Theoretical Study on Size-Structure Dynamics, Competition and Coexistence in Plant Communities

（植物群集におけるサイズ構造，競合そして共存に関する理論的研究）

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Chapter 1
Introduction

In natural vegetation, a plant population is composed of individuals having various sizes (e.g. plant weight, plant height, and stem diameter) and different crown architectures and competing with other individuals for light and nutrients. To investigate how competition and coexistence processes emerge from such a complex system is one of the most interesting subjects in plant ecology. Furthermore, to investigate size-structure dynamics and species coexistence conditions in plant communities is important for applied biological sciences such as agriculture and forestry. In this thesis, I study mechanisms of the size-structure dynamics of plant communities theoretically, and quantify the effects of competition between individuals on plant community dynamics, using dynamic canopy photosynthesis and continuity equation models. First, previous studies concerning size-structure dynamics, competition processes and coexistence among species in plant communities are briefly reviewed, and the subjects which will be discussed in this thesis are addressed.

Individual-based models of growth dynamics for plant populations

Many models so far proposed for the study of growth dynamics in plant populations divide into two categories, spatial and non-spatial models (e.g. review by Hara, 1988). Most of these models consider interactions between individuals based on the growth of each individual in a population. Spatial models take into account spatial distributions of individuals, whilst non-spatial models do not, assuming that the spatial distribution of individuals is homogeneous. Firbank and Watkinson's model (1985) is one of the most successful spatial models. It reproduced several well-known phenomena in plant ecology such as the reciprocal equation of crowding effect and the self-thinning rule (Yoda et al., 1963; White, 1981; Westoby 1984; but see Weller, 1987a, b; Osawa and Sugita, 1989; Lonsdale, 1990). Aikman and

Watkinson's non-spatial model (1980) also reproduced the self-thinning rule. These models as well as other successful individual-based models (e.g. Botkin, Janak and Wallis, 1972; West, 1987; Prentice and Leemans, 1990; Clark, 1990), however, assume some *a priori* growth equations and/or competition functions between individuals. West (1987) proposed a spatial, dynamic, canopy photosynthesis model with an *a priori* competition function and reproduced the self-thinning rule. Hara (1986a) proposed a canopy photosynthesis model for the growth of individual plants in a stand based on the diffusion model (Hara, 1984a, b). Assuming not any *a priori* growth or competition functions but an allometric relationship between plant height and weight (i.e. allocation-growth pattern), this model reproduced realistic size-dependent growth of individuals as affected by competition between them (Hara, 1986a, b). Hara's model is a non-spatial canopy photosynthesis model for one growth period.

Effects of variations in physiological traits on size structure dynamics and competition in plant populations

Temporal and spatial variations in the environmental conditions generate variation in physiological parameters of individuals in a plant population such as leaf photosynthetic rate, maintenance and growth respiration rates, etc., influencing the process and outcome of interactions between individuals and thus the dynamics of plant communities. Few ecophysiological studies have taken into account processes at the population level, such as size-structure dynamics, assuming instead that each species, genotype or population consists of identical individuals (e.g. Lambers and Dijkstra, 1987; Hirose, 1987, 1988a, b; Hirose et al., 1989; Lambers et al., 1990). Few size-structured models of plants have considered variation in physiological parameters, assuming that each species under consideration has fixed species-specific values of these parameters (e.g. Botkin, Janak and Wallis, 1972; Shugart and West, 1977; Shugart, 1984; Huston and Smith, 1987; Tilman, 1988). In the real world, however, a plant population consists of individuals of different sizes and ages, and physiological parameters of each individual even in a single-species population are varied by temporal and spatial variations of the environment.

Allometry and growth pattern of an individual and plant population dynamics

The growth pattern of an individual plant is generally species-specific, and two typical types have been recognized in trees, height-growth and diameter-growth type (e.g. Marks, 1975; Maruyama, 1978; Boojh and Ramakrishnan, 1982; Bicknell, 1982; Sakai, 1987, 1990; Kohyama, 1987; Kohyama and Hotta, 1990; King, 1990; Hara, Kimura and Kikuzawa, 1991). Trees of the height-growth type allocate more assimilates to height growth than to stem diameter growth and construction of lateral branches and foliage. The reverse is true with trees of the diameter-growth type. Therefore, the relationship between stem diameter and tree height reflects a species characteristic. This relationship is usually described by allometry. Allometry is given as a power equation between two sizes of individual plants in a population at one point in time. Allometry is given as a straight line on a log-log plot. However, it has been reported that the relationship between stem diameter and tree height in crowded tree stands at one point in time is usually curvilinear on a log-log plot. Kohyama et al. (1990) argued that the curvilinear *D-H* relationship is brought about by competition for light (asymmetric competition). Holbrook and Putz (1989) showed that sweet gum (*Liquidambar styraciflua*) trees respond to the presence of neighbours by changing stem biomass allocation patterns. Weiner, Berntson and Thomas (1990), Weiner and Thomas (1992) and Weiner and Fishman (1994) have also obtained the same results for several species of annual plants as those for trees mentioned above. However, few theoretical researches have been done for relationships between these allometries and allocation pattern in crowded plant populations.

Crown architecture and species coexistence in plant communities

Many researchers have investigated the relationships between species-specific crown architecture, successional status and responses to gaps in trees (Pickett and Kempf, 1980; Veres and Pickett, 1982; Kempf and Pickett, 1981; Shukla and Ramakrishnan, 1986). Horn (1971) suggested adaptive growth dynamics of modules in relation to crown architecture and light regimes in the foliage. Küppers (1989) discussed the adaptive significance of crown architecture based on cost-benefit relationships of carbon gain. However, most of these studies have simply discussed adaptive significances of species-specific tree crown architecture as simple allometries between crown dimensions (crown depth, crown width, crown area) and individual sizes (mass, stem diameter at breast height, stem height), and have not investigated the effects of individual crown architecture as vertical foliage profile on the interactions between individuals and population dynamics. Crown architecture is an important factor for photosynthetic production (Horn, 1971; Küppers, 1989; Kikuzawa et al., 1986). Tree communities are usually composed of species of various crown shapes (Kohyama, 1987; King, 1990; Kohyama and Hotta, 1990; note that these studies used simple allometries between crown dimensions and individual sizes for crown shape), and the crown architecture may play an important role in species coexistence. In the boreal and sub-boreal zones, forests are composed of two tree groups having distinct crown shapes (e.g. Youngblood, 1995), conifers having conic crowns and deciduous broad-leaved trees (hardwoods) having spheroidal crowns (e.g. Umeki, 1993). Conifers and hardwoods coexist at a large scale (Tatewaki, 1958; Ishikawa, 1990; Youngblood, 1995) and the difference in the crown architecture may contribute to species coexistence in the conifer-hardwood mixed-species forests. Several researchers have investigated the effects of crown shapes on stand dynamics and species diversity of sub-boreal forests. Ishizuka (1984) pointed out that spatial pattern of individual crowns affected the stand dynamics of sub-boreal forests. Fujimoto Hasegawa and Shinoda (1991) and Fujimoto (1993) suggested that the difference in crown shape between species affected the successional status of each species. However, few have investigated quantitatively the effects of crown shapes as a vertical foliage profile on community dynamics or species coexistence patterns.

