B-52.3.2 Global change impacts on regeneration of a temperate forest in Japan (IGBP-GCTE-TEMA)

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Abstract

This study was planed under "Global Change Inpacts on Terrestrial Ecosystems in Monsoon Asia (TEMA)", one of the core research of International Geosphere-Biosphere Programme (IGBP). Purposes of this study are to make clear physiological and morphological response of key species under natural environment condition, to make clear forest dynamics based on seed dispersal and survive, and to develop a long-term gap dynamics model.

We developed and analyzed a computer simulator (long-term gap dynamics model) for the forest dynamics based on the field measurements of long term and large area census plot of Ogawa Forest Reserve (OFR). The result of simulation for 400 years suggested that the component of tree species would change drastically by replacing the current present canopy trees with those whose recruitment rate are much higher. As a consequence of the replacement, the estimated total basal area (TBA) in the forest simulator decreased slightly. However, under the scenario in which the growth rate of all trees became higher by affected by any environmental change, the 400 years simulation generated the result of increasing TBA while the replacement in tree component happened as well as under without change.

Key Words Temperature deciduous forest, Long-term ecological research, Photosynthesis, Gap, Dynamics model

1. Introduction

This study was planed under "Global Change Inpacts on Terrestrial Ecosystems in Monsoon Asia (TEMA)", one of the core research of Global Change and Terrestrial Ecosystems (GCTE) in International Geosphere-Biosphere Programme (IGBP). The objectives of TEMA are to predict the effects of elevated CO2 and climate change on the distribution and structure of forest in Monsoon Asia, and to determine the associated feedback effects to the global carbon cycle.

TEMA consists of the following four components: 1) Screening of key species with respect of the response to Global Change. Identification and classification of functional types. 2) Modelling of forest structure as an integration of functional types. Prediction of the effect of Global Change on forest structure. 3) Biogeographical analysis of the distribution and structure of forest ecosystems in Monsoon Asia. Extension of the model from the patch to the regional scale. 4) Modelling of the carbon cycle of forest ecosystems in Monsoon Asia. Feedbacks to the atmosphere and the physical climate systems.

Under program of TEMA, this study was planed and conducted three sub-study-fields which are aiming to make clear physiological and morphological responses of trees to environmental factors, to make clear forest dynamics based on seed dispersal and survive, and to develop a long-term gap dynamics model at a deciduous forest, Ogawa Forest Reserve (OFR), Kitaibaraki, northeastern Japan.

2. Research Objective

A. Acclimation of properties of shoots and leaves to light environment in deciduous tree species

Under this research program, we conducted several basic studies which are aiming at understanding of responses of trees to environmental factors. In particular, we dealt with properties directly related to photosynthesis.

B. Demography of main component tree species in Ogawa Forest Reserve

To obtain the parameters for the submodel of reproduction in the individual based model (IBM model) of forest dynamics we investigated 1) reproductive schedule, 2) seed dispersal pattern, and 3) annual fluctuation of reproduction.

C. Development and analysis of a forest simulator for the Ogawa Forest Reserve

The objective of the study is the development of new methods to estimate the values for demographic parameters defined by Ogawa Forest Reserve (OFR) plot measurements and analysis the simulator unifying these submodels.

3. Research Method

A. Acclimation of properties of shoots and leaves to light environment in deciduous tree species

a) Effects of current-year and previous-year PPFDs on shoot gross morphology and leaf properties

in *Fagus japonica*

We examined how shoot gross morphology and leaf properties are determined in

Fagus japonica Maxim., a deciduous broad-leaved species with flush-type shoot phenology, in which all leaves are produced in a single flush at the start of each season. With a tree of 14 m height in a deciduous forest, we examined relationships between shoot properties and local light environment.

b) Estimation of internal resistance to CO_2 diffusion in a leaf in deciduous tree species.

