+}$), instead of those for gap sites.

Mean-field approximation

The dynamics of the global density ρ_+ of nongap sites are as follows:

$$\frac{d\rho_+}{dt} = b(1-\rho_+) - \{d + \delta(1-\rho_+)\} \rho_+ \quad , \quad (B1)$$

which is the same as Eq. 2.2 by rewriting $\rho_+ = 1 - \rho_0$.

Pair approximation and clumped distribution

The dynamics of global density ρ_+ are:

$$\frac{d\rho_+}{dt} = b(1 - \rho_+) - \{d + \delta(1 - q_{+/+})\} \rho_+ \quad , \quad (B2)$$

which holds exactly. To compute the dynamics of $q_{+/+}$, we first calculate the dynamics of doublet density ρ_{++} , the density of $(+,+)$ pairs, i.e. the probability for a randomly chosen pair to be both occupied:

$$\frac{d\rho_{++}}{dt} = 2b\rho_{+0} - 2\left(d + \delta\frac{z-1}{z}q_{0/++}\right)\rho_{++} \quad . \quad (B3)$$

Pair approximation is to replace $q_{0/++}$ in Eq. B3 by $q_{0/+}$. Note that this may in general differ from the pair approximation used in the text (where $q_{0/+0}$ is replaced by $q_{0/+}$).

The dynamics of local density $q_{+/+} = \frac{\rho_{++}}{\rho_+}$ is:

$$\frac{dq_{+/+}}{dt} = -\frac{\rho_{++}}{\rho_+^2} \frac{d\rho_+}{dt} + \frac{1}{\rho_+} \frac{d\rho_{++}}{dt}$$

After some arithmetics, we have

$$\frac{dq_{+/+}}{dt} = -q_{+/+} \left\{ \frac{b}{\rho_+} + \delta\frac{z-2}{z}(1 - q_{+/+}) + b + d \right\} + 2b \quad . \quad (B4)$$

Eqs. B2 and B4 constitute a closed dynamical system of two variables, ρ_+ and $q_{+/+}$. Now we apply standard analysis of nonlinear differential equations to these equations. The equilibrium of Eqs. B2 and B4 are:

$$\hat{q}_{+/+}^P = \frac{b+d+\delta \frac{z-1}{z} - \sqrt{\left(b+d+\delta \frac{z-1}{z}\right)^2 - 4b\delta \frac{z-1}{z}}}{2\delta \frac{z-1}{z}}, \quad (\text{B5a})$$

$$\hat{\rho}_+^P = \frac{b}{b+d+\delta(1-\hat{q}_{+/+}^P)}. \quad (\text{B5b})$$

In the limit when z is infinitely large, $\hat{q}_{+/+}^P$ converge to $\hat{q}_{+/+}^M (= \hat{\rho}_+^M)$.

$\lim_{z \rightarrow \infty} \hat{q}_{+/+}^P = \lim_{z \rightarrow \infty} \hat{\rho}_+^P = \hat{\rho}_+^M$. This implies that when the range of ecological interactions is

large and includes many sites, the dynamics become similar to the case of complete mixing.

Using a similar logic as in Appendix A, we can prove that $\hat{q}_{+/+}^P > \hat{\rho}_+^P > \hat{\rho}_+^M (= \hat{q}_{+/+}^M)$.

The global and local densities for gap sites are calculated from these densities for nongap sites:

$$\rho_0 = 1 - \rho_+ \quad \text{and} \quad q_{0/0} = 1 - (1 - q_{+/+})\rho_+ / (1 - \rho_+)$$

Appendix C: Analytical solutions from pair approximation (2)

Recovery rate proportional to global density of nongap sites

We here compute the dynamics of nongap sites (+), instead of gap site (0), because of mathematical tractability. We replace b by $\alpha \rho_+$ in Eqs. B1, B3 and B6, and we have the dynamics based on mean-field approximation:

$$\frac{d\rho_+}{dt} = \alpha \rho_+(1-\rho_+) - \{d + \delta(1-\rho_+)\}\rho_+, \quad (\text{C1})$$

and those based on pair-approximation:

$$\frac{d\rho_+}{dt} = \alpha \rho_+(1-\rho_+) - \{d + \delta(1-q_{+/+})\}\rho_+, \quad (\text{C2a})$$

$$\begin{aligned} \frac{dq_{+/+}}{dt} = & -q_{+/+} \{ \alpha(1-\rho_+) - (d + \delta - \delta q_{+/+}) \} \\ & + 2\alpha \rho_+(1-q_{+/+}) - 2 \left\{ d + \delta \frac{z-1}{z} (1-q_{+/+}) \right\} q_{+/+}. \end{aligned} \quad (\text{C2b})$$

The equilibria of the dynamics based on the mean-field approximation, Eq. C1, and of those based on the pair approximation, Eq. C2a, b can be solved explicitly. The system always has an equilibrium with $\rho_+^P = 0$, implying the extinction of the population. The stable positive equilibrium (ρ_+^P, q_+^P) is:

$$\hat{q}_{+/+}^P = \frac{\delta \frac{z+1}{z} - \alpha + \sqrt{\left(\alpha - \delta \frac{z-1}{z}\right)^2 - 4d\delta/z}}{2\delta/z}, \quad (C3a)$$

$$\hat{\rho}_+^P = \frac{\alpha - d - \delta(1 - \hat{q}_{+/+}^P)}{b}, \quad (C3b)$$

which exists only for $\delta < \delta_c$, where the critical δ_c is:

$$\delta_c = \frac{1}{2} \left(\alpha + \frac{4d}{z-1} - \sqrt{\left(\alpha + \frac{4d}{z-1}\right)^2 - 4\alpha^2} \right). \quad (C4)$$

An unstable equilibrium is the one with Eq. C3 if we replace a positive sign in front of the square-root symbol by a negative sign. At $\delta = \delta_c$, the stable and unstable equilibria merge and disappear. For $\delta > \delta_c$, there is no positive equilibrium, and δ a little smaller than δ_c , the system is bistable, as the positive equilibrium Eq. 2.3 and the trivial equilibrium are stable.

Fig. 2.3A and 3B are ρ_0 and $q_{0/0}$ calculated from Eq. C3.

Recovery rate proportional to local density of nongap sites

We replace α in Eq(C1) by β , $\alpha(1 - \rho_+)$ in Eqs. C2 and C3 by $\beta(1 - q_{+/+})$, we have the dynamics based on mean-field approximation:

$$\frac{d\rho_+}{dt} = \beta\rho_+(1-\rho_+) - \{d + \delta(1-\rho_+)\}\rho_+, \quad (C5)$$

and those based on pair-approximation:

$$\frac{d\rho_+}{dt} = \beta(1-q_{+/+})\rho_+ - \{d + \delta(1-q_{+/+})\}\rho_+ \quad , \quad (C6a)$$

$$\begin{aligned} \frac{dq_{+/+}}{dt} = & -q_{+/+} \{ \beta(1-q_{+/+}) - (d + \delta - \delta q_{+/+}) \} \\ & + 2\alpha \left(\frac{1}{z} + \frac{z-1}{z} q_{+/0} \right) (1-q_{+/+}) - 2 \left\{ d + \delta \frac{z-1}{z} (1-q_{+/+}) \right\} q_{+/+} . \end{aligned} \quad (C6b)$$

The equilibria of the dynamics based on the mean-field approximation, Eq. C5, and of those based on the pair approximation, Eq. C6a, b can be solved explicitly. The system always has an equilibrium with $\rho_+^P = 0$, implying the extinction of the population. The stable positive equilibrium $(\rho_+^P, q_{+/+}^P)$ is:

$$\begin{aligned} \hat{q}_{+/+}^P &= \frac{\beta - \delta - d}{\beta - \delta} \quad , \quad (C7a) \\ \hat{\rho}_+^P &= \frac{A}{(1 - \hat{q}_{+/+}^P) + A} \quad , \end{aligned}$$

where

$$A = \frac{z}{z-1} \left[\frac{\hat{q}_{+/+}^P}{\beta(1 - \hat{q}_{+/+}^P)} \left\{ d + \delta \frac{z-1}{z} (1 - \hat{q}_{+/+}^P) \right\} - \frac{1}{z} \right] \quad . \quad (C7b)$$

Appendix D: Maximum likelihood estimation of site transition rate

The statistical analysis of the effect of neighborhood, as shown in Fig. 2.8. We classify nongap sites in the forest according to the number of gap sites in their neighborhood. To be specific, let x be the number of gap sites within the neighborhood, L_x be the number of nongap sites with x gap neighbors in a given spatial data, and N_x be the number of nongap sites (with x gap neighbors) that made transition to gap sites before the following census. We assume that the probability of a nongap site in 1983 census becomes a gap site in 1984 census is $a + bx$, where a and b are positive parameters. The likelihood function is:

$$f = \prod_{x=1}^z \left(\frac{L_x}{N_x} \right) (a + bx)^{N_x} (1 - a - bx)^{L_x - N_x} \quad (D1)$$

For a given two-dimensional pattern, such as Fig. 2.7, Eq. D1 can be computed for Neumann neighborhood ($z = 4$) and for Moore neighborhood ($z = 8$), separately. The logarithm of the likelihood function was $\ln f = -3196.9 + \text{constant}$ for Neumann neighborhood, and $\ln f = -3200.4 + \text{constant}$, where "constant" term is common for both. Since the number of free parameters to fit is the same, we can conclude that the model with Neumann neighborhood gives a better fit to the data.

III. Sustainability of an isolated beech-dwarf bamboo stand:

analysis of forest dynamics with individual based model*

3.1. Introduction

The dwarf bamboos *Sasa* species have a strong impact on the forest regeneration (Nakashizuka, 1987 and 1988); they flower and wither synchronously over a large area once in several decades (Numata 1970). This phenomenon occurs widely in beech (*Fagus crenata*) forests in Japan. Nakashizuka and Numata (1982a) found that dense *Sasa* undergrowth not only destroys beech seedling bank, but makes synchronized age structure of beech trees by its simultaneous dying out. It is also observed that *Sasa* increases the proportion of gap area in forest (Nakashizuka, 1984), because the dense cover of *Sasa* prevents the development of new canopy trees for gaps in forest. Nakashizuka (1988) suggested that the interval between withering and the length of the recovery time are two important factors controlling the beech forests. There are few studies have investigated the regeneration process of *Sasa* species after their synchronous death (Makita, 1992; Makita *et al.*, 1993), but the relationship between *Sasa* undergrowth and beech dynamics has never been fully understood because this phenomenon might occur in every several decade.

Two studies about the modeling for forest dynamics with considering the *Sasa* activity were done. A matrix model for the dynamics of beech forest by Kawano and Iwasa (1993) confirmed that the synchronized death of *Sasa* generated the periodic cohort structure of beech stands. Takahashi (1997) showed that two conifers, *Picea* and *Abies* could coexist in forests with *Sasa* because of the increased relative success of regeneration on elevated sites (fallen logs buttresses) by *Picea* saplings.

The present study aims to answer an important question on beech forest dynamics: how much does dwarf bamboo *Sasa* prevent tree recruitment? To evaluate quantitatively the

* This chapter was done in collaboration with Dr. Hideyuki Ida. The original paper is submitted to Ecological

suppressing effects of *Sasa* on the recruitment of beech trees, we developed an individual based model (IBM) for a small isolated stand of beech population with *Sasa* undergrowth. The IBM can implement accurately some interactions such as one-directional competition acting between beech individuals and also between beech trees and *Sasa* foliage.

In modeling of forest dynamics, IBM has been used over 20 years (e.g. Botkin *et al.* 1972, Shugart 1984; Horn *et al.*, 1989). One of the recent achievement in this field is a realistic forest simulator SORTIE developed by Pacala *et al.* (1993 and 1996). In SORTIE, all the parameters are estimated directly from field measurements, the model has explicitly spatial structure and the output explains the real forest dynamics fairly accurately.

We will apply the Monte Carlo method to operate IBM which is the most direct way to realize vertical relations among individuals in beech population. We carry out the sensitivity analysis of the model by examining "sustainable probability for 500 years", or a P500 index. This is defined as the probability that a population of beech trees in a small stand isolated by forest fragmentation maintained over 500 years. In this analysis, we focus on how the index depends on the parameters, in particular, on those of *Sasa* life history.

3.2. Study area

The present study was carried out in a beech forest-oak (*Quercus mongolica* var. *grosseserrata*) forest-*Sasa* grassland series located on a northwestern slope toward the ridge of Mt. Jippo (34°34'N, 132°09'E, and 1318.9 m a.s.l.), southwestern Japan. Most present old-growth beech forests in Japan had already been diminished by past human activities. In addition, the beech forest on Mt. Jippo is fragmented and isolated from other beech forests.

A transect (280 m long and 20 m wide) was set up from old-growth beech stand on a slope to grassland dominated by *Sasa palmata* on the ridge, through the secondary oak stand. It was divided into 14 quadrats of 20 meters numbered from Q1 (beech stand) to Q14 (*Sasa* grassland). Ida and Nakagoshi (1994 and 1996) discussed the process of the zonation and

forest regeneration in the *Sasa* grassland. They concluded that the beech stand and the *Sasa* grassland had been maintained for more than 330 years. The oak stand, however, developed as a secondary forest after a disturbance event, and the disturbance could be due to human impact conducted more than 85 years ago.

3.3. Modelling and parameter estimation

We develop an IBM for the dynamics of an isolated beech stand. Because the beech stands on Mt. Jippo are isolated from each other for a long time, we focus on the dynamics of a single stand without seed flow from other beech stands.

Figures 1 outline the conceptual schemata of this model which is of discrete time with time step of one year. Figure 3.1A represents an isolated beech stand which includes some adult beech trees, many saplings and seedlings in a 20 m quadrat. *Sasa* foliage layer always exists at 2 meters height except the period after the synchronous dying out. We assume that the beech seedlings with height shorter than 2 meters are shaded by *Sasa* undergrowth. Figure 3.1B shows the grand design for developmental stages of beech trees. There are three major submodels: growth, surviving and seed production of beech trees. Their detail and parameterization will be described in the following sections.

Figure 3.1C explains the simplified model of the life cycle of the dwarf bamboo *Sasa*. A clone of *Sasa* covers a very broad area, and the shoots and underground part of *Sasa* die out every several decades and regenerate subsequently. Here we define that the longevity of *Sasa*, denoted by T , is equal to the range from an event of synchronous dying out to the next. *Sasa* life history is divided into two phases: "no-shading phase" of τ years and "shading phase" of $(T - \tau)$ years. The no-shading phase is the period for recovering of *Sasa* foliage from simultaneous withering. As we don't know the detail of the recovery process, we assume that *Sasa* has no foliage (*i.e.* no shading ability) during the no-shading phase for simplicity.