Outline of this thesis

The primary objective of this thesis is to study the plant ecological subjects mentioned above using size-structured dynamical models together with canopy photosynthesis of plant communities. I focus only on light competition, assuming that nutrients and water in the soil are homogeneously distributed. The effects of nutrients and water conditions can be indirectly incorporated in the photosynthetic ability of an individual. To investigate biological meanings of competition processes and size-structure dynamics, I mainly use a continuity equation for the size-structured dynamical model instead of a diffusion equation assuming that environmental conditions are homogeneous. With the continuity equation model and the dynamical canopy photosynthesis model, aspects of competition, stability of size structure for physiological and environmental variations, relationships between growth patterns of individuals and size-structure dynamics and relationships between crown architecture and species coexistence in plant communities are described theoretically, and implications about mechanisms of these processes are discussed based on actual data.

Chapter 2 describes the details of a continuity equation model together with dynamic canopy photosynthesis for the time development of size structure in plant populations, and addresses the competition modes not *a priori* but functionally using the model. In Chapter 3, using the model, effects of physiological and environmental variations on the dynamics of size structure and competition mode in a plant population are examined. In Chapter 4, the model is extended to a two-dimensional model which is capable of treating two different sizes (plant height and stem diameter) for investigating relationships between dynamic allocation patterns of individuals, size-structure dynamics and competition in plant populations. Chapter 5 deals with the coexistence of species with two different crown architectures, using the model of Chapter 1 extended to the case for multi-species plant community dynamics, and discuss the coexistence conditions. The overall findings and implications obtained by this study are summarized in Chapter 6.

Chapter 2

A canopy photosynthesis model for the dynamics of size-structure and self-thinning in plant populations

In this chapter, Hara's canopy photosynthesis model (1986a) is extended to describe the dynamics of stand structure based on a continuity equation (a simple version of the diffusion model; e.g. Hara, 1984a). This model has the foundamental structure which will be used and/or extended in the succeeding chapters. With this basic model, mechanisms of the dynamics of size structure and self-thinning and the relationships between density, size-dependence in individual growth, allocation-growth patterns of plant height and stem diameter and the mode of competition are discussed.

2.1 Model

Basic assumptions

Let consider an even-aged plant population which grows in a homogeneous environment, i.e. the plants have the same size distribution per unit area at any place in the stand we consider. Let $f(t,w)$ be a distribution density of individuals of plant weight w per unit area at time t. It is assumed that the basic equation governing the dynamics of $f(t,w)$ is given by

$$\frac{\partial f(t,w)}{\partial t} = -\frac{\partial}{\partial w}\left[G(t,w)f(t,w)\right] - M(t,w)f(t,w), \tag{2.1}$$

where $G(t,w)$ is the mean growth rate (instantaneous mean of increments of plant weight per unit time) of individuals of plant weight w at time t and $M(t,w)$ is the mortality rate of individuals of plant weight w at time t (Hara, 1984a; 1988). The density (number of individuals per unit ground area) at time t, $\rho(t)$, is given by

$$\rho(t)=\int_{w_0}^{w_{\max}} f(t,w)\mathrm{d}w, \tag{2.2}$$

where w_0 and $w_{\max}$ are the minimum and maximum plant weight, respectively.

The function forms of $G(t,w)$ and $M(t,w)$ are determined by the mode and degree of interactions between individuals. Competition is assumed to be only for light in this thesis. The equation (2.1) is the deterministic version of the diffusion model proposed by Hara (1984a). The diffusion model can describe fluctuations in species characteristics caused by environmental heterogeneity, genetic variation, spatial variation of individuals in the neighbourhood competition effects, etc.

Photosynthetic process of a single isolated plant

A population dynamic model must also simulate effectively the growth of individual plants. Therefore, I firstly describe a single isolated plant. It is assumed that each isolated plant has a similar conic canopy as illustrated in Fig. 2.1. For the conic canopy, total leaf area of an individual increases with its plant height. Thus It is further assumed that the foliage layer at height x from ground dies if the daily total net photosynthetic rate per unit leaf area at that height of an individual of plant height h, $p_n(x,h)$, is negative because of self-shading within the crown of a plant. The vertical distribution of leaf area density of an individual of plant height h at height x from ground, $f_{LA}(x,h)$, is therefore given by

$$f_{LA}(x,h)=\theta(h-x), \qquad (p_n(x,h)\geq 0); \tag{2.3a}$$

$$\qquad =0, \qquad (p_n(x,h)<0); \tag{2.3b}$$

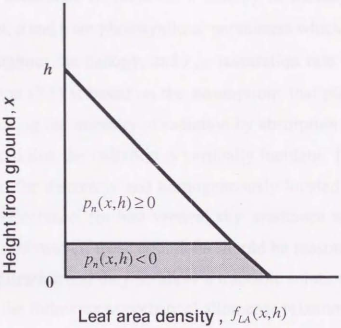

Fig. 2.1. A hypothetical vertical distribution of leaf area density of an isolated plant of height h at height x from ground. The foliage layer (shaded zone in the figure) dies if daily net photosynthetic rate per unit leaf area, $p_n(x,h)$, is negative.

where, using a rectangular hyperbola as an absorbed irradiance-photosynthetic rate curve (see Hara, 1986a),

$$p_n(x,h) = \int_0^{T_d} \left[\frac{bkI(t_d,x)}{1+akI(t_d,x)} \right] \mathrm{d}t_d - r_f, \tag{2.4}$$

$$I(t_d,x) = I_0 \sin\left(\frac{\pi t_d}{T_d} \right) \exp\left[-k \int_x^h f_{LA}(z,h) \mathrm{d}z \right]. \tag{2.5}$$

Here $I(t_d,x)$ is light intensity at height x from ground at time of day t_d and daylength T_d. I_0 is irradiance incident on a canopy at midday, k is light extinction coefficient, a and b are photosynthetic parameters which are assumed to be constant throughout the canopy, and r_f is respiration rate per unit leaf area per day. Equation (2.5) is based on the assumptions that plant foliage is homogeneously reducing the intensity of radiation by absorption according to Beer-Lambert law and that the radiation is vertically incident. This can only be an approximation for discretely and homogeneously located leaves, with transmittance and reflectance, for non-vertical sky irradiance and for direct sunlight in sunflecks. However, these equations should be reasonable approximations for this application and they do allow a tractable solution.

In the model, the following hypothetical allometric relationship between plant weight, w, and plant height, h, is assumed:

$$w = \alpha h^{\beta}, \tag{2.6}$$

where α and β are allometric parameters. The daily total net photosynthetic rate of a single isolated individual of plant height h is then obtained as

$$P_n(h) = \frac{1}{1+r_g}\left\{u\int_0^h p_n(x,h) f_{LA}(x,h)\mathrm{d}x - r_m\left(\alpha h^{\beta} - \frac{1}{s}\int_0^h f_{LA}(x,h)\mathrm{d}x\right)\right\}, \tag{2.7}$$

where u, r_g, r_m, s are conversion factor, growth respiration rate, maintenance respiration rate and specific leaf area, respectively. Finally, $P_n(h)$ is transformed to a function of w, $P_n(w)$, using eqn (2.6).