In tree leaves, thickness of cell walls of mesophyll cells tends to be thicker than in annual crops, which are usually used in photosynthetic studies. It is, therefore, important to know the magnitude of this resistance in tree species to examine photosynthetic responses of tree leaves to CO_2 concentration. We used the stable isotope technique based on the phenomenon that Rubisco discriminates $^{12}CO_2$ against $^{13}CO_2$. For controls, we also used annuals such as a bean plant.

a) Development of the photosynthetic machinery of the leaf in the course of leaf development

in tree leaves.

Rates of light-saturate net photosynthesis (Pmax) and dark respiration (Rd) on leaf area basis, leaf dry mass per area (LMA), leaf nitrogen content on a leaf area basis (LN) and instantaneous nitrogen use efficiency (NUE ≒ Pmax/LN) were followed during leaf development in several tree species and an annual. These species included *Castanopsis sieboldii*, *Quercus myrsinaefolia*, *Quercus glauca*, *Quercus serrata*, *Machilus thunbergii*, and *Phaseolus vulgaris*.

d) Re-examination of the Pipe-model theory of tree structure.

The pipe-model theory is also effective in examining tree architecture. This theory claims that the mass of non-photosynthetic parts between the height of z+Dz is proportional to dry mass of the leaves above the height z. Although this is simple, the tests so far made have supported this theory. However, this model lacks in physiological bases. In particular, light factor, which governs photosynthesis and transpiration, is neglected. We, therefore, paid our particular attention to light factor. We used *Acer mono* and *A. rufinerve* trees. We examined the leaf area (LA), leaf dry mass (LM) and relative photon flux density (R-PPFD) for each current year shoot. We harvested about 10 trees for each species at the end of the growing season and also examined cross sectional area of shoots and trunks (BA) and the area growth of the current year (DBA).

B. Demography of main component tree species in Ogawa Forest Reserve

We investigated demography of 16 main component tree species in a 6-ha plot, old-growing temperate deciduous forest, Ogawa Forest Reserve (OFR), central Japan. We have observed the flowering and fruiting of the sample trees for each species (18 to 726 individuals per species) together with measuring other demographic parameters since

1988. For the investigation on seed production and dispersal, we established sampling points (maximum 263 points) of regular distribution with a set of a seed trap and a quadrat in the central 1.2 ha area of the 6 ha plot. Seeds which fell into the seed traps have been collected every 2-4 weeks since 1987 and their viability was checked.

C. Development and analysis of a forest simulator for the Ogawa Forest Reserve

We started modeling by reviewing the previously used methods to describe forest dynamics. The most popular way of modeling is "density model" that is focusing only on the statistics, tree density (e.g. Kohyama and Takada 1998). Such kind of model keeps plain structure, and is calculated by some well-known methods like as transition matrix or partial differential equation. On the other hand, the model is often too simplified to generate various interesting patterns such as spatial structure observed in real forest (e.g. Pacala et al. 1996; comparison between spatial and mean filed forest dynamics). Moreover, It is pointed out that density model is sometimes inadequate to calculate dynamics including between-individual interactions (e.g. Kubo & Ida 1998; justification for using individual based model).

To avoid these difficulties and to construct more realistic simulator, several kinds of forest dynamics models based on the behavior of individual trees have been developed for long years (e.g. Botkin 1972, Shugart 1984, Pacala et al. 1993, Pacala et al. 1996, Kubo & Ida 1998).

We decided to develop our forest simulator as an individual based model, because it as necessary that the structure of the dynamics model should be consistent to the OFR census data. The data includes all tree whose Diameter at Breath Height (DBH) is equal to or larger than 5cm within 6ha plot calibrated in 1987, 1989, 1991 and 1993 (e.g. Masaki et al. 1992, Nakashizuka et al. 1992). Although the number of tree species in the focal quadrat is more than 50, we had to select only 23 for parameterization. They were chose because of its high density, so their total density is near to 90% of total density of whole community.