3.3.1. Beech growth

The submodel for growth of beech trees is stochastic and with three parameters: constant growth rate, size dependency and coefficient of competition between beech trees. For simplicity, we focus on a particular mode of competition between trees, that is, one-sided competition (a larger tree can suppress the growth of a smaller one but the opposite is impossible). The only one attribute for each beech individual is its diameter at breast height (DBH) which determines the direction of one-sided competition between beech trees. We will have individuals shorter than 2 meters high in our simulation and are covered by *Sasa* foliage. Even in such case, for simplicity, the size of a beech tree is assumed to have the corresponding DBH calculated from DBH-tree height relationship.

The DBH- H (tree height) relationship is represented by the "generalized allometric equation" (Ogawa, 1969; Kohyama, 1990). For various forest stands, the relation between DBH (cm) and H (m) shows an asymptotic curve suggesting a maximum height, or $H_{\max}$ for DBH, which is approximated by,

$$1/H = 1/(A \text{ DBH}^h) + 1/H_{\max} \quad , \quad (3.1)$$

where A , h and $H_{\max}$ are stand-specific positive parameters. We chose $A = 0.79$, $h = 1.26$ and $H_{\max} = 19.2$ by fitting Eq. 3.1 to the DBH-height relation on the Mt. Jippo research plot measured at 1991.

The model of one-sided competition adopted here is essentially the same as that of Kohyama (1989, 1991, 1992a, 1992b, 1993 and 1994), which has two assumptions; 1) the rank in the one-sided competition are determined by the DBH of trees; 2) The intensity of competition is characterized by the degree of growth inhibition which depends on the total of square DBH (*i.e.* total basal area) for all the larger than the focal one. We assume that *Sasa* has no direct effect the beech growth.

Let N_t be the total number of beech individuals at year t in a focal quadrat, and i be the index to distinguish each individual ($i = 1, 2, \dots, N_t$). Individual size $x_{i,t}$ (cm) is the DBH for the i -th beech tree in the year t . The annual growth of the i -th individual's growth is,

$$x_{i,t+1} = x_{i,t} + G(x_{i,t}) \quad , \quad (3.2)$$

where $G(x_{i,t})$ is a random variable, because we here assume that the growth of beech trees is stochastic. We assume that the growth follows an exponential distribution which is the simplest non-negative and continuous probabilistic distribution. To the probability that $G(x_{i,t})$ is in the range from z to $z + dz$ is,

$$\text{Prob}[z \leq G(x_{i,t}) < z + dz] = \lambda \exp(-\lambda z) dz \quad , \quad (3.3)$$

where the parameter λ is equal to the inverse of the expectation of $G(x_{i,t})$ or $\bar{G}(x_{i,t})$ ($\lambda = 1/\bar{G}(x_{i,t})$). we chose the expected growth per year $\bar{G}(x_{i,t})$ is,

$$\bar{G}(x_{i,t}) = x_{i,t} \exp[a_0 - a_1 \log(x_{i,t}) - a_2 B(x_{i,t})] \quad . \quad (3.4)$$

The parameter a_0 determined the initial growth rate under the circumstance without suppression. The parameters a_1 and a_2 are for self regulation and suppression by the larger, respectively. The function $B(x_{i,t})$ is the cumulative basal area of trees greater in size than the beech tree of size $x_{i,t}$ (Kohyama 1989, 1991, 1992a, 1992b, 1993 and 1994). This is defined as,

$$B(x_{i,t}) = \sum_{j=1}^{N_t} f(x_{j,t}, x_{i,t}) \quad , \quad (3.5a)$$

$$f(x, y) \equiv \begin{cases} \frac{1}{Q} \frac{\pi}{4} x^2 & , \text{ if } x > y \\ 0 & , \text{ if } x \leq y \end{cases} \quad (3.5b)$$

where Q is the area of a quadrat (*i.e.* 400 m²). The parameters a_0 , a_1 , and a_2 are estimated by maximum likelihood method using the measurements of beech growth which were observed on the Mt. Jippo plot (Table 3.2). The procedure of maximum likelihood method is explained in Appendix E.

3.3.2. Beech mortality

The submodel for beech trees includes two factors: size depending disturbance and the death by shading. The disturbance force is more significant when trees grow up because the effect of the wind is stronger for taller trees (Ida and Nakagoshi, 1998). In contrast, the death by shading becomes more important when trees are small (Fig. 3.2). We express the surviving probability of the i -th beech individual as a product of two functions,

$$[\text{Annual survivorship}] = p_1(x_{i,t}) \times p_2(x_{i,t}) \quad (3.6)$$

where $p_1(x_{i,t})$ and $p_2(x_{i,t})$ are the probability of escaping disturbance and the death by shading, respectively. In the following sections we choose the functional form and the parameter values for the two surviving probabilities. We adopt the mortality submodel (the combination of disturbance and shading) developed by Nakashizuka *et al.* (1992), in which the mortality processes in cool-temperature deciduous forest were analyzed in detail. We adopted the parameters for latter process, death by shading are estimated by Nakashizuka (1988).

3.3.2.1 Disturbances

First, let us specify the functional form of surviving probability, $p_1(x_{i,t})$. According to Fig. 1 in Nakashizuka *et al.* (1992), the disturbance rate of trees seems to be proportional to the square of DBH (*i.e.* basal area of a trunk). Hence the probability of disturbance per tree per year is expressed as,

$$p_1(x_{i,t}) = \begin{cases} 1.0 - c_1 x_{i,t}^2 & \text{if } x_{i,t} > \sqrt{1.0/c_1}, \\ 0.0 & \text{if } x_{i,t} \leq \sqrt{1.0/c_1}, \end{cases} \quad (3.7)$$

where c_1 is a coefficient of $x_{i,t}^2$. We chose $c_1 = 2.14 \times 10^{-6}$, which was obtained by fitting Eq. 3.7 to the measurements Nakashizuka *et al.* (1992, Fig. 1). Hiura (1993) also pointed out the size dependent mortality of beech trees in Japan.

3.3.2.2 Submodels for RLI extinction by beech and *Sasa*

Before constructing the submodel for death by shading, let us make formulas for relative light index (RLI) for the rate of light extinction in a beech stand. This index is needed to calculate the mortality submodels, which will be described in the next section.

Here we assume that the RLI can be calculated for each beech individual in its own light environment. As a consequence of one-sided competition, it is assumed that smaller trees are in worse condition than taller ones. RLI for each tree is the product of two factors: extinction by beech trees taller than itself and by *Sasa* if the focal beech tree is shorter than *Sasa* shoot.

The function form of RLI is,

$$RLI(x_{i,t}) = 100 \times \Delta RLI_Fagus \times \Delta RLI_Sasa, \quad (3.8)$$

where ΔRLI_Fagus and ΔRLI_Sasa are the RLI extinction rates by beech trees and *Sasa*, respectively. Because the height of the *Sasa* shoots on the plot is about 2 meters, *Sasa* shades

only beech trees with size shorter than that height. The DBH of beech trees of 2 meters height is about 1.6 cm from Eq. 3.1. We denote $x^* = 1.6$ a critical size, so that *Sasa* shades the beech trees with DBH smaller than x^* .

Figure 3.2A illustrates that the rate which is calculated by using the RLI measured at 2 meters high in Mt. Jippo plots at 1991. We can see that the extinction rate is an exponentially decreasing function of the total basal area in quadrat, $B(x^*)$ which is defined in Eqs. 3.5

Therefore we choose the following function form for ΔRLI_Fagus ,

$$\Delta RLI_Fagus = \exp(-d B(x_{i,t})) \quad , \quad (3.9)$$

where d is a coefficient of light extinction by beech trees. We chose $d = 9.52 \times 10^{-2}$, which was obtained by fitting to the measurement. This light extinction submodel is essentially the same as that of Monsi and Saeki (1953).

Figure 3.2B plots the light extinction rate by *Sasa* on Mt. Jippo. Here we can see a negative correlation between the density of *Sasa* foliage (*i.e.* light reducing ability) and that of beech canopy trees. This might mean that the biomass of upper-ground part of *Sasa* is suppressed by beech canopy trees. In addition, as mentioned above, *Sasa* has no shading function during its no-shading phase of τ years while *Sasa* is needed for to recover after its dying out synchronized over a large area. Hence the functional form of *Sasa*'s light extinction rate is,

$$\Delta RLI_Sasa \equiv \begin{cases} 1 & \text{if } x_{i,t} > x^* \quad \text{and/or } t_s \leq \tau \\ \exp(s_0 - s_1 B(x^*)) & \text{if } x_{i,t} \leq x^* \quad \text{and } t_s > \tau \end{cases} \quad , \quad (3.10)$$

where s_0 and s_1 are the parameters to specify the light extinction rate of *Sasa*. The values of s_0 and s_1 are -3.24 and 4.04×10^{-2} , respectively, estimated by fitting to the measurement on Mt. Jippo (Ida and Nakagoshi, 1994).

3.3.2.3 Death of beech trees by shading

In this model, the mortality rate of beech tree is assumed a function of $RLI(x_{i,t})$ which is a combination of beech and *Sasa* shading as described in the last section. To estimate the functional forms and parameters for the model, we used the data of beech seedlings mortality in Nakashizuka (1988). Figure 3.3 represents the mortality of beech seedlings for different RLI observed at Mt. Iizuna, in central Japan by Nakashizuka (1988). Nakashizuka pointed out that the mortality rate for current-year seedlings was higher for the current-year seedlings than for older seedlings. It is suggested that just after emergence seedlings are likely to be killed by fungal attack (Sahashi *et al.*, 1994) and seedlings a few years old are likely to be cut off by rodents (Ida and Nakagoshi, 1996).

From the observations mentioned above, the functional form of light dependent survivorship of beech trees becomes,

$$p_2(x_{i,t}) = 1 - \exp(-c_2 RLI(x_{i,t})) \quad , \quad (3.11)$$

where c_2 is estimated from the data on Mt. Iizuna (Fig. 3.3 which is based on Nakashizuka, 1988). The parameter c_2 has two different values, depending on whether the beech seedling is of current-year or older.

3.3.3. Seed production and regeneration of beech

Here we write down the recruitment rate, by considering processes from seed production to germination based on Hashizume (1987) who studied beech forests on Mt. Daisen near Mt. Jippo. The recruitment of beech trees by seed production occurs every two

years. The number of seeds produced depends on the density of adult beech trees in the focal quadrat. The details of the process are as follows;

- (1) Seed are produced every two years.
- (2) Maximum number of seed production increases with size : $S_{\max}(x_{i,t}) = 0.111 x_{i,t}^{3.44}$, where $x_{i,t}$ is the DBH. This relationship equation was shown in Hashizume (1987).
- (3) Masting factor: $F_1 = 10^{-3p}$, where p is a random number uniformly distributed between 0 and 1 ($0 < p < 1$), which is chosen every seed producing year and is common for all the trees in a stand. This factor represents the intensity of masting (Hashizume, 1987). The functional form of F_1 are determined empirically to be consistent with the observation that masting of beech trees occurs every 6 years or so.
- (4) The fraction of healthy seeds which can germinate is a random variable uniformly distributed between 0 to 0.3: $F_2 = 0.3p$, where p is the same as p in (3). This relationship equation was shown in Hashizume (1987).
- (5) The current-year seedlings that escape from predation is about 10%: $F_3 = 0.1$. This also comes from Mt. Jippo research plot (Ida and Nakagoshi, 1996).

All these things make the expected number of germination at next spring by seeds which is produced by an individual beech is that,

$$S(x_{i,t}) = S_{\max}(x_{i,t}) \times F_1 \times F_2 \times F_3, \quad (3.12)$$

which is determined for each individual beech every seed producing year. We didn't consider seed dormancy, because it is known that the seeds of *Fagus crenata* have no dormancy stage.

3.4. Results

3.4.1 Computer simulation trials

Before analyzing the statistics describing the behavior of this model, here we will illustrate the model's behavior by few examples of trial. In this section, all the computer

simulations for the individual based model were performed by starting from the same situation as Q1 stand in 1991 (see Table 3.2) under the baseline parameter set estimated from the Mt. Jippo research plot given by Table 3.1. It was assumed that *Sasa*'s longevity (T) and its recovery time (τ) were 60 years and 20 years, respectively.

Figures 5 indicates an example of simulation, and illustrates the sizes of individual trees in a stand. After the removal of old canopy trees by a disturbance, during the periods when *Sasa* foliage was absent, newly settled beech seedlings could start to grow and some of them become new canopy trees in the quadrat. In this trial, about 380 years after the start of simulation, all beech trees disappeared and the beech stand went extinct. In contrast, as shown in Fig. 3.5, an isolated beech stand survived by chance throughout the whole trial period of 500 year, although this trial was done under the same conditions as Fig. 3.4. Here we can see the importance of demographic stochasticity in understanding dynamics for a small population of beech trees with *Sasa* undergrowth.

The final example in Fig. 3.6 is a controlled trial in which all *Sasa* were removed from the beech stand, in order to evaluate *Sasa*'s exacerbating effect on the recruitment of beech seedlings. In Fig. 3.6A, synchronous regeneration of beech trees were still observed because of the one-directional competitions between large and small beech trees. However, as in Fig. 3.6B, the change in beech population over time were less clear than Figs. 3.4B and 5B. This suggests that a number of seedlings are always present in the beech stand in this trial, and therefore extinction by chance is unlikely to occur.

3.4.2 Sensitivity analysis

3.4.2.1 "P500": the probability of sustaining for five hundreds years

Our final goal is to evaluate how the Sustainability of a beech stand depends on the life cycle of *Sasa*. We introduced a statistical index, named "500 years Sustainability" or abbreviated as P500. The chosen period, 500 years, was approximately equal to the twice of the expected waiting time for the extinction of beech stand under the same condition as in Figs.

3.4 and 3.5. In the following, the index was calculated from 500 of independent replications.

Table 3.3 shows the P500 values with using the baseline parameter set given by Table 3.1. We chose the initial state of the same as Q1, Q2, Q3 and Q5 in 1991 (Table 3.2) and examined indexes were estimated for different initial conditions. For each case, the indexes were calculated by using two models: the model with and without *Sasa* undergrowth. The former corresponds to the situation in Figs. 3.4 and 3.5, while the latter to the case in Fig. 3.6. Index P500 for the model with *Sasa* were within the range of 0.10 and 0.13. The sustaining probability of an isolated beech stand for 500 years was about 10%. The value was insensitive to the initial state of beech stand. On the other hand, the P500 for the model without *Sasa* condition were always one, implying that a beech stand is likely to be maintained for a very long time if it had no *Sasa* undergrowth. In the following, we use the state of Q1 in 1991 as the initial condition for all the replicates.