Photosynthetic process of individual plants in a crowded stand

In this section, let consider an individual in a crowded stand to formulate the function form of $G(t,w)$. At first, I briefly review the canopy photosynthesis model proposed by Hara (1986a). Now let $f_H(t,h)$ be a distribution density of plant height h per unit area at day t in a stand. Thus the vertical leaf area density in the stand at height x from ground at day t is given by

$$\phi(t,x)=\int_0^{h_{\max}} f_{LA}(x,h)f_H(t,h)\mathrm{d}h, \tag{2.8}$$

where $h_{\max}$ is the maximum plant height in the stand. From the assumption of homogeneity of the stand, light intensity at height x from ground at time of day t_d at day t is given as (cf. eqn (2.5))

$$I(t,t_d,x)=I_0\sin\left(\frac{\pi t_d}{T_d}\right)\exp\left[-k\int_x^{h_{\max}}\phi(t,z)\mathrm{d}z\right]. \tag{2.9}$$

Then daily net photosynthetic rate per unit leaf area at x from ground for an individual of plant height h in the stand at day t, $p_n(t,x,h)$, is given as follows (cf. eqn (2.4)):

$$p_n(t,x,h)=\int_0^{T_d}\left[\frac{bkI(t,t_d,x)}{1+akI(t,t_d,x)}\right]\mathrm{d}t_d-r_f. \tag{2.10}$$

In this case, leaves in the foliage layer at height x from ground also dies if $p_n(t,x,h)$ is negative. The height of leaf death depends on the crowdedness of the stand. Let $f_{LA}^*(x,h)$ represent $f_{LA}(x,h)$ in the crowded stand and let $p_n^*(t,x,h)$, which is calculated using $f_{LA}^*(x,h)$, represent $p_n(t,x,h)$ in the crowded stand. Therefore, daily net photosynthetic rate of an individual of plant height h in the stand at day t is obtained as follows:

$$P_n^*(t,h) = \frac{1}{1+r_g}\left\{u\int_0^h p_n^*(t,x,h) f_{LA}^*(x,h)\mathrm{d}x - r_m\left(\alpha h^\beta - \frac{1}{s}\int_0^h f_{LA}^*(x,h)\mathrm{d}x\right)\right\}, \quad (2.11)$$

where u, r_g, r_m, s are the same parameters as in the case of an isolated individual. The above equation is given in terms of plant height h. Therefore, we can transform it into a function of plant weight, $P_n^*(t,w)$, using the hypothetical allometric relationship between plant height, h, and plant weight, w [eqn (2.6)]. In the transformation of distribution density, we should take account of the following relationship:

$$f_H(t,h)\mathrm{d}h = f(t,w)\mathrm{d}w, \quad (2.12)$$

where dh and dw are infinitesimal intervals of plant height and weight, respectively. Finally, the function form of $G(t,w)$ in the basic equation (2.1), which is identical to $P_n^*(t,w)$, is obtained.

Mortality process

Throughout this thesis, it is assumed that light mainly governs competition processes between individuals. In fact, many studies have suggested that competition between plants in a monoculture stand is principally for light and one-sided (asymmetric; e.g. Kuroiwa, 1960; Ford, 1975; Ford and Diggle, 1981; Cannell, Rothery and Ford, 1984; Hara, 1986b; Weiner and Thomas, 1986; Weiner, 1990). Thus the growth rate of an individual surrounded by large plants is reduced and it can be negative. In the model, it is assumed for simplicity that mortality occurs when daily net photosynthetic rate of an individual is negative. Then, I assume the function form of $M(t,w)$ as

$$\begin{aligned} M(t,w) &= 0, \quad (P_n^*(t,w) \geq 0); && (2.13a) \\ &= 1, \quad (P_n^*(t,w) < 0). && (2.13b) \end{aligned}$$

2.2 Simulation procedure

Since the above model cannot be solved analytically, numerical calculations are used to investigate the dynamics of size distribution of plant weight w, $f(t,w)$. The simulation procedures are as follows:

0) Assume an initial size distribution of plant weight (normal distribution in this simulation) and calculate its plant height distribution using the allometric relationship given by eqn (2.6)
1) Calculate the vertical distribution of leaf area density of individuals using eqn (2.8) and the size distribution of plant height.
2) Calculate the vertical distribution of light intensity using eqn (2.9) for the canopy structure given by step 1).
3) Remove the foliage layer where daily net photosynthetic rate per unit leaf area given by eqn (2.10) is negative.
4) Calculate the growth rate in plant weight of individuals using eqns (2.11) and (2.12), which gives rise to the $G(t,w)$ function. If it is negative, these individuals die, giving rise to the $M(t,w)$ function defined as eqn (2.13). Then calculate the size distribution of plant weight at the next time-step using the continuity equation (2.1)
5) Calculate the size distribution of plant height at the next time-step from plant weight using the allometric relationship given by eqn (2.6). Then proceed to step 1).

Calculations of numerical integration were executed by the spline integration method (e.g. Davis and Rabinowitz, 1984). For the time development of the basic equation (2.1), I used the Lax-Wendroff method (e.g. Smith, 1985). A normal distribution with a mean plant weight 1.0 (g) and a standard deviation 0.1 was used as the initial distribution of plant weight for each simulation set, and the simulations were conducted over the time interval from 0 to 500 (in days).

Parameter values used for simulations are given in Table 2.1 and are the same as used in Hara (1986a). Two sets of simulations were performed as follows:

i) variation in the allometric parameter, β,

ii) variation in the initial density of the stand, $\rho(0)$.

Table 2.1. *Parameter values used for simulations in Chapter 2*

Parameter	Units	Definition
$\alpha=4.2\times10^{0}$	$(gm^{-\beta})$ for $\beta=2.0$	Allometric parameters: eqn (2.6)
$=3.9\times10^{1}$	for $\beta=2.5$	
$=3.7\times10^{2}$	for $\beta=3.0$	
$=3.6\times10^{3}$	for $\beta=3.5$	
$\theta=1.0\times10^{-3}$	(m^2m^{-2})	Parameter for leaf area distribution: eqn (2.3a) and (2.3b)
$u=0.65$	$(g_{dwt}g_{CO_2}^{-1})$	Conversion factor: eqn (2.7)
$k=0.70$		Light extinction coefficient: eqns (2.4), (2.5), (2.9) and (2.10)
$a=0.01$	$(W^{-1}m^2)$	Parameters for light-photosynthetic rate curve: eqns (2.4) and (2.10)
$b=0.05$	$(g_{CO_2}W^{-1}h^{-1})$	
$I_0=250$	(Wm^{-2})	Irradiance incident on the canopy at midday: eqns (2.5) and (2.9)
$T_d=14$	(hour)	Day length: eqns (2.5) and (2.9)
$r_f=0.06$	$(g_{CO_2}m^{-2}d^{-1})$	Respiration rate of leaves: eqns (2.4) and (2.10)
$r_m=0.05$	$(gg^{-1}d^{-1})$	Maintenance respiration rate: eqns(2.7) and (2.11)
$r_g=0.30$	(gg^{-1})	Growth respiration rate: eqns (2.7) and (2.11)
$s=0.02$	(m^2g^{-1})	Specific leaf area: eqns (2.7) and (2.11)

2.3 Simulation results

As the allometric parameter, β, in eqn (2.6) decreases, there is more allocation to height growth giving plants which may be termed as 'height-growth' type, because for the same value of w, plants with smaller β have greater height h. Similarly, plants with large values of β is defined as 'diameter-growth' type. On the other hand, α in eqn (2.6) is a scaling factor: dimensionless statistics such as CV (coefficient of variation) and skewness are independent of α. Direct comparison of the absolute value of mean plant weight for different values of α is meaningless, because the mean of w is proportional to α.