Our forest simulator consists of 6040 of 5m quadrat. Each quadrat is given altitude which is estimated from topography data of OFR plot. On the quadrats, individual trees (exactly, not individual but trunk) are arranged. Each tree (trunk) acts independently but sometimes affected by the interaction between neighbors

The observed growth rate of DBH had a large variation ith and without trend, hence we assumed that the growth rate of DBH was generated by a probabilistic distribution determined by a few parameters depending on tree species, size and interaction between neighbors. The expectation of growth rate is given as a variation of Gompertz-type growth model which is modified by the intensity of one directional competition. "One directional" represents a kind of mode of competition between individuals defined as higher tree can reduce the growth and survivability of lower tree. We introduced an index to indicate the intensity of competition such that it gave a best statistical explanation to the observed pattern of DBH growth rate.

The values of the parameters for the growth submodel are estimated by applying maximum likelihood method to the tree growth data in OFR. The numerical calculation to solve the likelihood equations was done by Newton-Raphson method.

In this model, growth of tree height is assumed to be entirely subordinated to the growth of DBH given as above. Here we use Ogawa's generalized allometricequation to calculate height growth. The parameterization for the equation was done by applying nonlinear fitting to DBH-height relationship data.

The mode of tree mortality in OFR plot is understood that it mainly consists of two factors (Nakashizuka et al. 1992): DBH depending disturbance and withered by shading. We also constructed the submodel for tree mortality (exactly, not individual tree but trunk elimination) similar to the above. All the value of parameters for the submodel was obtained from field measurements by using maximum likelihood method.

We developed a recruitment rate estimator which is resemble to the method of Kohyama and Takada (1998). The essential idea is the construction of "time distribution of recruitment" which is a kind of projection by applying growth and mortality submodels to DBH distribution of small trees. Once such distribution of estimated time is generated for each tree species, we can easily obtain some statistics needed by the submodel for recruitment such as mean recruitment rate.

4. Results & Discussion

A. Acclimation of properties of shoots and leaves to light environment in deciduous tree species

a) Effects of current-year and previous-year PPFDs on shoot gross morphology and leaf properties

in *Fagus japonica*

Leaf number (LNo), total leaf area (TLA), and length (SL) of the current-year shoot increased with the increasing PPFD in a deciduous forest. Thickness of the leaf, dry mass per leaf area and nitrogen content on a leaf area basis increased, whereas chlorophyll/N ratio decreased with increasing PPFD. To separate the effects of current-year PPFD from those of previous year(s), we artificially shaded a part of the uppermost leaf tier. Reciprocal transfers of the seedlings between controlled PPFD regimes were also made. The results showed that characteristics of shoot gross morphology such as LNo, TLA and SL were largely determined by the PPFD of the previous year. The exception was long 'long shoots' with many leaves, where shoot elongation appeared to be also influenced by current-year PPFD. In contrast, leaf properties were determined by current-year PPFD. These results indicate that both the current-year and previous-year PPFDs are important in the determination of shoot propitious. It is also shown that tree seedlings at very low relative PPFD retained leaves. On the other hand, the mature tree did not have leaves at very low PPFDs. This is obvious when the mass of non-photosynthetic organs to be supported by a but photosynthetic organ is considered. This is important when tree function is studied based on branch autonomy of C budget.

b) Estimation of internal resistance to CO_2 diffusion in a leaf in deciduous tree species.

The results indicate that the leaf internal resistance in deciduous tree species is greater than that in most annual crops but smaller than that in evergreen tree species. It is also indicated that the thick leaves are advantageous because they have large internal surfaces of mesophyll cells. Drop of CO_2 concentration in the intercellular spaces is less than a few Pa even in thick leaves, and thus the resistance to CO_2 diffusion in the intercellular spaces is small compared with the rest of the internal resistance.

b) Development of the photosynthetic machinery of the leaf in the course of leaf development

in tree leaves.

When expansion of leaf area was completed Pmax was near the maximum level in *P. vulgaris*, while it was one third in ever green species. In the evergreen species, Pmax continued to increase for upto 45 days. *Q. serrata* showed intermediate values. In evergreen species, Rd at full leaf expansion was about 1.5 to 3.5 times greater than that at the steady state level. These facts suggest that, in tree leaves, leaf development was still underway at full leaf area expansion. Low Pmax at full leaf expansion was caused both by low leaf nitrogen content and low NUE. Pmax increased with the increase in LMA. Plotting of the period required for photosynthetic maturation against LMA of the present data and the data from the literature showed a strong, unique correlation . This indicate that, with the increase of LMA, the energy and photosynthate allocated to nitrogenous compounds in chloroplasts are small compared with that to structural component such as cell walls. This explains the slow development of photosynthetic activity in tree species. This is very important to study acclimation capacity in tree species.

d) Re-examination of the Pipe-model theory of tree structure.