3.4.2.2 Sustainability of beech stand and the life cycle of *Sasa*

In order to know the impact of *Sasa* on the Sustainability of a beech stand, we estimated the P500 with two different values of two important life cycle parameters of *Sasa*: *Sasa* longevity T and *Sasa* recovering time τ . We selected various values for these parameters; the range for T was 40-120 years and 15-40 years for τ .

The results of sensitivity analysis are shown in Fig. 3.8. There were a trend that the P500 became small as *Sasa* longevity T increased, while the index became larger as the length of no-shading phase τ increased. We could ignore the effect of more complicated term of T and t , because the logarithm of P500 could be reduced to,

$$\log(\text{P500}) = -1.27 - 2.18 \log(T) + 3.19 \log(\tau) \quad , \quad (3.13)$$

by using step-wise multiple regression ($r^2 = 0.93$, $p < 0.0001$). By Eq. 3.13, we can infer the effects of these parameters separately and clearly.

3.4.2.3 Sensitivity analysis for growth and mortality parameters

Now we study on the sensitivity of P500 to parameters of beech trees. We focused on two parameters which relate to the shade tolerance: the sensitivity of growth rate to shading denoted by a_2 and the shade tolerance of mortality c_2 . Figure 3.8 represents the results. The P500 indexes were calculated under the condition in which only one parameter was changed gradually from the estimated value in the baseline parameter set. The P500 had a small response to the change of a_2 , while the index was keenly sensitive to the change in c_2 . In short, shade tolerance of survivorship of beech seedlings was more important to sustainability than the shade tolerance of growth rate.

3.5. Discussion and conclusions

From the analyses of the index of Sustainability, or P500, we obtained a simple and clear understanding of the maintenance mechanism an isolated beech stand. Although, in our model, *Sasa* can reduce only the survivorship of beech trees but not the growth rate, the results of computer simulation indicate that *Sasa* undergrowth has a very harmful effect on the Sustainability of the beech stand. As shown in Eq. 3.13, the P500 index can be approximated as a product of a factor depending on T (the longevity of *Sasa* clone) and another factor depending on τ (the recovery time of *Sasa* foliage). Based on this result, we can compare the sustainabilities of different beech stand for each research site, even if we had only incomplete data (e.g. *Sasa* recovering time τ) about the clonal plant *Sasa* which has very long life cycle assuming that the longevity T is common to all sites.

The sensitivity analysis to the shade tolerance parameters with respect to beech growth and survival revealed that the importance of mortality in shady environment by *Sasa*. Beech

stand always survived and the P500 value for the model without *Sasa* undergrowth is always equal to one (Table 3.3). The magnitude of the sensitivity of beech growth rate on shading is smaller. This suggested that more accurate information on the surviving processes in the early stage of beech development could improve the prediction on the sustainability of the beech stand.

One of the further studying in this IBM is analyzing the time change of size distribution of beech trees. By doing it, we could discuss the clear cohort structure of beech trees as mentioned in Peters *et al.* (1992), and compare the difference between this model and real forest in detail.

Appendix E: Maximum likelihood estimate of growth parameters

In this Appendix, we explain the method to estimate the parameters on tree growth based on field measurements on Mt. Jippo. Let x_i and g_i be the DBH of beech tree on Mt. Jippo at 1991 and its growth rate, respectively. For simplicity, the growth rate is defined as,

$$g_i = (x_{i,1993} - x_{i,1991}) / (1993 - 1991) \quad (E1)$$

The likelihood function for growth rate is,

$$f(a_0, a_1, a_2) = \prod_{i=1}^N \lambda_i \exp(-\lambda_i g_i) dg_i \quad (E2)$$

where $\lambda_i = x_i \exp(a_0 - a_1 \ln x_i - a_2 B(x_i))$. Here we take the logarithm of Eq. E2

$$\begin{aligned} \ln f &= \sum_{i=1}^N \ln \lambda_i - \sum_{i=1}^N \lambda_i g_i + [\text{terms without } a_0, a_1 \text{ or } a_2] \\ &= - \sum_{i=1}^N (a_0 - a_1 \ln x_i - a_2 B(x_i)) \\ &\quad - \sum_{i=1}^N \frac{g_i}{x_i \exp(a_0 - a_1 \ln x_i - a_2 B(x_i))} + [\text{terms without } a_0, a_1 \text{ or } a_2] \quad (E3) \end{aligned}$$

By calculating the derivative of both sides of Eq. E3, we obtain the following three equations:

$$\frac{\partial \ln f}{\partial a_0} = -N + \sum_{i=1}^N \frac{g_i}{x_i \exp(a_0 - a_1 \ln x_i - a_2 B(x_i))} \quad (E4a)$$

$$\frac{\partial \ln f}{\partial a_1} = \sum_{i=1}^N \ln x_i - \sum_{i=1}^N \frac{g_i \ln x_i}{x_i \exp(a_0 - a_1 \ln x_i - a_2 B(x_i))} \quad (E4b)$$

$$\frac{\partial \ln f}{\partial a_2} = \sum_{i=1}^N B(x_i) - \sum_{i=1}^N \frac{g_i B(x_i)}{x_i \exp(a_0 - a_1 \ln x_i - a_2 B(x_i))} \quad (\text{E4c})$$

By setting these equations to zero, we can obtain the value of maximum likelihood estimators, which can be calculated by Newton method. The results are listed in Table 3.1.

IV. Acknowledgements

I sincerely thank Professors Yoh Iwasa, Akira Sasaki and Yasuhiko Takeda for their helpful advices and encouragemnts throughout the study. I also thank the following people for their comments and criticisims: Shin-Ichiro Aiba, Nobuhiro Akashi, Edward Cooper, Naoki Furumoto, Hiroshi Hakoyama, Yuko Harada, Yoshihiro Haraguchi, Tsutomu Hiura, Kousuke Honma, Hideyuki Ida, Masashi Kamo, Mamoru Kanzaki, Hideyuki Kawaguchi, Takashi Kohyama, Norio Konno, Hirotugu Matsuda, Hiroyuki Matsuda, Atsushi Mochizuki, Mayuko Nakamaru, Satoshi Nanami, Satomi Nishitani, Satoki Sakai, Akiko Satake, Tetsuo Shirota, Akio Takenaka, Akio Takesue, Hiroshi Tanaka, Shusaku Tohya and Shin-Ichi Yamamoto. This work is supported by a grant-in-aid from the JSPS Research Fellowships for Young Scientists.

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VI. Tables

Table 2.1. Perimeter polynomials for the site percolation process on two-dimensional regular square lattice (from Sykes and Glen, 1983).

k	$f(x)$
1	x^4
2	$2x^6$
3	$4x^7 + 2x^8$
4	$9x^8 + 8x^9 + 2x^{10}$
5	$x^8 + 20x^9 + 28x^{10} + 12x^{11} + 2x^{12}$
6	$4x^9 + 54x^{10} + 80x^{11} + 60x^{12} + 16x^{13} + 2x^{14}$
7	$22x^{10} + 136x^{11} + 252x^{12} + 228x^{13} + 100x^{14} + 20x^{15} + 2x^{16}$
8	$4x^{10} + 80x^{11} + 388x^{12} + 777x^{13} + 818x^{14} + 480x^{15} + 152x^{16}$ $+ 24x^{17} + 2x^{18}$
9	$28x^{11} + 291x^{12} + 1152x^{13} + 2444x^{14} + 2804x^{15} + 2089x^{16}$ $+ 856x^{17} + 216x^{18} + 28x^{19} + 2x^{20}$
10	$4x^{11} + 154x^{12} + 986x^{13} + 3676x^{14} + 7612x^{15} + 9750x^{16}$ $+ 8192x^{17} + 4330x^{18} + 1416x^{19} + 292x^{20} + 32x^{21} + 2x^{22}$

Table 3.1. Parameters for growth and mortality.

Parameter		estimated value	unit	source
Initial growth rate	a_0	1.59×10^{-1}	year ⁻¹	Mt. Jippo (Table 3.2)
Size dependent growth rate	a_1	3.26×10^{-2}	cm ⁻¹	Mt. Jippo (Table 3.2)
Shade dependency of growth rate	a_2	3.35×10^{-2}	cm ⁻²	Mt. Jippo (Table 3.2)
Size dependent survivorship	c_1	2.14×10^{-6}	cm ⁻²	Ogawa Forest Reserve (Nakashizuka <i>et al.</i> , 1992, Fig. 1)
Shade dependent survivorship for current-year seedlings	c_2	4.20×10^{-1}	% ⁻¹	Mt. Iizuna (Nakashizuka, 1988, Fig. 1 and table 1)
Shade dependent survivorship for the older seedlings	c_2	6.68×10^{-1}	% ⁻¹	Mt. Iizuna (Nakashizuka, 1988, Fig. 1 and Table 1)

Table 3.2. The growth of beeches in Mt. Jippo forest research plot

Quadrat No.	DBH (cm) 1991	DBH (cm) 1993
1	71.5	72.2
1	57.5	57.1
1	52.0	51.1
1	44.7	45.3
1	41.1	41.4
1	21.5	21.6
1	21.4	21.0
1	17.3	17.4
2	85.1	85.2
2	63.0	62.2
3	100.1	102.0
3	72.0	72.0
3	46.3	47.1
5	60.5	61.8
7	52.0	54.0
7	26.6	27.1
7	18.8	19.3
7	10.8	11.5
7	10.3	11.1
7	7.5	8.2
8	3.7	4.1

Table 3.3. P500 index.

Quadrat No.	P500	P500 (No <i>Sasa</i>)
1	0.13	1.00
2	0.12	1.00
3	0.10	1.00
5	0.10	1.00

VII. Figure Legends

Figure 2.1 Spatial patterns generated by the model at the equilibrium. Open squares are gap sites, and gray area are nongap sites. (A) a transition between two states, from a gap site to an occupied site by the growth of trees within the site, and the transition of a site from a nongap to a gap due to the death of canopy trees by disturbances. Assume that the rate of transition from a gap to a nongap occurs at rate b per year, and that of transition from a nongap to a gap occurs at rate d . The spatial pattern is very simple, because each site experiences transition between a gap and a nongap randomly and independently, fraction $d/(b+d)$ of the sites are gaps and others are nongaps. Parameters are: $b = 0.400$, $d = 0.0348$, and $\delta = 0$; observed global and local density are: $\rho_0 = 0.0804$ and $q_{0/0} = 0.0779$ (not significantly different). (B) the transition rate is an increasing function of the number of surrounding gap sites. A new gap tends to be next to existing gaps, rather than in an isolated location. Parameters are: $b = 0.400$, $d = 0$, and $\delta = 0.6$; observed global and local density are: $\rho_0 = 0.0804$ and $q_{0/0} = 0.3286$, which are significantly different. Here we present one fourth (50×50) of the whole lattice.

Figure 2.2 Equilibrium global density ρ_0 and local density $q_{0/0}$ for different maximum gap expansion rates δ . Circles and triangles in this figure are the results from computer simulation. Solid circles imply global density of gaps ρ_0 , and triangles are for local density $q_{0/0}$. Open circles imply global density of non-gaps ρ_+ , and squares are for local density $q_{+/+}$. Mean field approximation does not distinguish these two densities, and ρ_0^M as shown by broken line. Solid curves are ρ_0^P and ρ_+^P , and gray one is $q_{0/0}^P$ and $q_{+/+}^P$. The local density $q_{0/0}$ (or $q_{+/+}$) is clearly larger than the global density ρ_0 (or ρ_+). This implies that the gap sites (or non-gap site) are clumped. (A) one dimensional system ($z = 2$, lattice size is 1000). $b = 0.20$, $d = 0.01$. (B) two-dimensional system ($z = 4$, lattice size is 100×100). $b = 0.20$, $d = 0.01$.

Figure 2.3 Global and local gap density for the case in which the supply of recruitment is limiting the process of recovery. (A) and (B): The rate of recovery from a gap is directly proportional to global density of nongap sites. Parameters are $\alpha = 0.20$ and $d = 0.01$. Horizontal axis is gap expansion rate δ . (A) is for one-dimensional system ($z = 2$) and (B) is for two-dimensional system ($z = 4$). Solid black line is the prediction for the average density (global density) of gaps at the stable equilibrium ρ_0 , and solid gray line is the prediction for the local gap density $q_{0/0}$ (the fraction of gap sites among neighbors of gaps), both of which predicted by the pair approximation, Eq. C3. These fit well with the result of computer simulation shown by solid circles and triangles, respectively. Thin curve is for unstable equilibria. Broken line is the prediction given by the mean-field approximation, which considerably overestimates the gap fraction. It predicts neither the bistability nor the difference between local and global density.

(C): The rate of recovery from a gap is directly proportional to the number of surrounding nongap sites. The one-dimensional system ($z = 2$). Symbols are the same as in (A) and (B). Parameters are: $\beta = 0.50$, and $d = 0.01$. No bistability is predicted by pair approximation. The mean-field approximation gives ρ_0^M that is the same as $q_{0/0}^P$.

Figure 2.4 Definition of "gap" on regular two-dimensional square lattice for Neumann neighborhood. We denote an aggregate of gap sites that are connected with each other by a "cluster" of gap sites, or simply a gap, and the cluster size or the gap size by the number of gap sites included. There we illustrate three clusters, of different sizes.

Figure 2.5 Gap size distribution on the one dimensional system. Solid circles are from computer simulation of the model ($b = 0.20$, $d = 0.01$). Vertical axis is for the

number of gaps included in one-dimensional lattice of size $L = 1000$, and horizontal axis is the cluster size. A gray line is the gap size distribution expected for a random spatial pattern with the same ρ_0 as the model. A solid line is the cluster size distribution predicted by Eq. 2.9 using the observed parameters of ρ_0 and $q_{0/0}$. A broken line is the prediction by pair approximation, Eqs. 2.7 and 2.9. Neighbor-dependent mortality δ , indicating gap expansion, are: (A) $\delta = 0.0$ (random spatial pattern). (B) $\delta = 0.2$, and (C) $\delta = 0.4$. We see that gap size distribution of the spatial pattern generated by computer simulation is very different from random patterns for positive δ , but is predicted accurately by the pair approximation.

Figure 2.6 Gap size distribution on the one dimensional system. Solid circles are from computer simulation of the model ($b = 0.20$, $d = 0.01$). Vertical axis is the number of gaps of a given size in two-dimensional lattice of size $L = 100 \times 100$ with periodic boundary condition, and horizontal axis is gap size k . Parameters are the same as in Figure 2.5. (A) $\delta = 0.0$, (B) $\delta = 0.2$, (C) $\delta = 0.4$.

Figure 2.7.. Map data used for the analysis to illustrate the model's application. These are from Fig. 3.4 in Hubbell and Foster (1986), in which the leftmost column and the bottom row are removed as they are unreadable. Gray squares indicate 5x5 m plots with canopy below in 1983. Black squares indicate plots with canopies 20m or above in 1983, but with canopies lower than 20m in 1984, white squares are for those with canopies higher than 20 m both in 1983 and 1984.