Growth of a single isolated plant

If the relationship between the relative growth rate (RGR) given by $P_n(w)/w$, and plant weight, w, is given as a straight line with a negative slope, then the growth of w is the logistic curve. If the relationship between RGR and $\log w$ is given as a straight line with a negative slope, then the growth of w follows the Gompertz curve. β=2.0 except for large values of w approximately corresponds to the logistic growth, and β=2.5, 3.0 and 3.5 except for large values of w approximately correspond to the Gompertz growth (Fig. 2.2).Therefore, this canopy photosynthesis model approximates the well-known *a priori* growth curves for an isolated individual. Moreover, this model shows that a single isolated plant of 'height-growth' type (small β) tends to follow the logistic growth in plant weight, and that of 'diameter-growth' type (large β) tends to follow the Gompertz growth (or Richards growth) in plant weight. Generally, the following Richards equation (e.g. see Causton and Venus, 1981) can be used as the $G(t,w)$ function of a single isolated plant over a wide range of the allocation-growth pattern in terms of β (Fig. 2.2):

$$G(t,w) = w(a_0 - a_1 w^m), \tag{2.14}$$

where a_0, a_1 and m are constants. In particular m=1 represents the logistic growth (Fig. 2.2A).

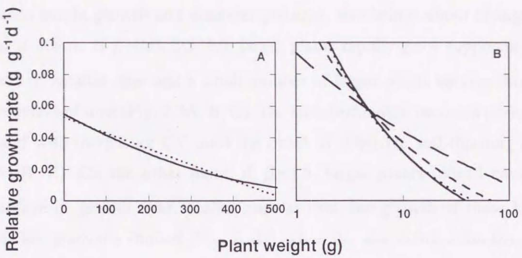

Fig. 2.2. Simulated relationships between relative growth rate (RGR) and weight of a single isolated plant. A, allometric parameter β =2.0; B, β=2.5 (— —); β=3.0 (– – –); and β=3.5 (——). Curves, ······· , represent regressions by the Richards equation [$\mathrm{RGR} = a_0 - a_1 w^m$ for β=2.0 (A, m=1.0 i.e. logistic equation) and for β=3.5 (B, m=-0.48)]. Other parameters as in Table 2.1.

Dynamics of stand structure

It is well documented that as plants grow size distribution of individual weight (or stem diameter) becomes positively skewed (e.g. Koyama and Kira, 1956; Obeid, Machin and Harper, 1967; White and Harper, 1970; Ford, 1975; Mohler, Marks and Sprugel, 1978; Hara, 1984a, b; Westoby, 1984) with increasing CV (e.g. Hara, 1986b; Weiner and Thomas, 1986; Bonan, 1988; Knox and Peet, 1989), but intensive self-thinning reduces skewness (e.g. Mohler, Marks and Sprugel, 1978; Hara, 1984a, b; Hara et al., 1990; Westoby, 1984) and CV (e.g. Kohyama and Fujita, 1981; Hara, 1986b; Weiner and Thomas, 1986; Knox and Peet, 1989) or keeps them rather constant (e.g. Hara, 1985;

Hara et al., 1990; Knox and Peet, 1989). These phenomena are well reproduced in simulations of this chapter (Figs. 2.3 and 2.4 together with Fig. 2.7).

In the model, the value of allometric parameter, β (i.e. allocation pattern between height growth and diameter growth), also brings about changes in stand structure. If β=2.0, 2.5, 3.0, larger plants rapidly grow suppresing the growth of smaller ones and a small number of larger plants survive through the progress of time (Fig. 2.3A, B, C). The size distribution becomes positively skewed with increasing CV until the onset of intensive self-thinning (Fig. 2.4A, B, C). On the other hand, if β=3.5, larger plants indeed have the advantage of growth over smaller ones at first, but growth of these larger plants are gradually limited (Fig. 2.3D). Then the size distribution becomes negatively skewed with constant CV (Fig. 2.4D). Generally, plants of 'height-growth' type (small β) tend to exhibit larger CV and skewness than those of 'diameter-growth' type (large β) (Fig. 2.4C, D).

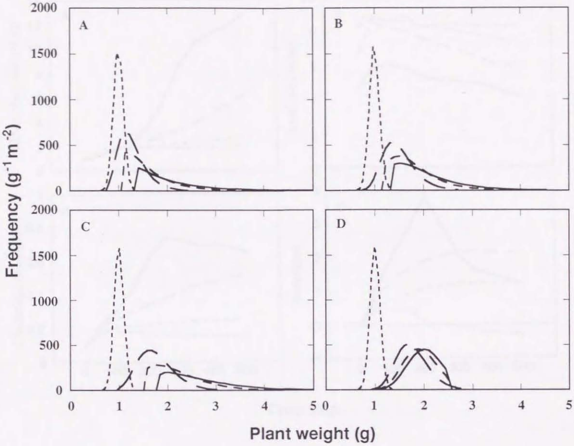

Fig.2.3. Simulated changes in size distribution, $f(t,w)$, of plant weight w at time t. In all cases, initial density is 400 (m^{-2}) with the initial normal distribution of plant weight (mean plant weight, 1.0 (g); standard deviation, 0.1). A, allometric parameter β=2.0; B, β=2.5; C, β=3.0; and D, β =3.5. Other parameters as in Table 2.1. Time steps are t=0 (········), t=50 (— —), t=100 (- - -), and t=150 (——) for β=2.0, 2.5; t=0 (·······), t=100 (— —), t=300 (- - -), and t=500 (——) for β=3.0, 3.5.

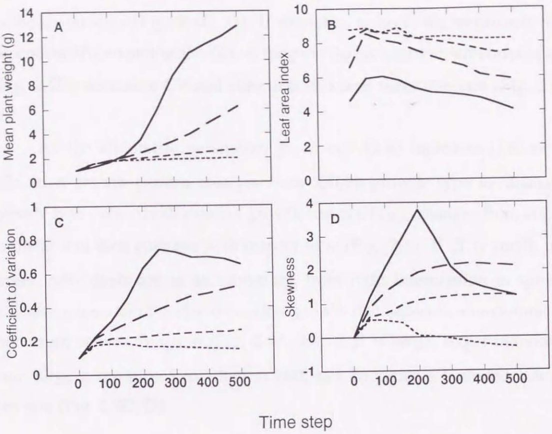

Fig.2.4. Simulated changes over time in A, mean plant weight; B, leaf area index (LAI); C, coefficient of variation (CV); and D, skewness. Allometric parameter β=2.0 (——), β=2.5 (— —), β=3.0 (- - -), and β=3.5 (........). Other parameters as in Table 2.1.