The results were as follows;

i. There is a strong relationship between the cross sectional area at a particular position and the cumulated leaf mass above the section position. However, the relationship between the light interception by the leaves above the particular position and the cross sectional area at the position is scattered.

ii. There is a strong correlation between cumulated light interception and the DBA. These results indicate that the current-year wood growth is influenced both by the current-year PPFD as well as the conditions of the previous years. Tree growth may be thus analyzed in a derivative way. The deciduous trees serve as an ideal system for studying mode of tree growth.

B. Demography of main component tree species in Ogawa Forest Reserve

a) Reproductive schedule

We found; 1) To make reproduction or not was depended not only by tree size, but also by growth rate of the individual tree, suggesting the amount of the resource production to be the critical factor. 2) The minimum size of reproduction was almost proportional to the maximum size of the species, and all the trees exceeded about 40% of the maximum size of each species reproduced irrespective to their growth rate (Nakashizuka et al. 1998, Shibata and Nakashizuka 1998).

We think that the reproductive tree size could be treated as a function of the maximum size of the species in the IBM model. We should consider growth rate of each trees, if we construct submodel of reproductive schedule of each trees.

b) Seed dispersal

The observed patterns of seed dispersal could be mechanistically explained by Greene-Johnson model. The model involves parameters which can be biologically interpreted; 1) terminal seed velocity, 2) tree height and 3) amount of dispersed seed per reproductive individual. The relationship between dispersed seed density and distance from a single seed source were explained well by the model. Two dimensional distribution of seed density dispersed from multiple seed sources was simulated by the model (Fig. 1). This model could be used as the submodel of seed dispersal.

c) Annual fluctuation of reproduction

From these quantitative long-term data, we found that many species had rather large annual fluctuation of seed production (Fig. 2). As an index of masting, coefficients of variation (CV, presented as fractions) of annual sound seed production from 1987 to 1994 were more than 1.5 for 11 species out of 16 species. *Fagus crenata* (CV was 2.7) had largest annual fluctuation of seed production. While *Quercus serrata* (CV was 0.6) produced seeds rather constantly. We also found a strict synchronized annual fluctuation among same genus by PCA of seed production.

To consider the factor related to annual fluctuation of seed production, predator satiation hypothesis were tested for 13 species which suffered from predation by insects at pre-dispersal stage. The percentage of seeds suffering predation had negative correlations with the annual seed production and with the ratio of seed production to that of the previous year for most species. This tendency was also found when the species of same genus were pooled. These results suggests the predator satiation operated for each population and guild. Such traits of seed production should be parameterize in the submodel of seed production pattern.

C. Development and analysis of a forest simulator for the Ogawa Forest Reserve

The forest configuration of OFR in 1987 is used the initial state for all the run of individual based simulator, and the simulation period is 400 years. With the value set of parameter calibrated by field measurements(base-line set), the result of simulation predicted that the total basal area(TBA) within the plot decreased to 26.6m^2/ha after 400 years, while the initial value was 32.2m^2/ha. This is caused by tree species replacement: the density of some current canopy species such as *Quercus* and *Castanea* fell down due to their small recruitment rate, and they were replaced with trees of larger recruitment rate such as *Acer*, *Carpinus* and *Styrax*. As the maximum DBH of the latter species was smaller than those of former, the TBA in forest was reduced.

Due to some environmental change, the demographic parameter could be different from the estimated values in above. To check the behavior of the simulator under such situation, we also simulated the forest dynamics with a modified parameter set in which the growth rate for all species increases extra 10% of the observation. The 400 years simulation generated the prediction that suggested slightly increasing in TBA, 35.9m^2/ha, while the replacement of tree species component occurred again as well as under the scenario with base-line set. It turned out that the change in TBA was caused by the increasing of mean basal area of future dominant trees such as *Acer* thanks to the extra growth.