Figure 2.8.. Probability of a canopy fall in a 5x5 m plot and the number of surrounding 5x5 m plots with low canopy height within its neighborhood. Data are from Fig. 2.7. Both Neumann neighborhood (each site has four neighbors: $z = 4$), and

Moore neighborhood (each site has eight neighbors: $z=8$) are analyzed, and both give very good fit to a straight line, with regression line $y = 0.069x + 0.024$ for Neumann neighborhood, and $y = 0.035x + 0.018$ for Moore neighborhood. According to the likelihood analysis in Appendix D, Neumann neighborhood gives a better fit.

Figure 2.9.. Percolation probability. Vertical axis is the fraction of runs that has at least one cluster of gap sites that stretch through the whole lattice (from the leftmost column to the rightmost column, or from the top row to the bottom row). Horizontal axis is for the total fraction of gap sites ρ_0 . Open circles are gap percolation probabilities for random distributions with different probability of being gaps, and solid squares are those for the clumped spatial pattern generated by the gap expansion model with for different values of δ . Other parameters are: $b = 0.20$ and $d = 0.01$. Percolation probabilities for nongap sites are also shown for random distribution (open triangles) and for gap-expansion model (solid triangles).

Figure 3.1. Schemata of individual based model for Mt. Jippo beech forest. (A) A fragmented beech stand. The quadrat of 20 meters includes some adult beech trees and many saplings and seedlings. The dwarf bamboo, *Sasa*, foliage layer exists at 2m height except during the period after its synchronous dying out. (B) Developmental stages of beech trees. The growth rate of beech trees is affected by the density of *Sasa* foliage when beech trees are below the *Sasa* layer. The growth rate is also affected by larger beech trees. (C) *Sasa* life cycle. The upper-ground part of *Sasa* dies out every T years. For simplicity, *Sasa*'s life cycle is divided into two: no-shading phase (τ years) and shading phase ($T-\tau$ years). During the shading phase, the mortality of beech seedlings is higher than in the no-shading phase.

Figure 3.2. (A) Relative light index (RLI) extinction rates by beech, ΔRLI_Fagus is plotted against the total basal area in quadrat on Mt. Jippo. There are 14 quadrats. These observed rate are calculated by using the measurements indicated in Ida and Nakagoshi (1994). Solid line is the regression line determined by using Eq. 3.10. (B) RLI extinction rates by *Sasa*, ΔRLI_Sasa is plotted against the total basal area of each quadrat. Solid line is the regression line determined by using Eq. 3.11.

Figure 3.3. The annual mortality of beech seedlings against RLI observed at Mt. Iizuna, in central Japan (from Nakashizuka, 1988). Closed circles represent the observed mortality of current-year beech seedlings, and triangles are for the observed mortality of the second year or older. Two solid lines are derived from these data by using Eq. 3.12. The negative slope of the regression line indicates that an increase in RLI is accompanied by a decrease of mortality rate. The mortality rates for the current-year seedlings were higher than older seedlings.

Figure 3.4. An example of simulation run of the model. (A) Time change of size of each individual. The horizontal axis indicates years since the start of the simulation, and the vertical axis is the DBH of each individual beech tree. Shaded areas are for the periods of the existence of *Sasa* foliage. *Sasa*'s longevity (T) and recovery time (τ) were 60 and 20 years, respectively. After the removal of old canopy trees by a disturbance event, during the periods when *Sasa* foliage is absent, newly settled beech seedlings can start to grow and some of them become new canopy trees in the quadrat. In this trial, after about 380 years, all beech trees disappeared and the beech stand went extinct. (B) Time change of total number of beech trees (including saplings and seedlings).

Figure 3.5. Another example of simulation run of the model. This trial was done under the same conditions as in Fig. 3.4. In this trial, the fragmented stand of beech trees survived throughout the whole period (500 years). (A) Time change of size of each individual. (B) Time change of the total number of beech trees.

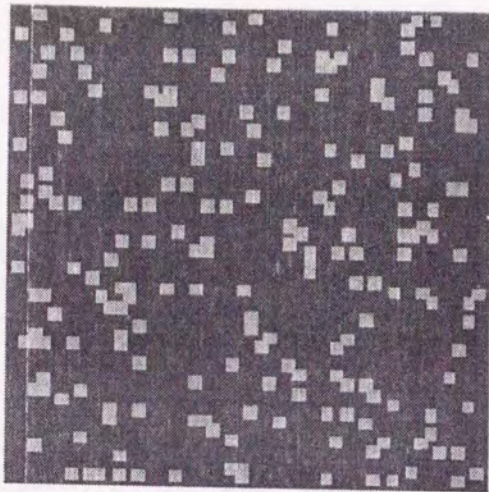
Figure 3.6. A **controlled** trial without *Sasa*. To evaluate *Sasa*'s adverse effect on the recruitment of beech seedlings, this simulation was done without *Sasa* foliage. (A) Time change of size of each individual. (B) Time change of the total number of beech trees.

Figure 3.7. Sensitivity analysis to the length of *Sasa*'s longevity T and its recovery time τ . The vertical axis represents the sustainability for 500 years, denoted by P500, of an isolated beech stand. The replicated trials were simulated with the baseline parameter set shown in Table 3.1 and its initial condition is the same as Q1 (Table 3.2). By multiple regression, we obtained Eq. 3.13. The interaction between T and τ was not significant.

Figure 3.8. Sensitivity analysis for shade-tolerance parameters and the vertical axis is P500. The replicated trials were done with the baseline parameter set (Table 3.1) except the parameter to study. The initial condition was the same as in Q1 (Table 3.2). The circles are the base line parameters shown in Table 3.1. (A) The effect of changing the shade responding parameter for growth rate, a_2 . (B) The effect of changing the shade responding parameter for mortality, c_2 . The P500 was more sensitive to the change in mortality parameter.