Growth of individual plants in a crowded stand

Size-dependent growth rate of individuals at each growth period, $G(t,w)$ (Fig. 2.5), explains these dynamics of stand structure (Fig. 2.4) theoretically (Hara, 1984a, b). If mortality is low, the $G(t,w)$ function is monotonically increasing convex with respect to w (Fig. 2.5A, B) and brings about increases in CV and skewness (Fig. 2.4C, D), whilst a $G(t,w)$ function that is linearly dependent on w (at the early time-step in Fig. 2.5C) brings about little changes in these statistics (Fig. 2.4C, D). If mortality is high, the negatively size-dependent $M(t,w)$ and/or the $G(t,w)$ function that is concave with respect to w (Fig. 2.5D) decreases CV and skewness or keeps them constant (Fig. 2.4C, D).

As the allometric parameter, β, in eqn (2.6) increases (i.e. as the allocation-growth pattern changes from 'height-growth' type to 'diameter-growth' type), the size-dependent growth curve, $G(t,w)$, changes from convex to linear and then concave with respect to w (Fig. 2.5). If β is small, then larger individuals are at an advantage from light interception in spite of respiration loss, and the size-dependent growth rate becomes a monotonically increasing convex function (Fig. 2.5A, B). If β is large, larger individuals have large respiration loss, then growth rate becomes a bounded concave function (Fig. 2.5C, D).

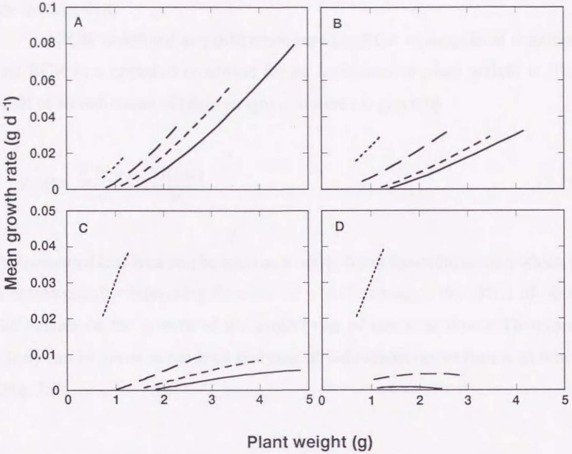

Fig. 2.5. Simulated relationships between plant weight w and mean growth rate at time t, $G(t,w)$. A, allometric parameter β=2.0; B, β =2.5; C, β=3.0; and D, β=3.5. Other parameters as in Table 2.1. Time steps are t=0 (········), t=50 (——), t=100 (– – –), and t=150 (——) for β=2.0, 2.5; t=0 (·······), t=100 (——), t=300 (– – –), and t=500 (——) for β=3.0, 3.5.

Mode of competition

The growth rate of an individual plant surrounded by larger neighbours is reduced because of their shading effect, which is generally regarded as asymmetric one-sided competition for light (e.g. Kuroiwa, 1960; Ford, 1975; Ford and Diggle, 1981; Cannell, Rothery and Ford, 1984; Hara, 1986b; Weiner and Thomas, 1986; Weiner, 1990). Therefore, relationships between RGR of an individual plant and the accumulated leaf area of other neighbouring plants are investigated.

ΔRGR is defined as a difference between RGR in an isolated condition and RGR in a crowded condition for an individual of plant weight w. The RGR of an individual of plant weight w at time t is given by

$$\mathrm{RGR} \equiv \frac{P_n^*(t,w)}{w} = \frac{G(t,w)}{w}. \tag{2.15}$$

Accumulated leaf area can be used as a competition function, $C(t,w)$, which is a monotonically decreasing function of w and expresses the effect of other individuals on the growth of the subject one of size w at time t. Therefore, $C(t,w)$ can be given as the total leaf area of individuals larger than w at time t (Fig. 2.6),

$$C(t,w) = \int_{h(w)}^{h(w_{\max})} \left\{ \int_0^{h'} f_{LA}^*(x,h')\mathrm{d}x \right\} f_H(t,h')\mathrm{d}h'. \tag{2.16}$$

We see that $C(t,w_0)$=LAI (leaf area index) and $C(t,w_{\max})$=0, where w_0 and $w_{\max}$ represent the minimum and maximum plant weights in the stand, respectively. Under completely one-sided competition, the relationship between ΔRGR and $C(t,w)$ at a given time t is given as a monotonically increasing function passing through the origin, whereas under completely symmetric two-sided competition ΔRGR is a constant irrespective of $C(t,w)$ (Hara, 1992; "two-sided competition" there means completely symmetric two-sided competition in this study). The model in this chapter shows that the mode of competition is between these two extremes, two-sided but asymmetric, even though competition was assumed to be only for light (Fig. 2.6). Moreover, it is notable that the ΔRGR-$C(t,w)$ relationship converges to a nearly-linear stationary curve as the stand develops and LAI becomes more or less constant (Figs. 2.4B and 2.6), even when size structure still changes greatly (Figs. 2.3 and 2.4). Therefore, from Fig. 2.6 we have

$$\Delta \mathrm{RGR} = c_1 C(t,w) + c_2 C(t,w_0), \tag{2.17}$$

over a wide range of stand development except for the early growing stage, where c_1 and c_2 are constants, c_1 represents a slope of the linear ΔRGR-$C(t,w)$ relationship, and $c_2C(t,w_0)$ (=c_2LAI) is the intercept on the ordinate. c_1=0 and c_2=0 represent the extremes of symmetrically two-sided and completely one-sided competition, respectively.

The slope of ΔRGR-$C(t,w)$ relationship, c_1, becomes gentler and c_2 increases as the value of β increases (Figs. 2.6 and 2.7), indicating that the asymmetry in competition decreases as the allocation-growth pattern becomes 'diameter-growth' type from 'height-growth' type. This is also supported by small CV and skewness and by the linear or concave $G(t,w)$ function of the 'diameter-growth' type with large β as compared with the 'height-growth' type with small β (Figs. 2.4 and 2.5), which are regarded as the characteristics of symmetric two-sided competition (e.g. Hara, 1986b, 1988, 1992 ; Weiner and Thomas, 1986 ; Weiner, 1990).

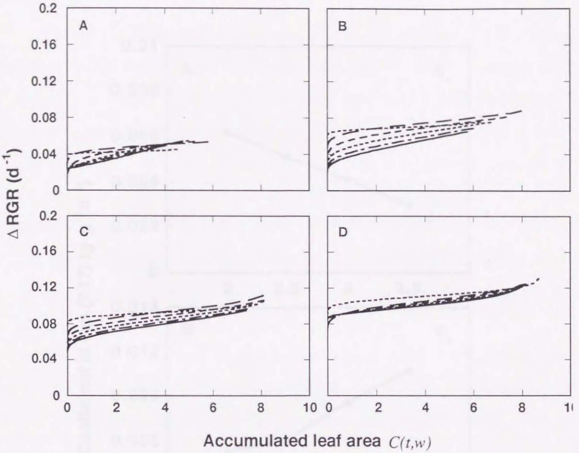

Fig. 2.6. Simulated relationships between ΔRGR and accumulated leaf area of individuals larger than plant weight w at time t, $C(t,w)$. ΔRGR denotes a difference between RGR in an isolated condition and RGR in a crowded condition for an individual of plant weight w at time t. A, allometric parameter β=2.0; B, β=2.5; C, β=3.0; and D, β=3.5. Other parameters as in Table 2.1. In all cases, time steps are t=0 (········), t=100 (— —), t=200 (– – –), t=300 (–––––), t=400 (–·–·–), and t=500 (———).