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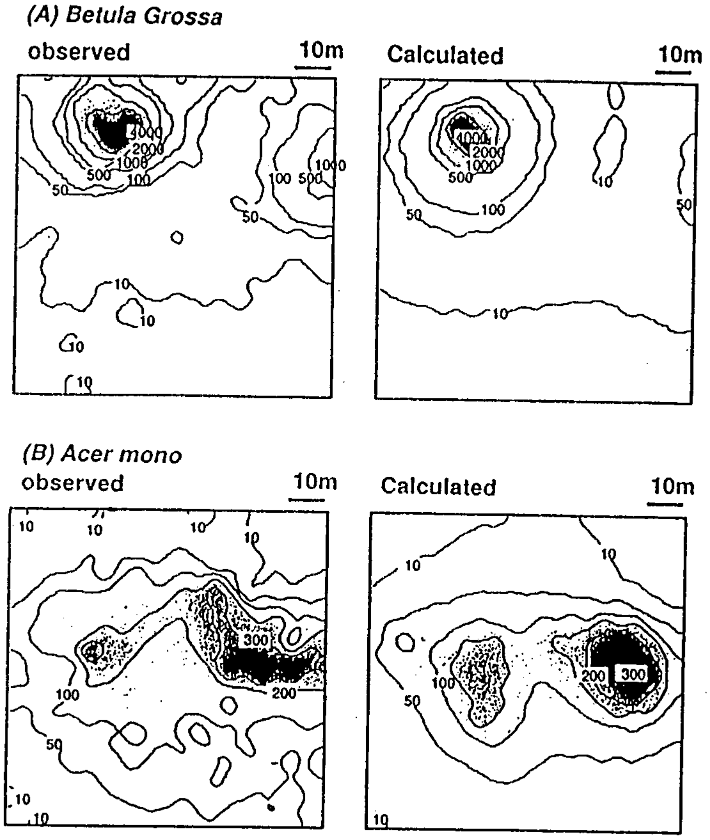

Figure 1 Seed dispersal pattern of *Betura grossa* (A) and *Acer mono* (B). Observed (left) and calculated seed dencity (right) from the regression by the Greene-Johnson model are shown (from Tanaka *et al.* 1998).

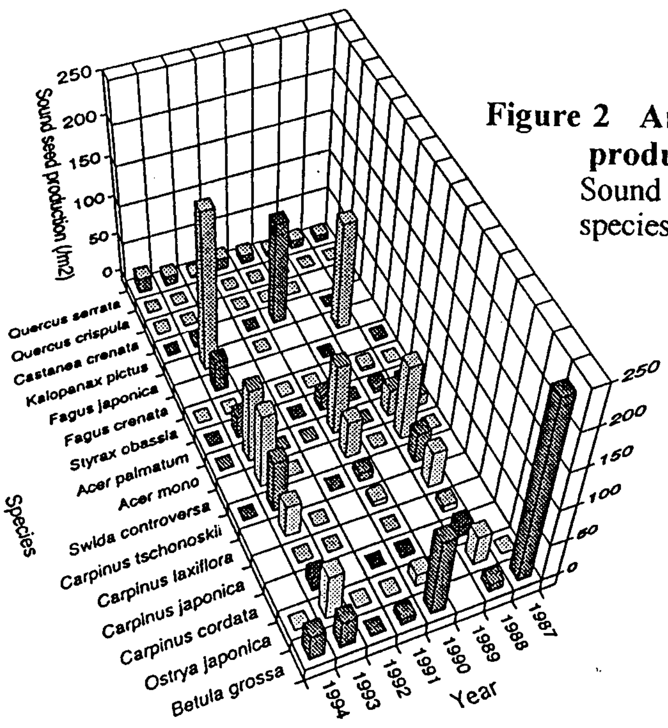

Figure 2 Annual fluctuation of sound seed production in Ogawa Forest Reserve. Sound seed production of main component species (/m2) are shown.(from Shibata 1999).