Figure 2.1

A



B

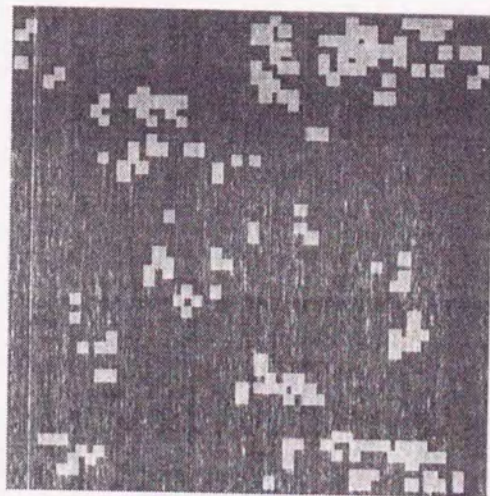


Figure 2.2A

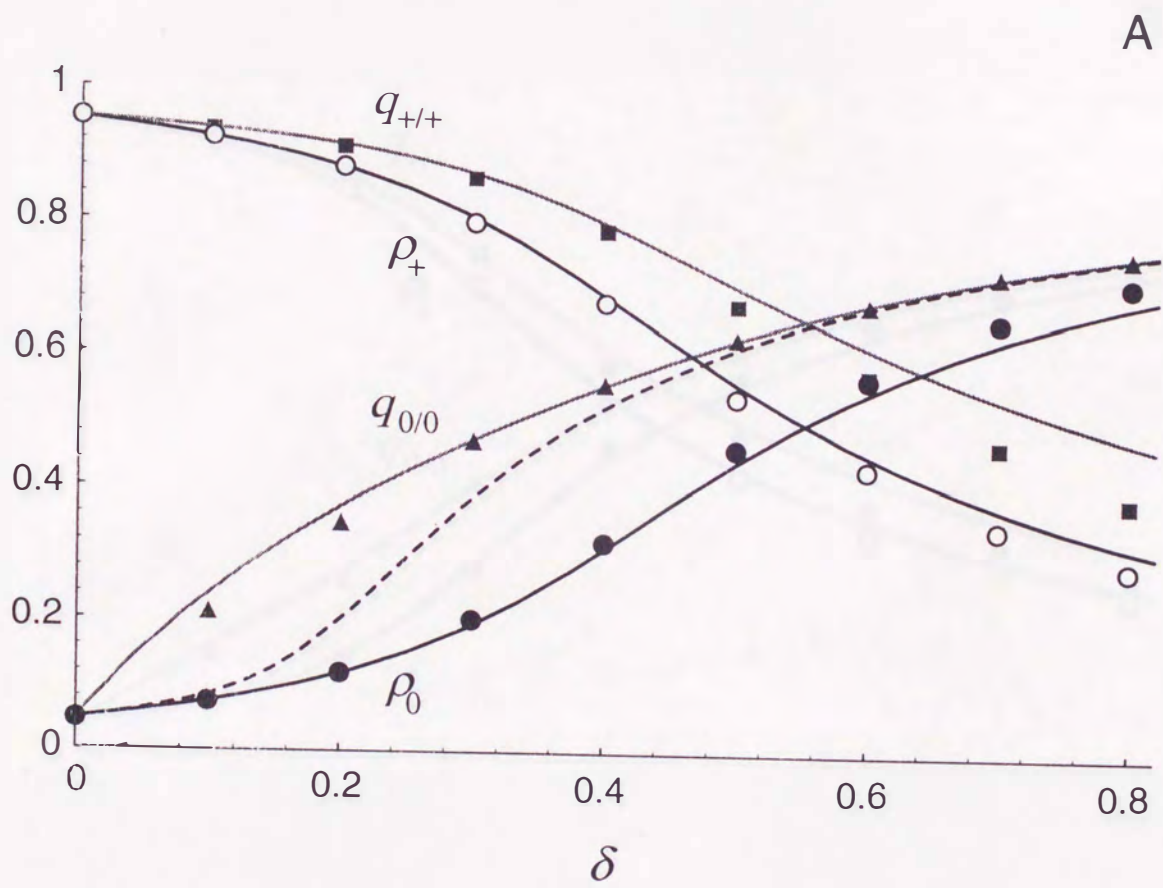


Figure 2.2B

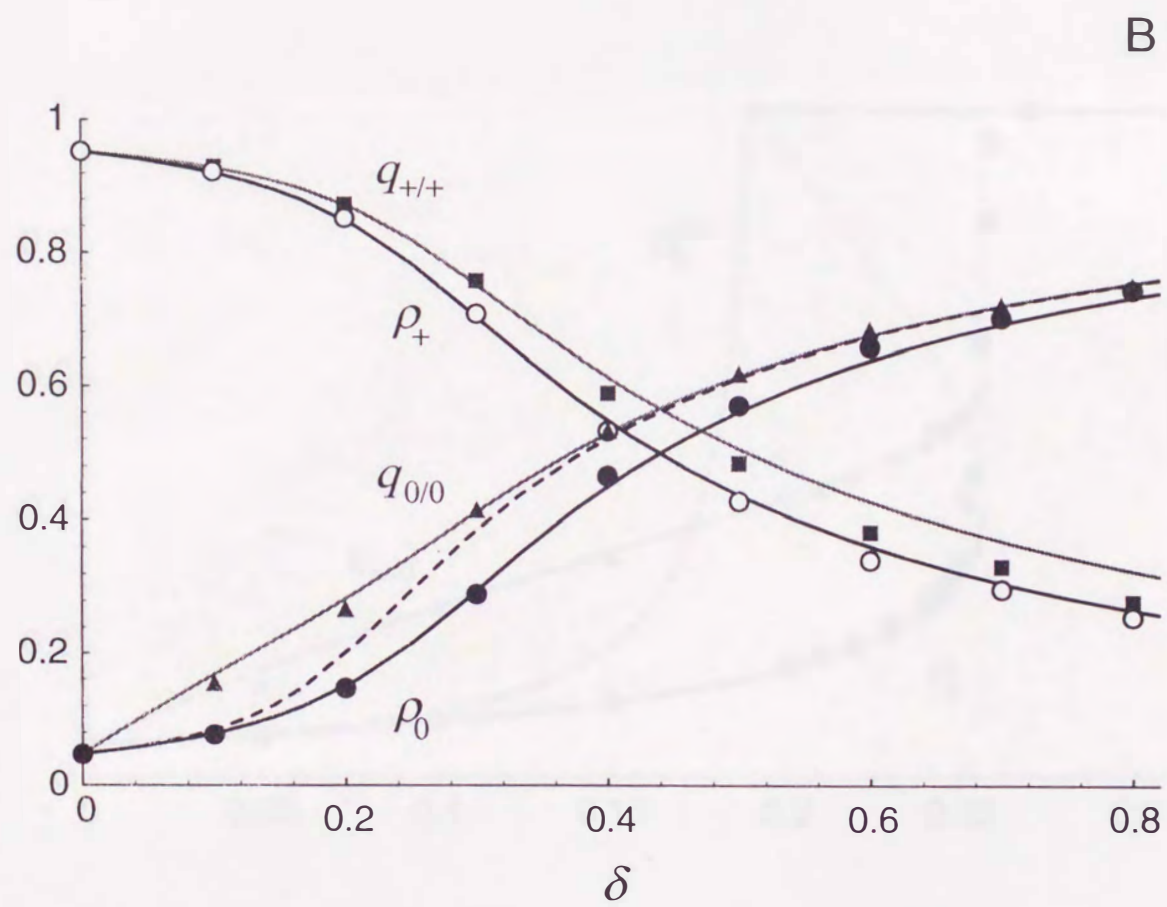


Figure 2.3A

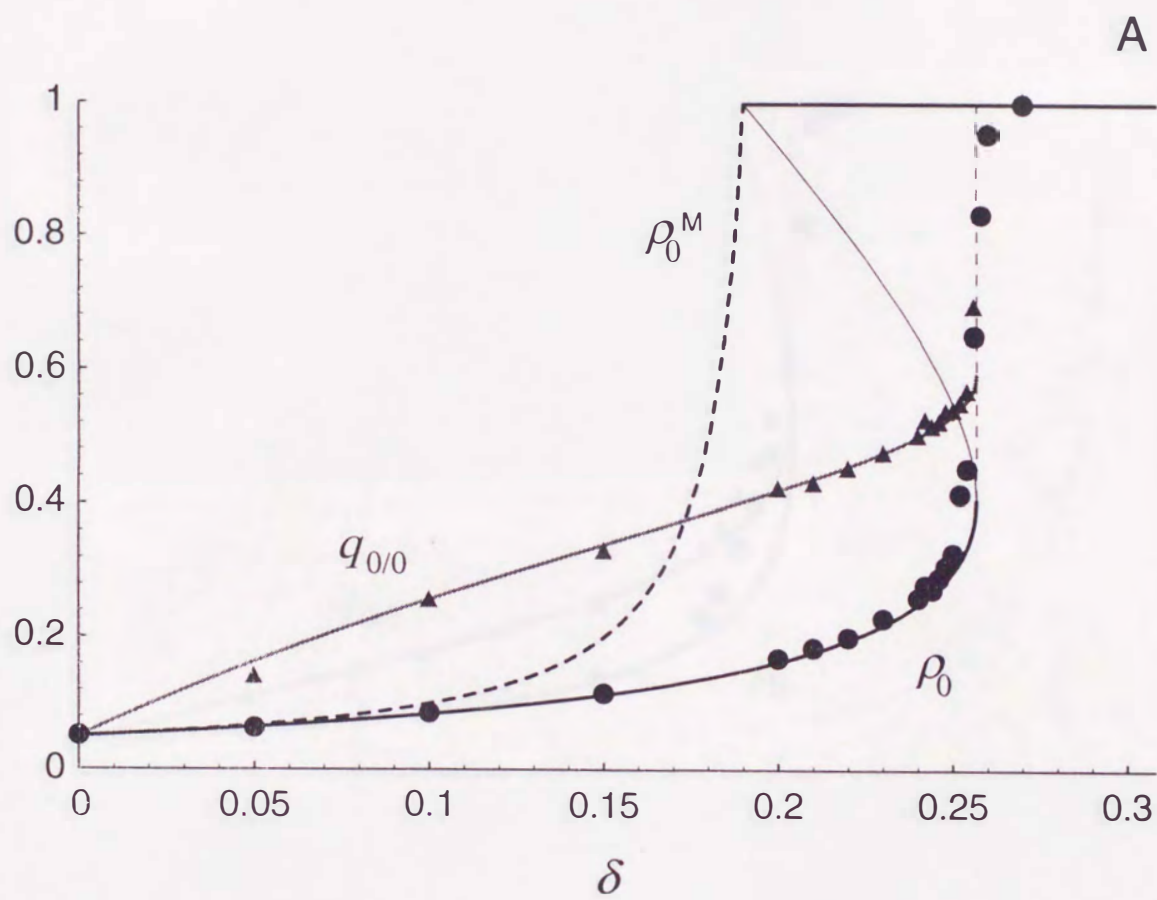


Figure 2.3B