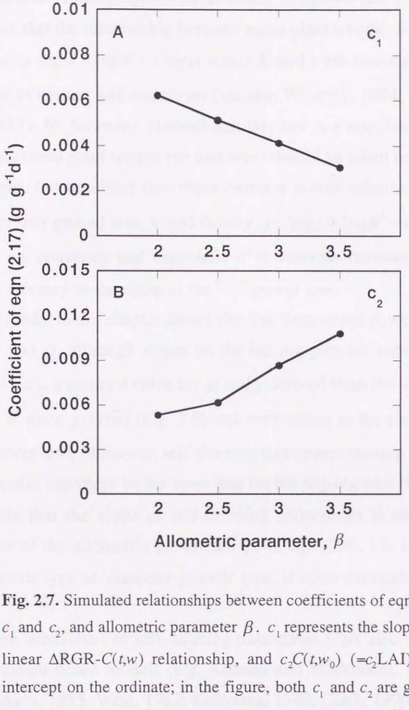

Fig. 2.7. Simulated relationships between coefficients of eqn (2.17), c_1 and c_2, and allometric parameter β. c_1 represents the slope of the linear ΔRGR-$C(t,w)$ relationship, and $c_2C(t,w_0)$ (=c_2LAI) is the intercept on the ordinate; in the figure, both c_1 and c_2 are given as an average between time steps t=300 and t=500. A, coefficient c_1; B, coefficient c_2. Other parameters as in Table 2.1.

Self-thinning rule

Yoda et al. (1963) proposed the so-called '-3/2 power law of self-thinning', which states that the relationship between mean plant weight, $\overline{w}$, and density, ρ, is given as $\log\overline{w} = \log K + c\log\rho$ where K and c are constants and $c \approx -3/2$ irrespective of species and conditions (see also Westoby, 1984; White, 1981). Weller (1987a, b), however, claimed that this law is a statistical artifact and that biomass (total plant weight per unit area) should be taken instead of mean plant weight, but admitted that there exists a power relationship between biomass per unit ground area, y, and density, ρ: $\log y = \log K' + c'\log\rho$, where K' and c' are constants and especially c' is variable between species and conditions contrary to the claim of the '-3/2 power law'.

The model in this chapter shows also that there exists power relationships between y and ρ, although slopes on the log-log plot are somewhat greater than -1/2 (-1/2 is a claimed value for ρ and y derived from the -3/2 power law for ρ and $\overline{w}$ since $y = \rho\overline{w}$) (Fig. 2.8), not conforming to the claimed value of the '-3/2 power law'. Moreover, self-thinning trajectories starting from different initial densities converge to the same line on the log-log plot (Fig. 2.8). It is also notable that the slope of self-thinning trajectories is nearly constant irrespective of the allometric parameter, β, in eqn (2.6), i.e. irrespective of 'height-growth' type or 'diameter-growth' type, if other parameters remain the same.

These behaviours of self-thinning trajectories were also reproduced by other individual-based models (e.g. Aikman and Watkinson, 1980; Firbank and Watkinson, 1985; West, 1987; Kohyama, 1989; Clark, 1990; Prentice and Leemans, 1990). Especially Prentice and Leemans' result (their Fig. 4) resembles the Fig. 2.8, that is, little increase in biomass per unit ground area during the course of intensive self-thinning, which also agrees to a statistical finding by Weller (1987a).

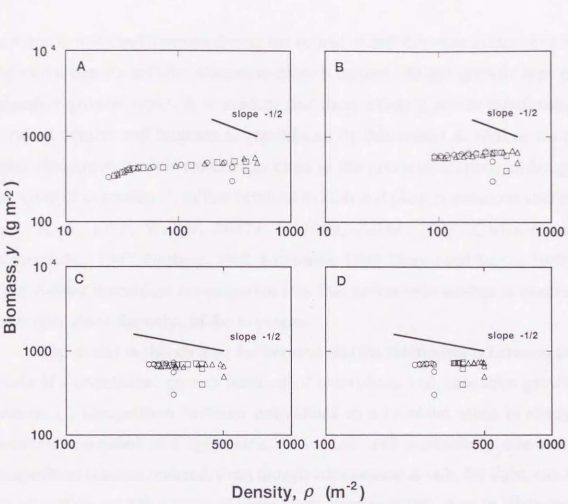

Fig. 2.8. Simulated developments of biomass per unit ground area, y, and density, ρ, at 50 time-step intervals until t=500 in stands starting from initial densities, 300 (○), 400 (□) and 500 (△) (m^{-2}). The solid line has a slope of -1/2 on a log-log plot. A, allometric parameter β=2.0; B, β=2.5; C, β=3.0; and D, β=3.5. Other parameters as in Table 2.1.

2.4 Discussion

Growth pattern and the mode of competition

The theoretical model in this chapter can reproduce several well-documented phenomena in plant population ecology except for the effects of spatial distribution on the growth dynamics: (1) correspondence between the dynamics of size structure and the $G(t,x)$ and $M(t,x)$ functions; (2) a power relationship between density and biomass during the course of self-thinning irrespective of the initial density and the allocation-growth pattern ('height-growth' type or 'diameter-growth' type). It is evident that there exists a power relationship between density and biomass as reproduced by this model as well as many other simulation models (references cited in the previous section), although the value of exponent, c', differs between models and plant populations studied (e.g. Hara, 1985; Weller, 1987a, b, 1989; Zeide, 1987; Carleton and Wannamaker, 1987; Norberg, 1988; Kikuzawa, 1988; Osawa and Sugita, 1989). Thus further theoretical investigation into this power relationship is needed, especially about the value of the exponent.

The model in this chapter further revealed the relationships between the mode of competition, growth function of individuals and allocation-growth pattern: (i) competition between individuals in a crowded stand is always between one-sided and symmetric two-sided, and completely one-sided competition is never realised, even though competition is only for light; (ii) as the allocation-growth pattern changes from 'height-growth' type to 'diameter-growth' type, the mode of competition changes from a highly asymmetrical to more symmetrical, with the $G(t,w)$ function changing from convex to linear and then concave with respect to w and also with decreasing size variability in terms of CV and skewness. Therefore, it should be noted that plants of 'diameter-growth' type tend to exhibit a two-sided competition effect that is close to symmetric, even though competition is only for light, suggesting that *competition for light is not always one-sided as hypothesized so far* (e.g. review by Weiner, 1990).

The above-stated theoretical result (i) is supported by Thomas and Weiner (1989) who demonstrated, using an *a priori* competition-growth model, that competition in *Ambrosia artemisiifolia* and *Pinus rigida* populations was between one-sided and symmetric two-sided. However, their model showed the best fit (the highest r^2 value) of completely one-sided competition in

Impatiens pallida (r^2=0.44, P<0.01), but the 70~90% proportions of one-sided competition were also significant at P<0.01 (r^2=0.39~0.42) and even completely symmetric two-sided competition was still significant at P<0.05 (r^2=0.26). Therefore, their results do not necessarily demonstrate complete one-sidedness of competition in *Impatiens pallida*, because a slight change of the empirical model may bring about a different result.