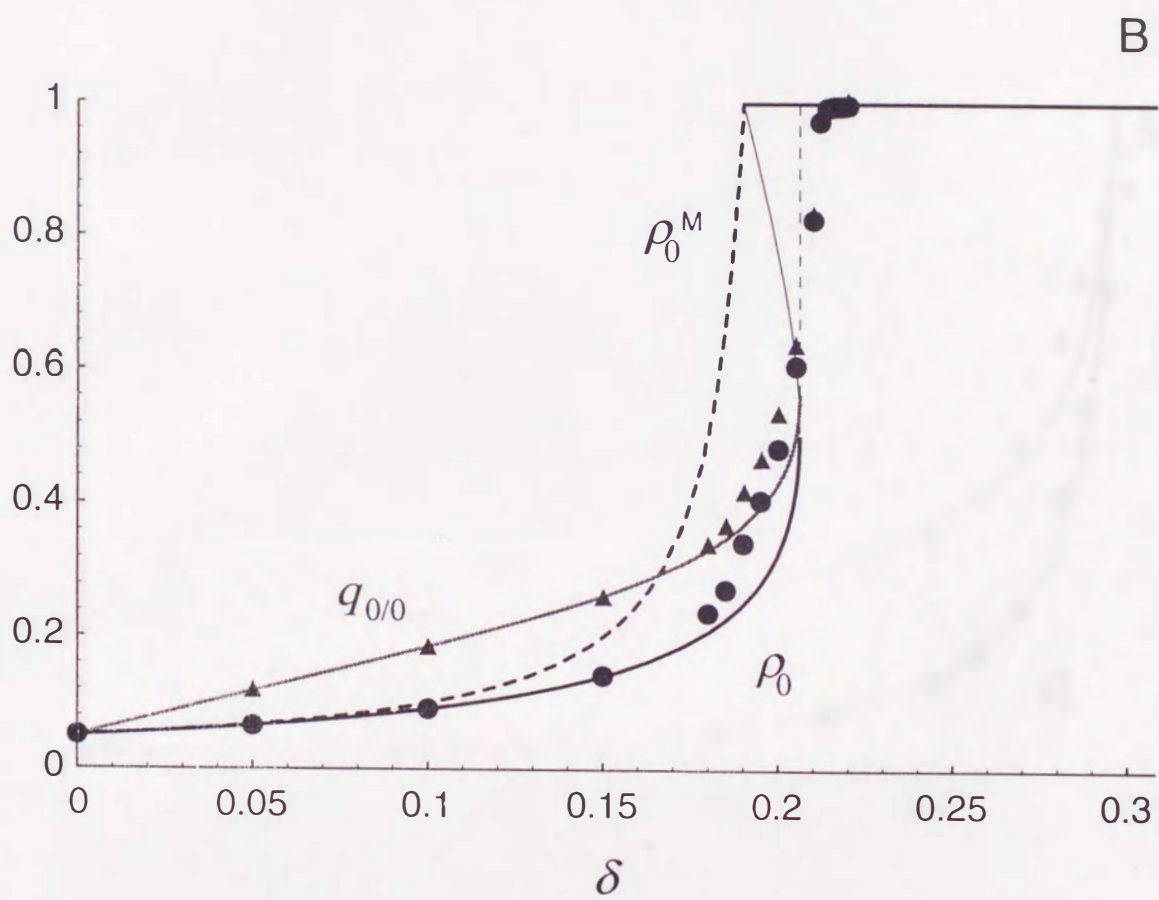


Figure 2.3C

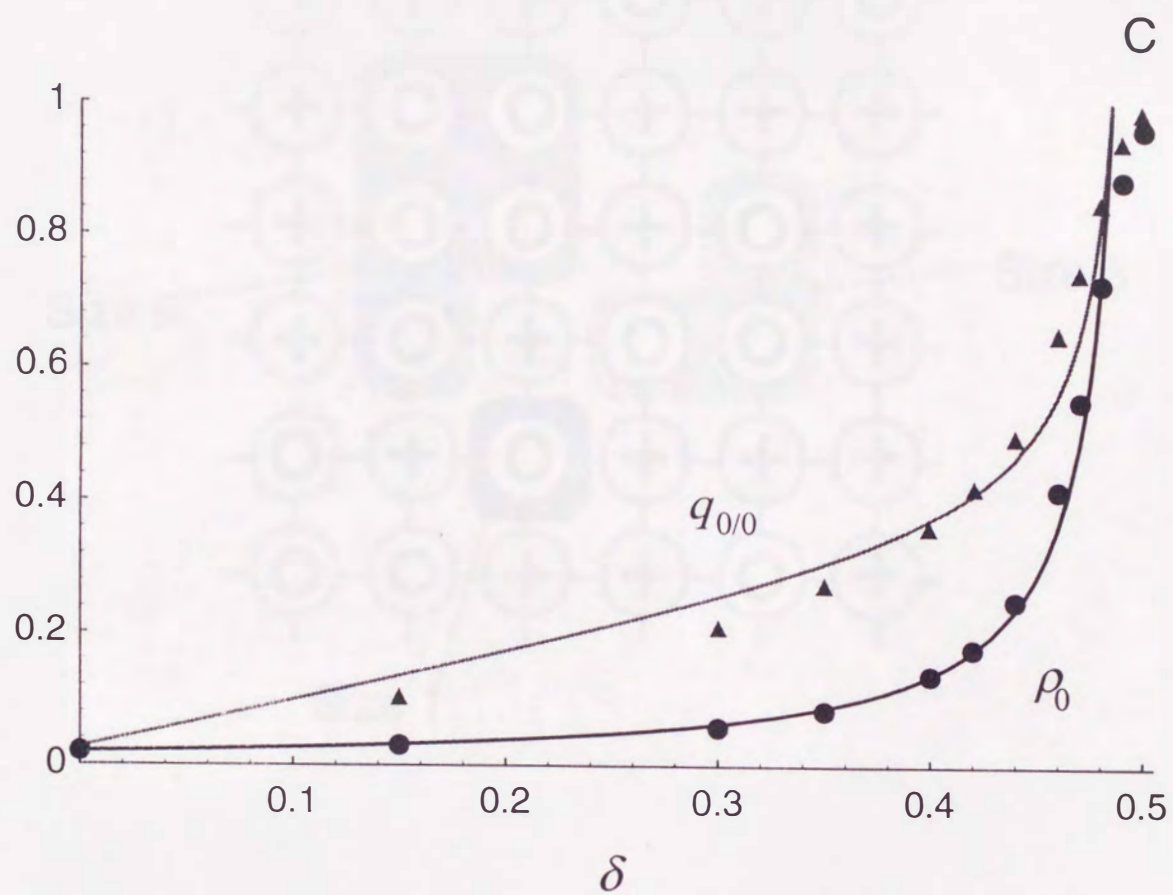


Figure 2.4

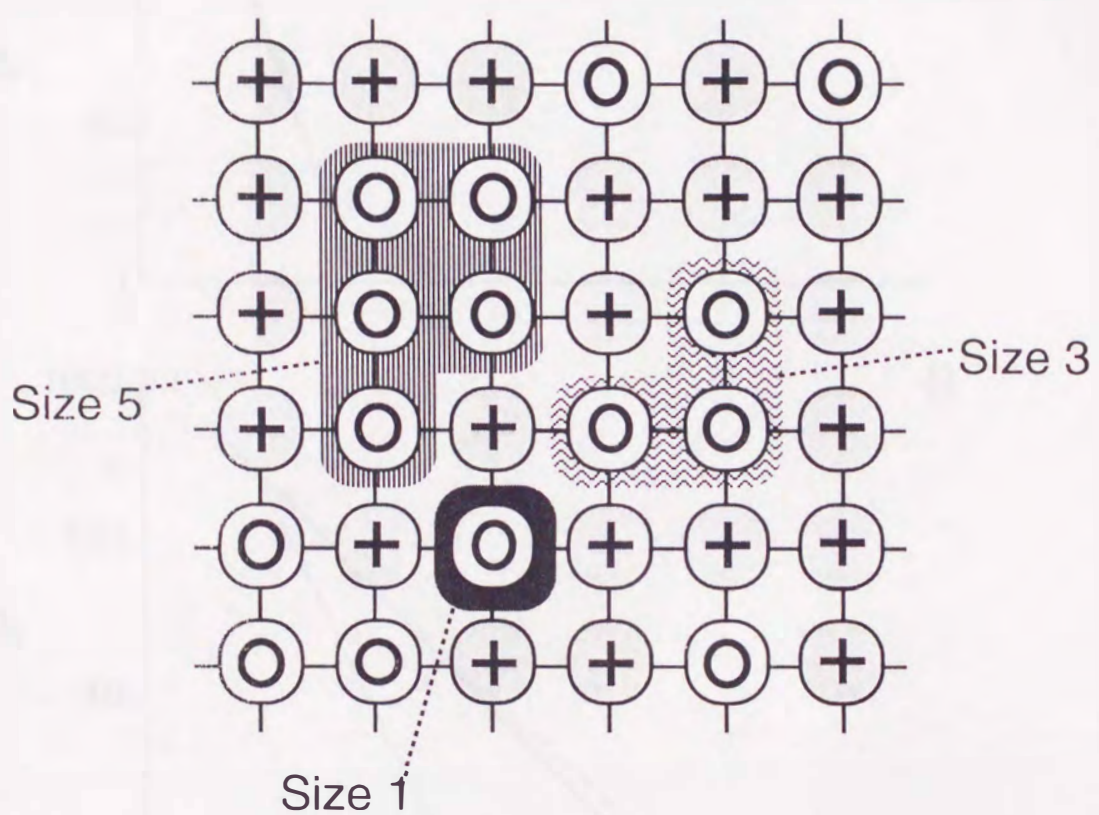


Figure 2.5

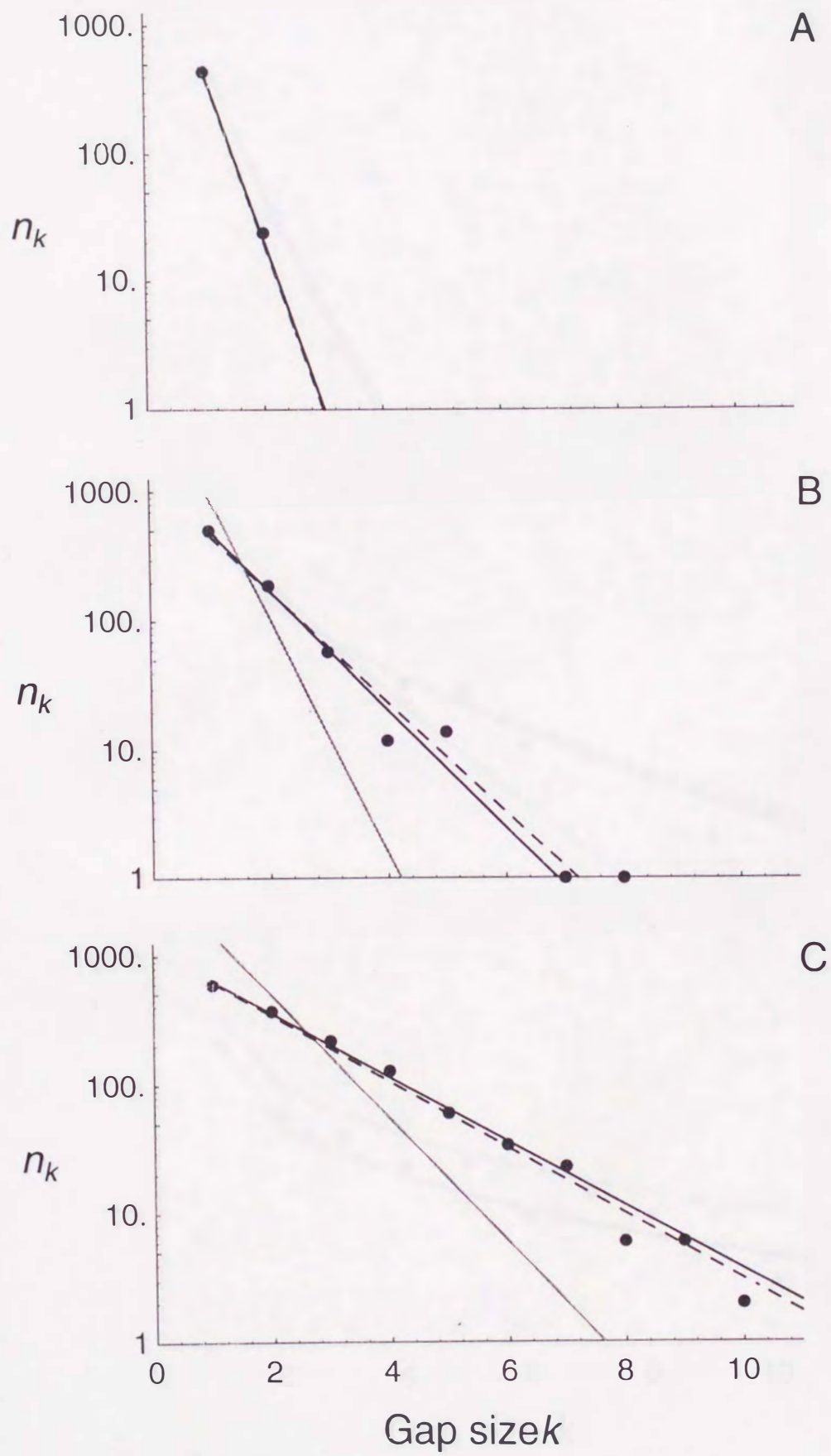
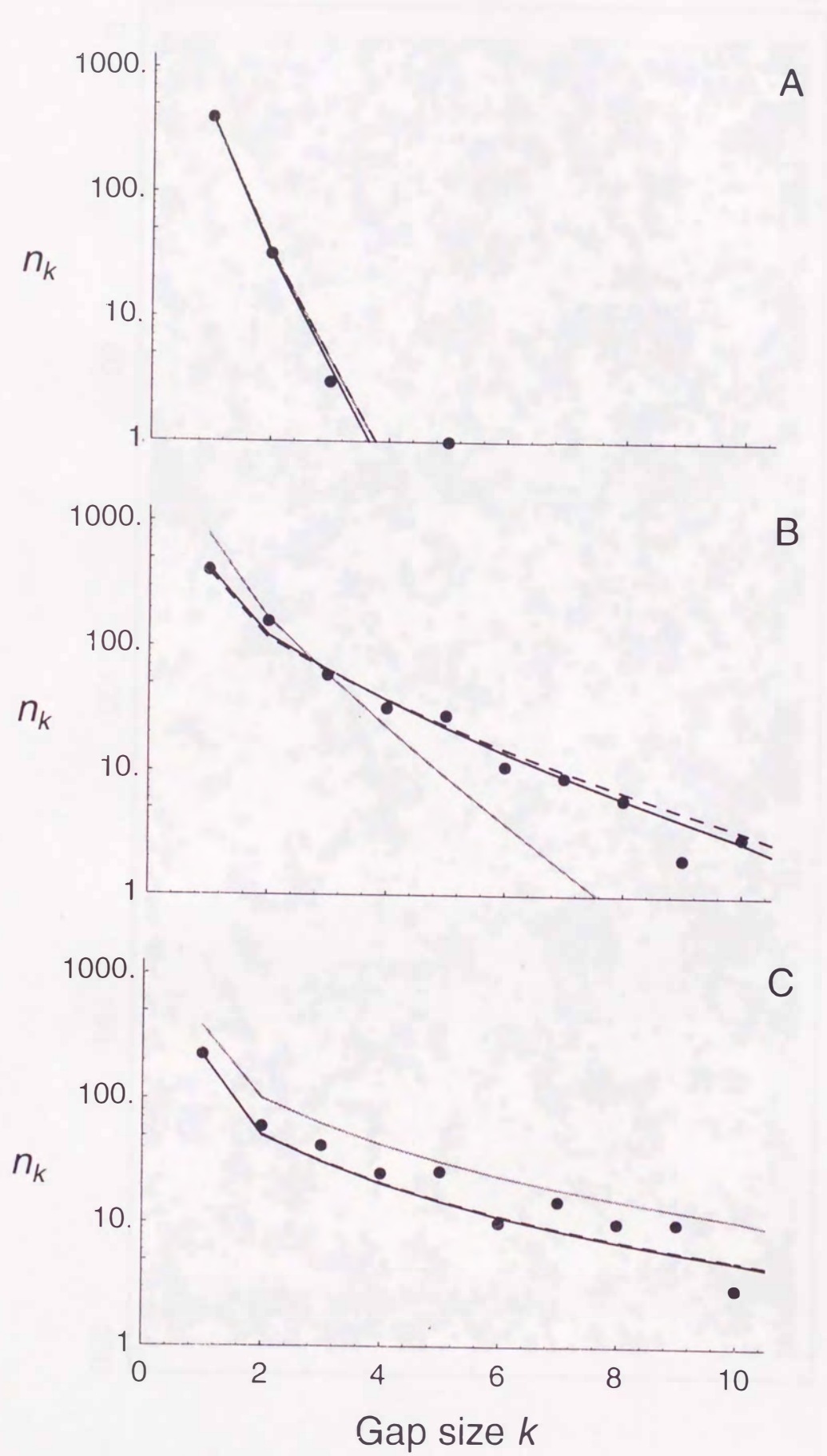