Plants of 'height-growth' type are regarded as early-successional shade-intolerant species, whilst plants of 'diameter-growth' type are regarded as late-successional shade-tolerant species (Hara, Kimura and Kikuzawa, 1991). Although direct comparison between shade-tolerance and shade-intolerance, which are expressed in terms of the photosynthetic and respiration parameters in the model, was not performed in this chapter, the theoretical result (ii) conforms to the findings by Hara et al. (1991; "two-sided competition" there means completely symmetric two-sided competition in this study) that diameter growth of *Abies veitchii* and *A. mariesii* (species of 'diameter-growth' type) is less affected by one-sided competition than is diameter growth of *Betula ermanii* (a species of 'height-growth' type); dynamics of diameter growth are parallel to those of weight growth rather than to those of height growth (e.g. Hara, 1984a, b).

It should be noted that 'one-sided competition' and 'symmetric two-sided competition' are an *a priori* conception and the two extremes that are never realised in the real world; the mode of competition in nature is always in between: two-sided but asymmetric. The mode of competition as well as the stand structure is not the cause but the consequence of growth and allocation dynamics based on the canopy photosynthetic process. In this respect, I agree with Bonan (1988, 1991) that the study of size hierarchies should be shifted away from considerations of one-sided versus two-sided competition as an *a priori* starting point and toward a direct understanding of the consequences of neighbourhood competition. But I still believe that the mode of competition is a useful conception and should play an important role in looking at the growth dynamics in the real world, as shown in this chapter.

Growth of individuals and competition function

From eqns (2.14) and (2.17), I propose the following equation as the general $G(t,w)$ function for individuals in a crowded stand, which covers a wide range of stand development, allocation-growth pattern and the mode of competition:

$$G(t,w) = w\{a_0 - a_1 w^m - c_1 C(t,w) - c_2 C(t,w_0)\}, \tag{2.18}$$

where a_0, a_1, m, c_1 and c_2 are positive constants. Here m decreases from 1 and c_1 approaches 0 as the allocation-growth pattern changes from 'height-growth' type to 'diameter-growth' type [i.e. as β increases in eqn (2.6)].

An empirical finding by Kohyama (1989, 1991) is a special case of eqn (2.18). He obtained

$$G(t,x) = x\{a - a_1 \ln x - a_2 B(t,x)\}, \tag{2.19}$$

for trees of mixed species in a warm-temperate rain forest which can be assumed to be at a stationary state as a climax forest. Here x represents dbh (stem diameter at breast height). $B(t,x)$ was defined as

$$B(t,x) = \int_x^{x_{\max}} z^k f(t,z)\mathrm{d}z, \tag{2.20}$$

where k is a positive constant, $f(t,z)$ is the distribution density function of dbh z at time t, and $x_{\max}$ is the maximum dbh. Leaf area of an individual competing tree of dbh z is assumed to be proportional to z^k in an allometric relationship.

Therefore, $B(t,x)$ is proportional to total leaf area of individual trees larger than the tree of dbh x at time t. According to the pipe model theory (Shinozaki et al., 1964a, b), leaf area is proportional to basal area, i.e. $k=2$ in eqn (2.20), which was also assumed in Kohyama's simulations (1989, 1991). Therefore, Kohyama's $B(t,x)$ is a simplified functional form but a good approximation of the $C(t,x)$ function given by eqn (2.16). Kohyama (1989, 1991) empirically assumed the Gompertz growth curve for a single isolated tree, which is also supported by the theoretical result in this chapter (Fig. 2.2B). His assumption of completely one-sided competition, however, will bring about overestimation for growth of large-sized trees.

Benjamin (1988) proposed an empirical single equation for weight growth of individual plants in monocultures. Benjamin's model [his eqn (3)] can be described in terms of the $G(t,w)$ function as follows:

$$G(t,w) = rw\left\{1 + Kn\ln\left[\frac{w}{\bar{w}}\right]\right\}\left(1 - \frac{w}{\bar{w}}\right)\left(1 - \frac{\bar{Y}}{Y}\right), \tag{2.21}$$

where r, K, W ($w<W$) and Y are positive constants, n is density ($=\rho(t)$) given as eqn (2.2) in the model of this chapter, a time-invariant constant if mortality is zero, $\bar{w}$ is the mean of w, and y is biomass per unit ground area ($= n\bar{w} < Y$). Let $B_k(t,w) \equiv B(t,w)$ to express the exponent k explicitly in eqn (2.20). Then define the competition function, $C(t,w)$, as

$$C(t,w) \equiv \ln\left[\frac{B_1(t,w_0)}{nw}\right], \tag{2.22}$$

where w_0 is the minimum weight in the stand and $B_1(t,w_0)/n$ represents the mean plant weight, $\bar{w}$, by definition. Then Benjamin's model, eqn (2.21), can be rewritten as

$$G(t,w)=\left\{rw\left(1-\frac{w}{\overline{w}}\right)\right\}\left\{1-d_1C(t,w)\right\}\left\{1-d_2\exp\left[C(t,w_0)\right]\right\}, \tag{2.23}$$

where $d_1=Kn$ and $d_2=nw_0/Y$. The first term expresses the logistic growth equation for a single isolated individual. The second and third terms express effects of one-sided and symmetric two-sided competition, respectively.

The effects of one-sided and symmetric two-sided competition is multiplicative in eqn (2.23), whilst those in the model of this chapter, eqn (2.18), are additive. This is a major structural difference in these two models, but both models can describe all the possible mode of competition. Which model is appropriate and what is the best function form for $C(t,x)$ are determined only by the agreement between observed and predicted results. However, there may be little difference between the additive and multiplicative representations if reduction in growth are small: the cross-terms generated in an expansion of the multiplicative form would be of second order in magnitude. Significant differences would only appear between the two representations if two or more sources of limitation are simultaneously large in effect. The function form of $G(t,x)$ given by eqn (2.18), which is not an *a priori* function but derived from the canopy-photosynthetic process, is realistic, although simple, and Kohyama's $B(t,x)$, eqn (2.19), can be used as a simple and good approximation for the competition function $C(t,x)$. Therefore, the $G(t,x)$ function given by eqn (2.18) can be used for further investigations of the dynamics of growth and competition in plant populations.

The $D(t,x)$ function in the diffusion model (Hara, 1984a) represents variance in growth rate of individuals of size x at time t, and describes environmental heterogeneity, genetical variation, variation in the neighbourhood effects (*i.e.* spatial distribution of individuals), etc. The present model in this chapter cannot describe these effects on the growth dynamics, because the present model is non-spatial and deals with only averaged size-dependence of individual growth expressed by $G(t,x)$ and $D(t,x)=0$. However, assuming that eqn (2.1) describes a local phenomenon, we can investigate the effects of variation in terms of $D(t,x)$ by integrating these local phenomena with varying parameter values.

The present model assumes an *a priori* allometric relationship between plant height and weight. But such a relationship should be also derived from a basic model. To do so, the two-dimensional (plant height and stem diameter) diffusion model (Hara et al., 1990, 1991) should be employed. This will be dealt with in Chapter 4.