Figure 2.6



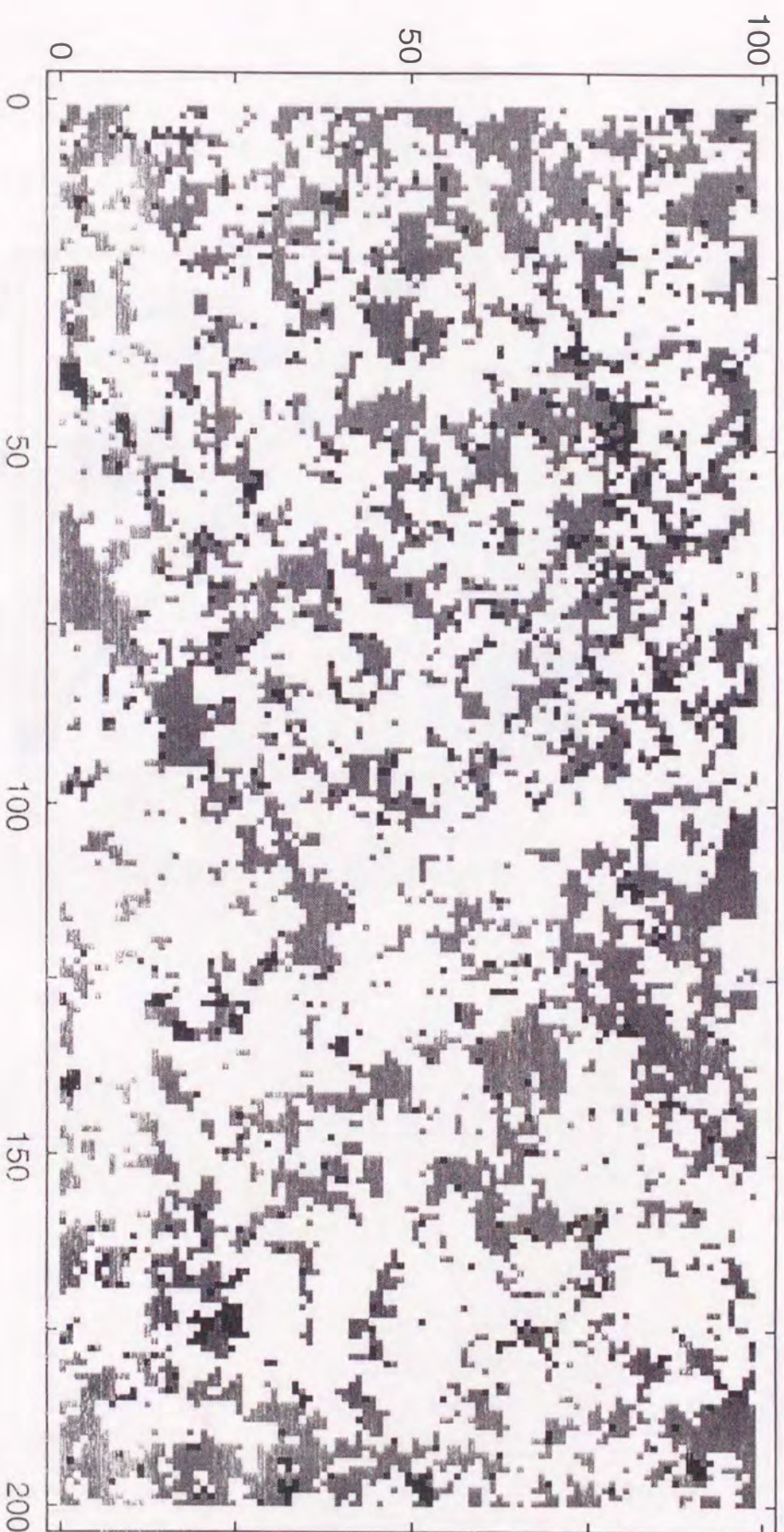


Figure 2.7

Fig. 2.8

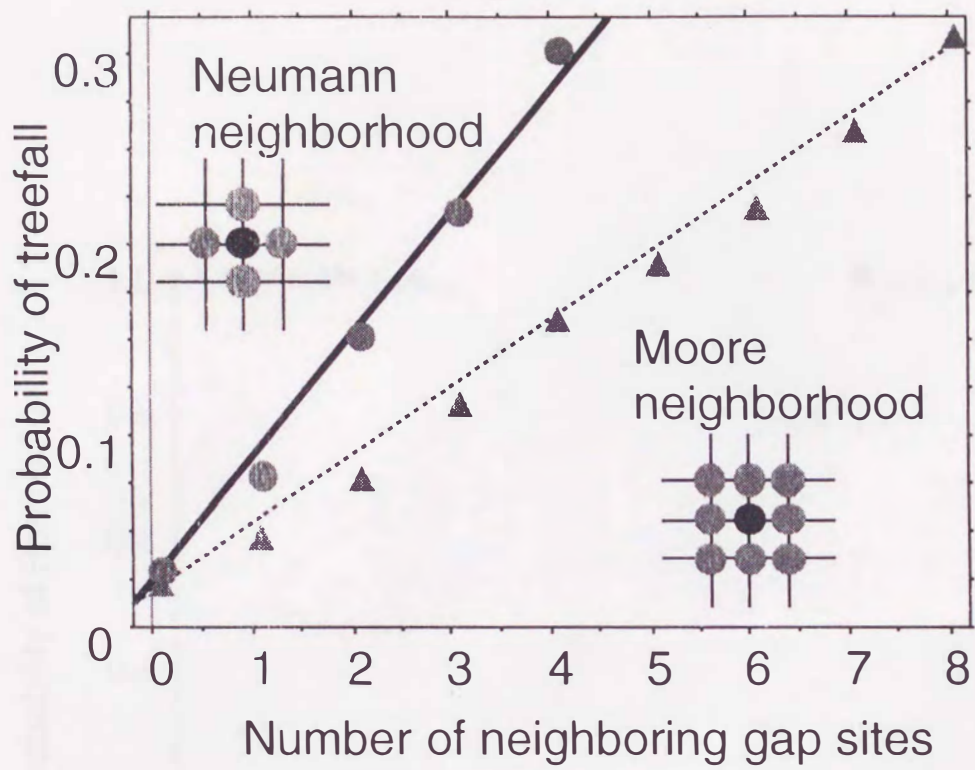


Figure 2.9

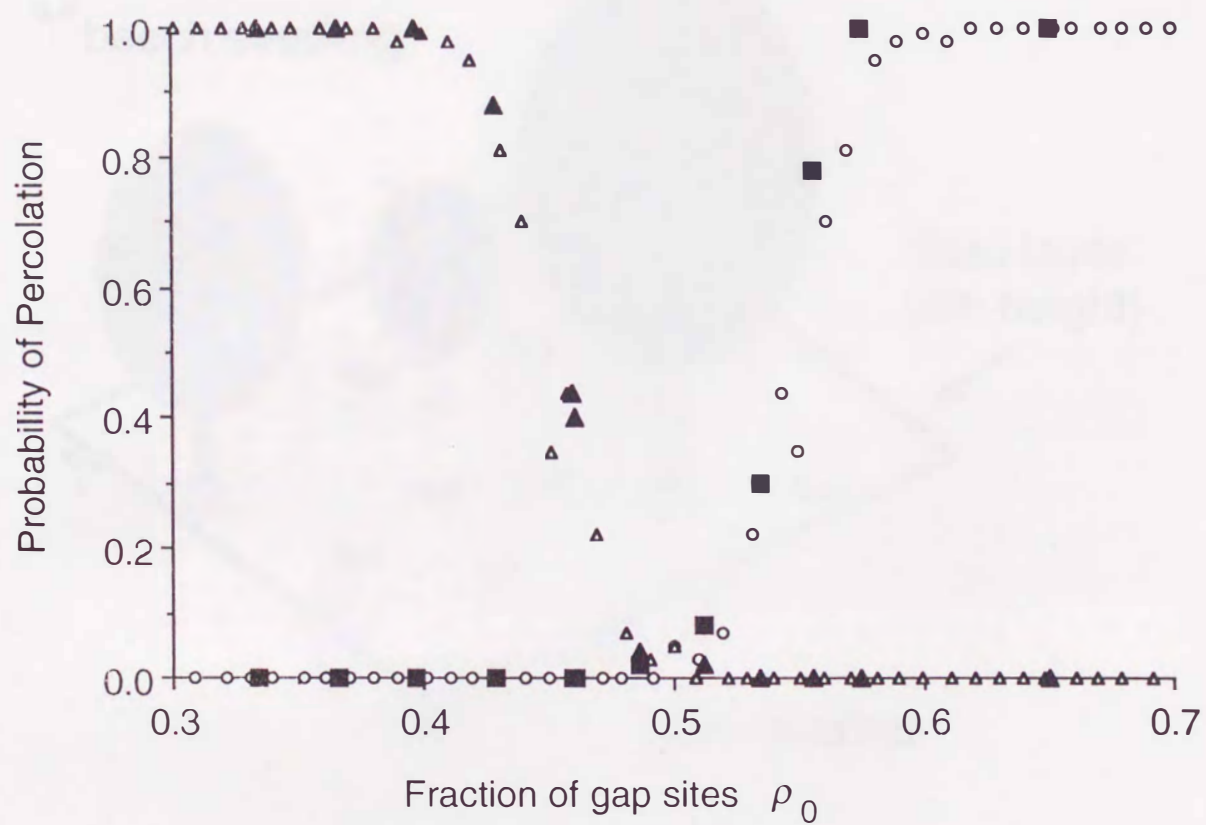


Figure 3.1 A

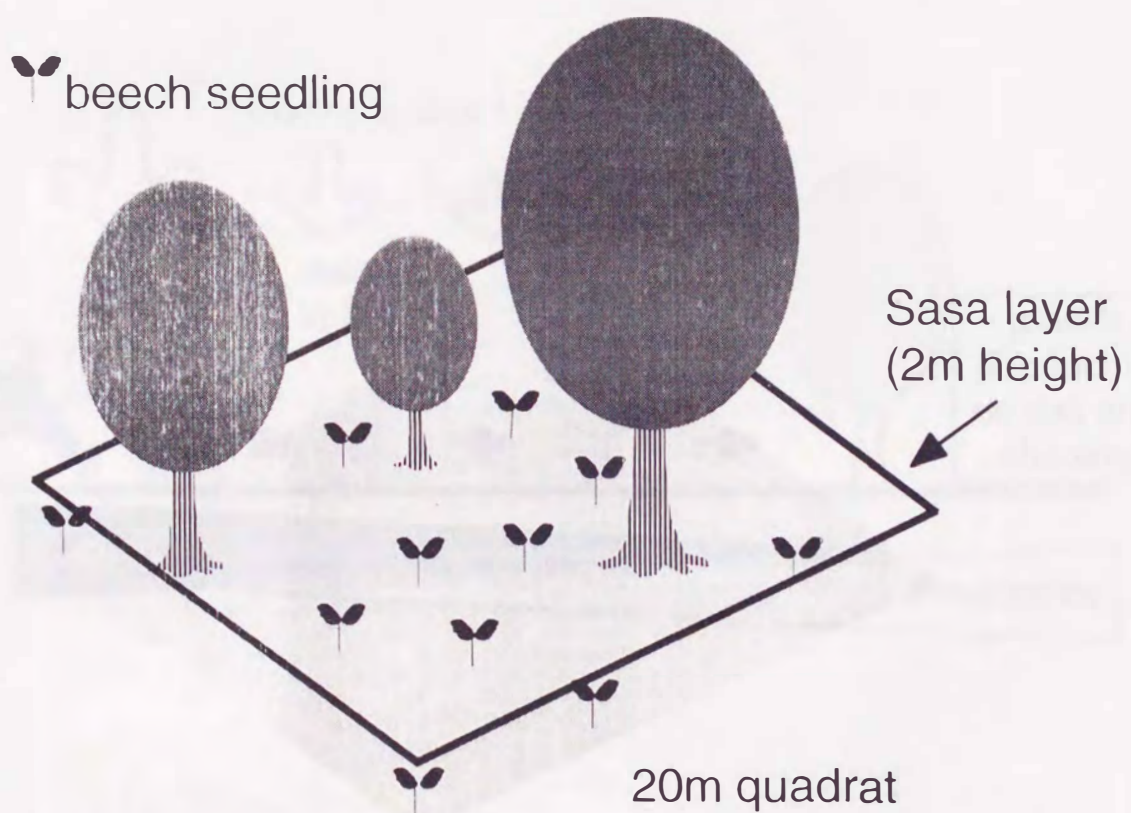


Figure 3.1 B

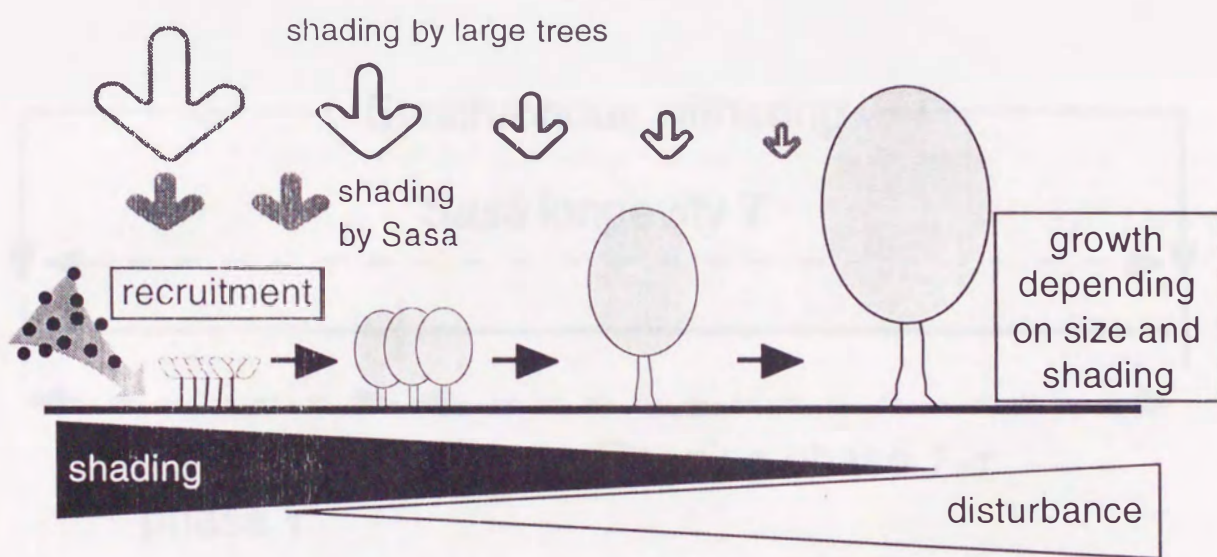


Figure 3.1 C

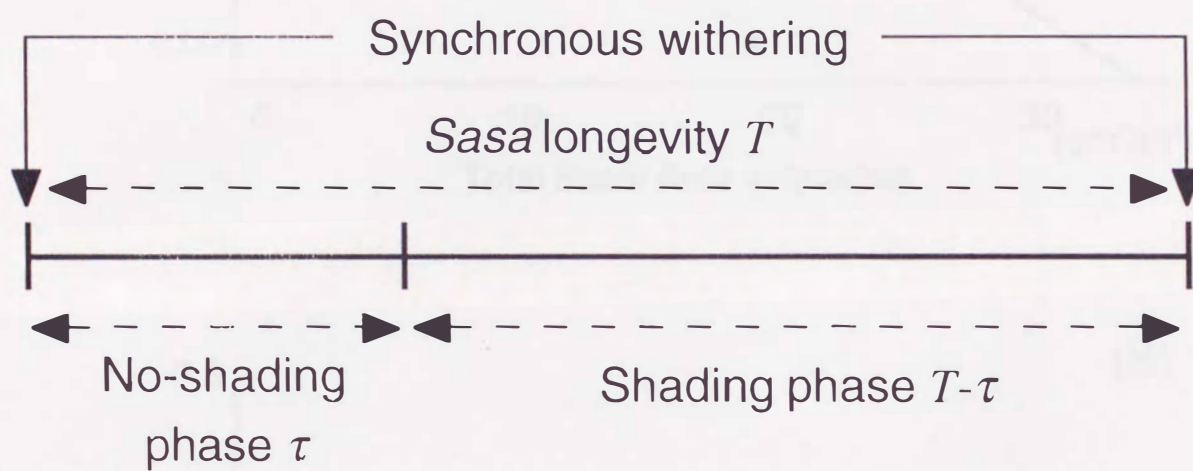


Figure 3.2

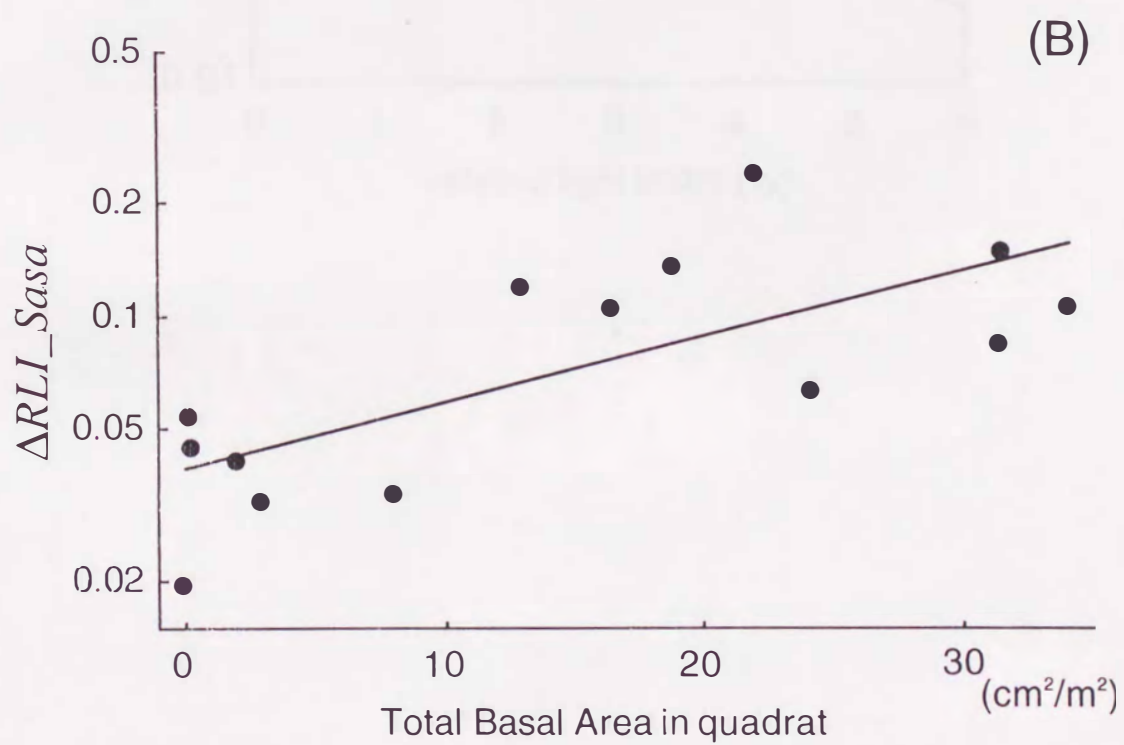
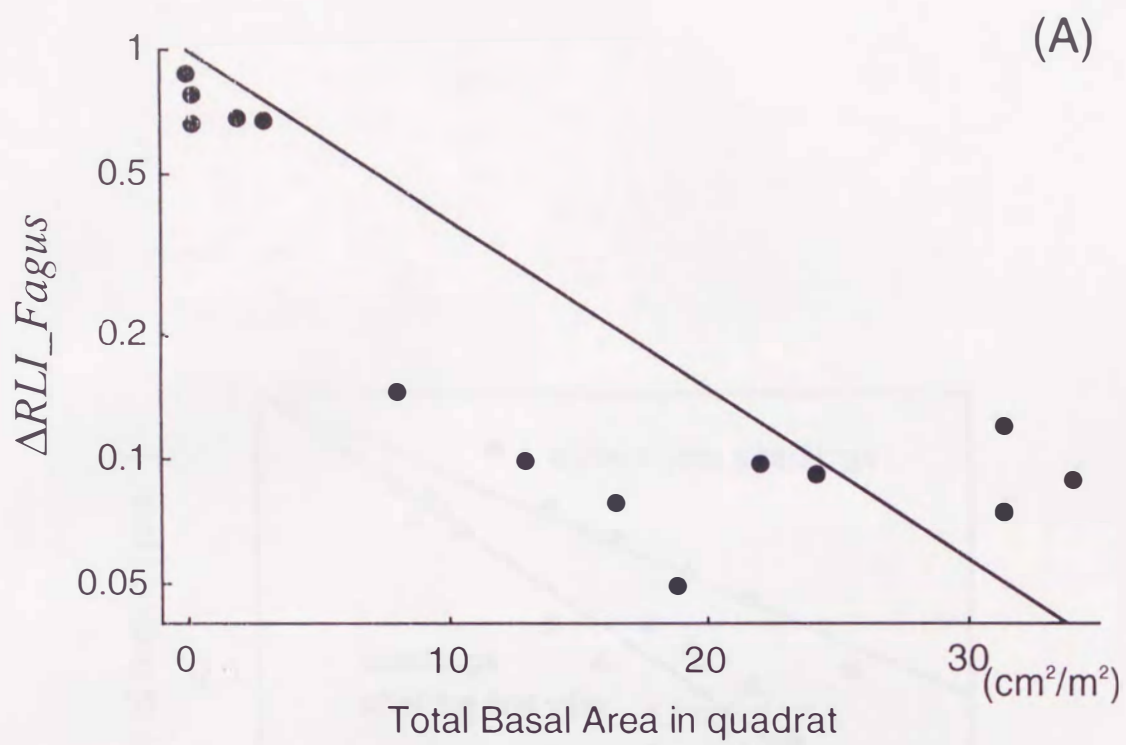


Figure 3.3

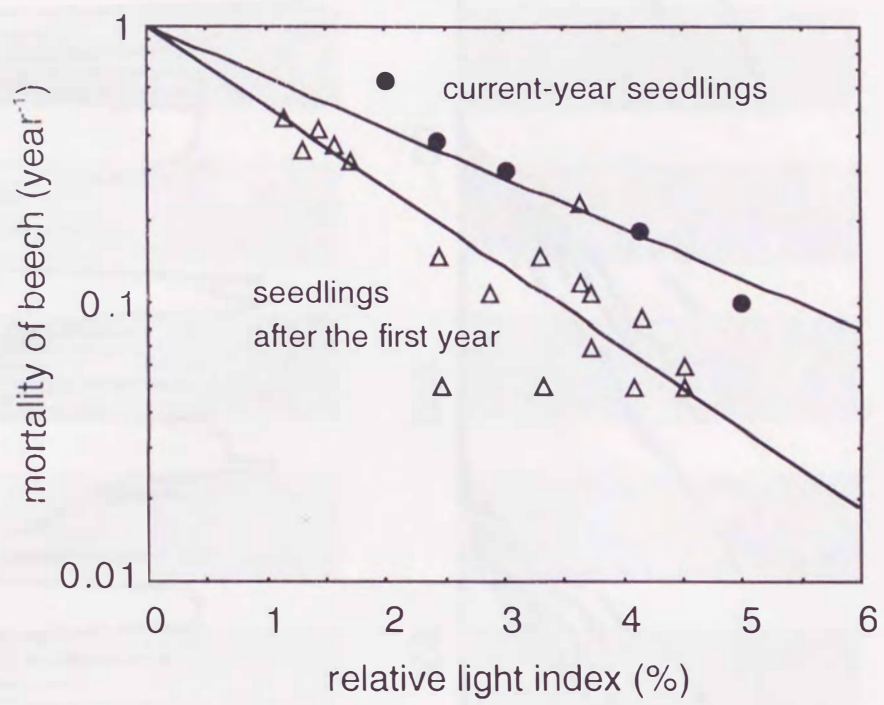


Fig.3.4

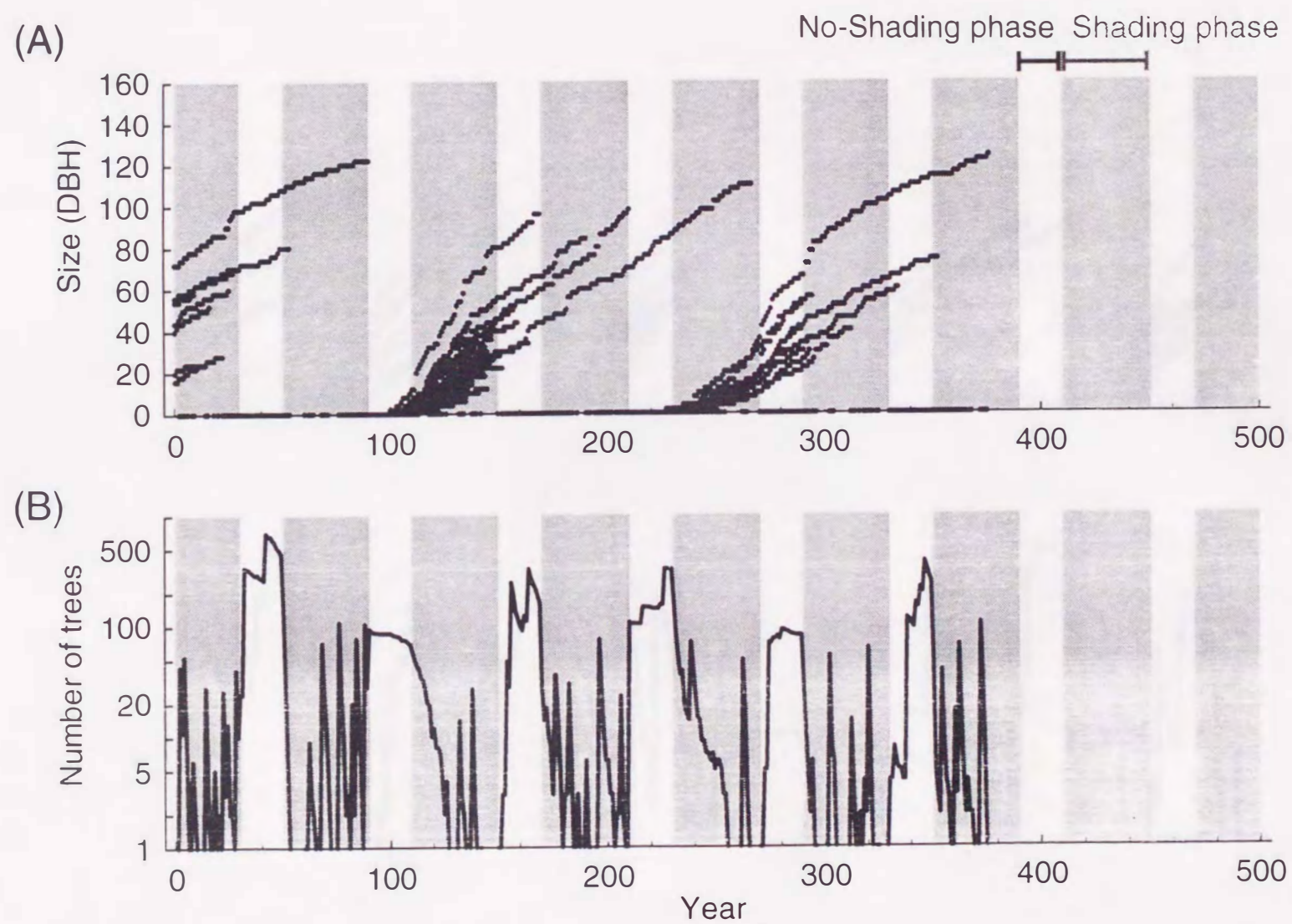


Fig. 3.5

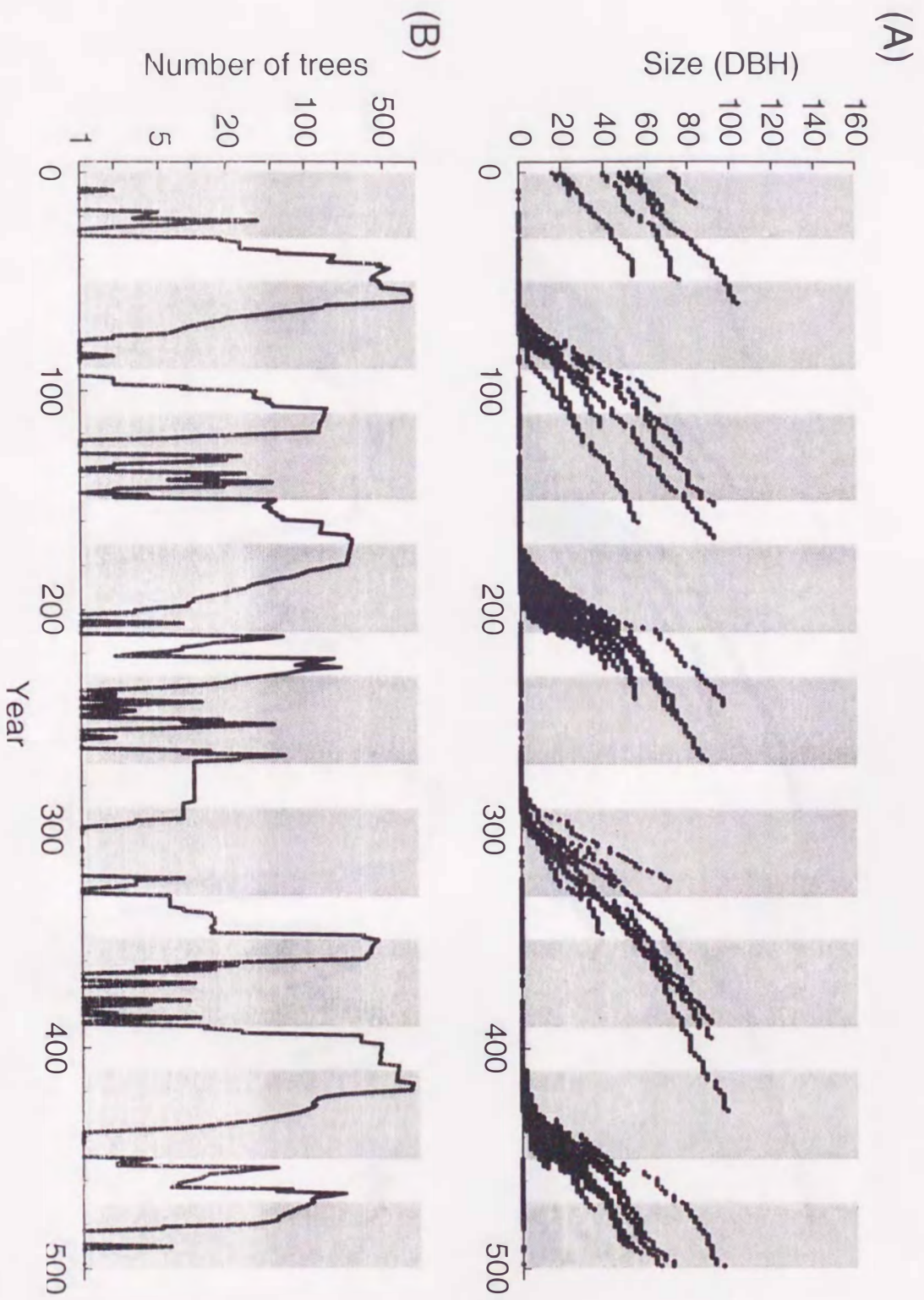


Fig.3.6

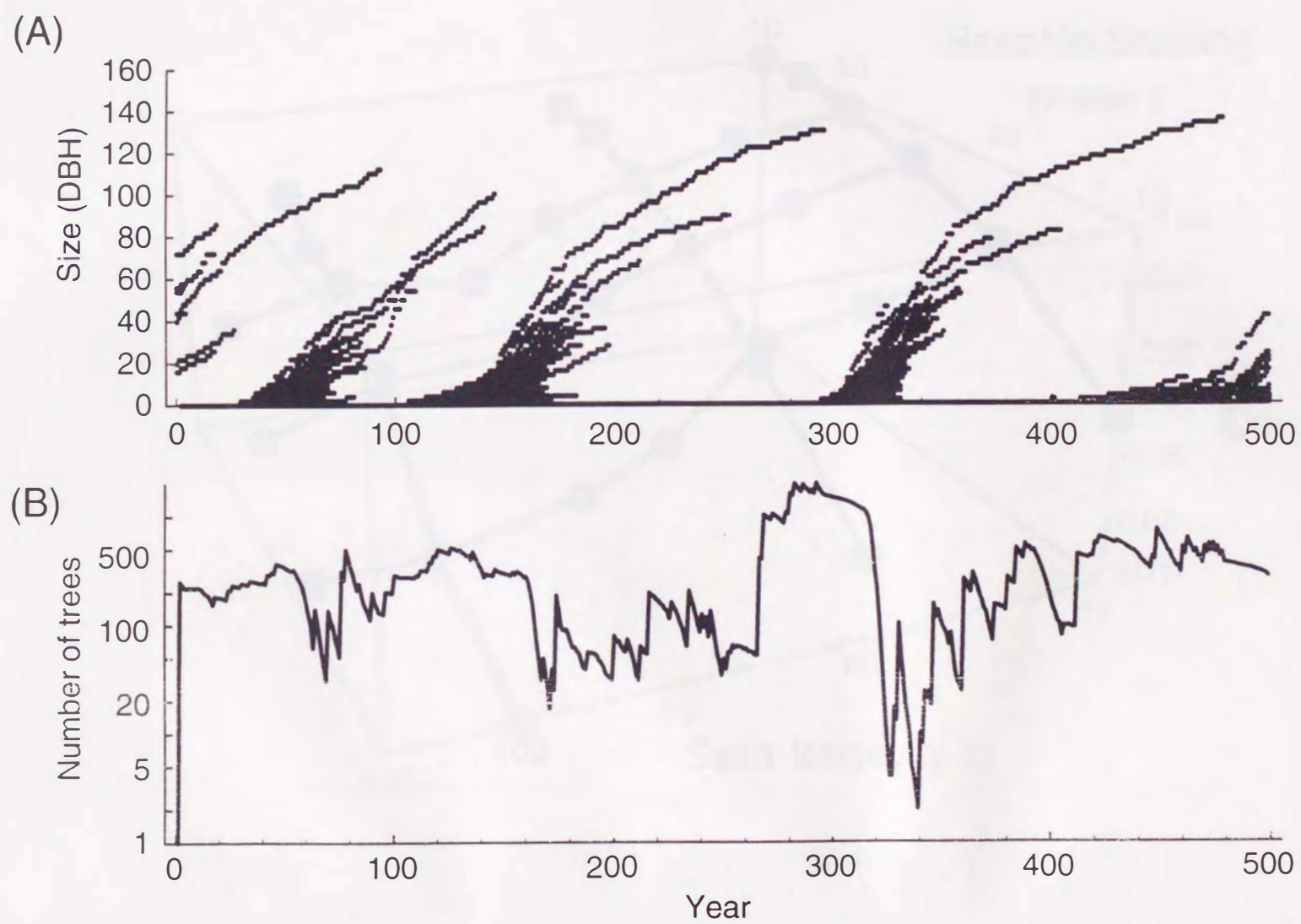


Figure 3.7

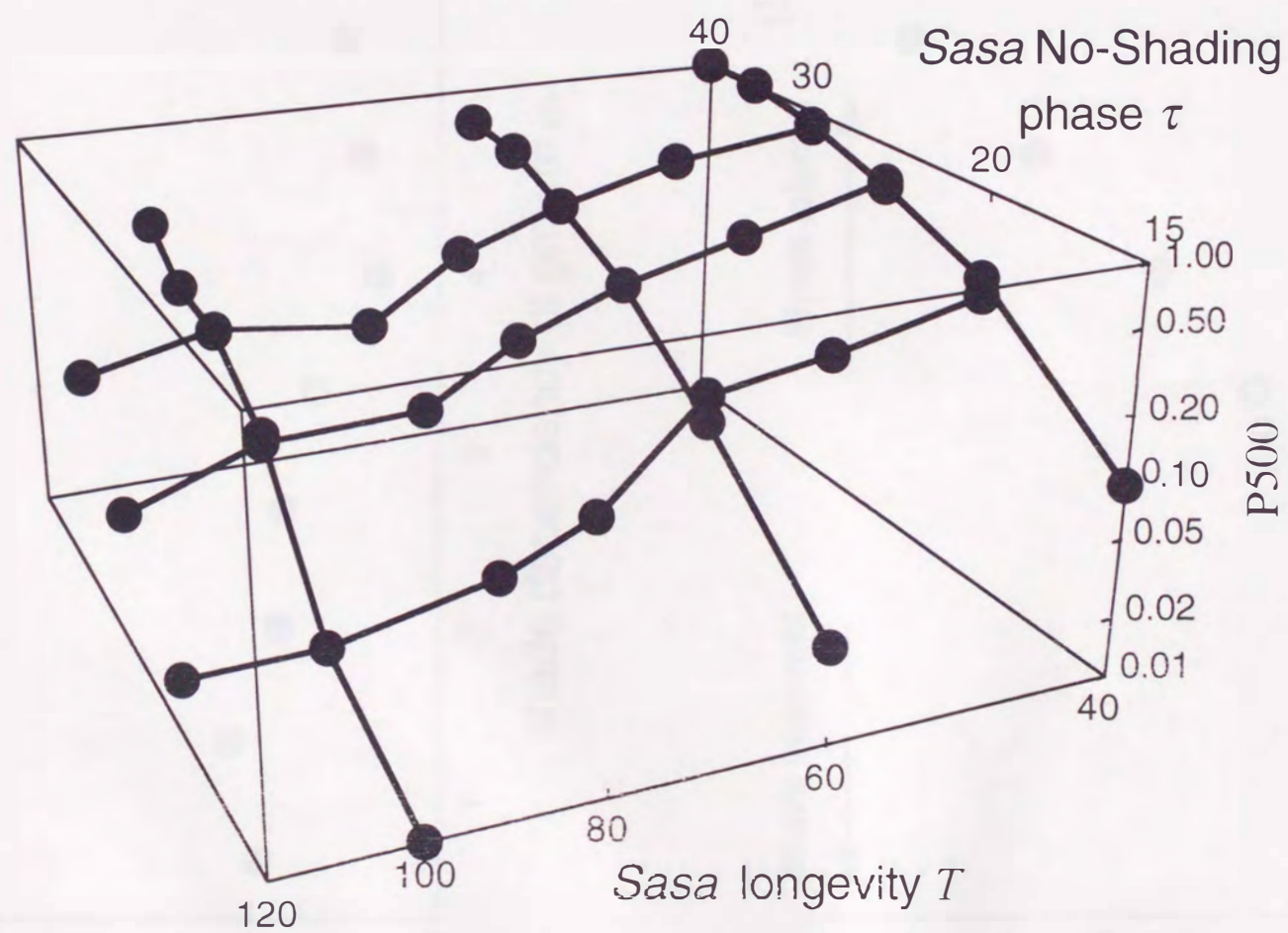


Figure 3.8