Chapter 3
Effects of physiological and environmental variations on size-structure dynamics in plant populations

In Chapter 2, a dynamic canopy photosynthesis model was developed for the growth of individual plants in a stand based on a continuity equation model for investigating mechanisms of size-structure dynamics in relation to allocation-growth patterns. The objective of this chapter is to evaluate, based on the canopy photosynthesis and continuity equation models, the effects of variation in physiological parameters on the size-structure dynamics in relation to the degree of asymmetry in competition or the allocation-growth pattern. Then effects of temporal and spatial variations of the environments on the dynamics of plant communities are evaluated, and mechanisms of species coexistence are discussed.

3.1 Simulation method

Details of the canopy photosynthesis and continuity equation models have been given in Chapter 2. Here, two different forms of vertical distribution of leaf area density of an individual of plant height h at height x from ground, $f_{LA}^{*}(t,x,h)$, are examined: a trianglular form as used in Chapter 2,

$$\begin{aligned} f_{LA}^{*}(t,x,h) &= \theta(h-x), && (p_n^{*}(t,x,h) \geq 0); && (3.1\text{a}) \\ &= 0, && (p_n^{*}(t,x,h) < 0); && (3.1\text{b}) \end{aligned}$$

and a rectangular form,

$$\begin{aligned} f_{LA}^{*}(t,x,h) &= \theta h, && (p_n^{*}(t,x,h) \geq 0); && (3.2\text{a}) \\ &= 0, && (p_n^{*}(t,x,h) < 0); && (3.2\text{b}) \end{aligned}$$

where θ is a constant parameter which determines the shape of the crown and $p_n^{*}(t,x,h)$ is daily net photosynthetic rate per unit leaf area at height x from ground for an individual of plant height h in the stand at day t, given as the integral over a day of the instantaneous photosynthetic rate.

In Chapter 2, simulations of size-structure dynamics were conducted by changing the value of the allometric exponent β in eqn (2.6) (from 2.0 to 3.5 in steps of 0.5) with fixed values of other physiological parameters. In this chapter, simulations are conducted for two fixed values of β, 2 and 3, and changed other parameter values; photosynthetic parameters (a and b), respiration rate per unit leaf area (r_f), maintenance respiration rate per unit weight (r_m), growth respiration rate per unit weight (r_g), extinction coefficient of the canopy (k), canopy shape parameter (θ) and the other allometric parameter (α), for initial stand densities of 200, 300, 400, 500 and 600 (m^{-2}) (Table 3.1). When changing one parameter value, other parameter values were fixed at the 'standard values' given in Table 3.1, which were also used in Chapter 2. A normal distribution with a mean plant weight 1.0 g and a standard deviation 0.1 was used as the initial size distribution of plant weight at t=0 d for each simulation set as in Chapter 2, and the simulations were conducted over the time interval from 0 to 400 d.

Table 3.1. *Parameter values used in simulations in Chapter 3*
When changing one parameter out of I~IX, other parameters are fixed at the standard values given in bolds.

Conversion factor (fixed)
u=0.65 ($g_{dwt}g_{CO_2}^{-1}$)

Irradiance incident on the canopy at midday (fixed)
I_0=250 (Wm^{-2})

Daylength (fixed)
T_d=14 (hour)

Specific leaf area (fixed)
s=0.02 (m^2g^{-1})

I. Variation in photosynthetic parameter: a ($W^{-1}m^2$)
for fixed b=0.050 ($g_{CO_2}W^{-1}h^{-1}$)
(b/a in parentheses)

0.025	0.017	0.013	**0.010**	0.008	0.007	0.006
(2.0)	(2.9)	(3.8)	(**5.0**)	(6.3)	(7.1)	(8.3)

II. Variation in photosynthetic parameter: b ($g_{CO_2}W^{-1}h^{-1}$)
for fixed a=0.010 ($W^{-1}m^2$)
(b/a in parentheses)

0.020	0.030	0.040	**0.050**	0.060	0.070	0.080
(2.0)	(3.0)	(4.0)	(**5.0**)	(6.0)	(7.0)	(8.0)

III. Variation in leaf respiration rate: r_f ($g_{CO_2}m^{-2}d^{-1}$)

0.03	0.04	**0.06**	0.10	0.30	0.60	1.00

IV. Variation in maintenance respiration rate: r_m ($gg^{-1}d^{-1}$)

0.020	0.030	**0.050**	0.055	0.060	0.065

V. Variation in light extinction coefficient: k

0.4	0.6	**0.7**	0.8	0.9	1.0

VI. Variation in growth respiration rate: r_g (gg^{-1})

0.10	0.20	0.25	**0.30**	0.35	0.40	0.50

VII. Variation in canopy shape parameter: θ ($\times 10^{-3}m^2m^{-2}$)

0.8	0.9	**1.0**	1.1	1.2

VIII. Variation in allometric parameter: α

3.2	4.0	**4.2**	4.4	5.2	6.2	($\times 10^0 gm^{-2}$) for β=2.0
2.7	3.5	**3.7**	3.9	4.7	5.7	($\times 10^2 gm^{-3}$) for β=3.0

IX. Variation in initial stand density: $\rho(0)$

200	300	**400**	500	600	(m^{-2})

3.2 Simulation results

In Chapter 2, it was shown by simulation that asymmetry in competition decreases as β increases (i.e. as the allocation-growth pattern shifts from 'height-growth' to 'diameter-growth'). In this chapter, I investigate by simulation the effects of variation in the above parameters on the size-structure dynamics for two cases: β=2 ('height-growth' type, thus more asymmetric competition) and β=3 ('diameter-growth' type, thus less asymmetric competition). There was little difference in the qualitative trends among initial stand densities and also between the triangular and rectangular forms of $f^*_{LA}(t,x,h)$ [eqns (3.1) and (3.2)]. Therefore, only the results for a stand density of 400 (m^{-2}) and a triangular form of $f^*_{LA}(t,x,h)$ [eqn (3.1)] are shown here.

Effects of variation in photosynthetic rate

Variations in a and b both gave almost the same results, and only the results for variation in a with a constant b are shown (Fig. 3.1). The mean, coefficient of variation (CV) and skewness of plant weight for different values of maximal photosynthetic rate per unit leaf area at infinity light intensity, b/a, eventually converge with time for β=2 (Fig. 3.1A, C, E), whilst those for β=3 diverge with time (Fig. 3.1B, D, F). Time lag in the convergence is only the difference between the varied parameter values for β=2. These results indicate that effects of variation in maximal photosynthetic rate per unit leaf area on the size-structure dynamics become more apparent with an increasing β.

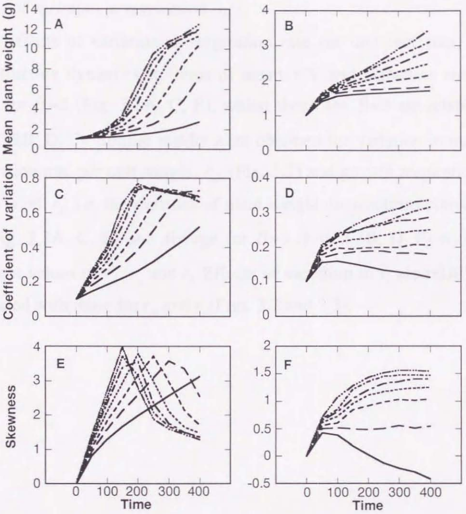

Fig. 3.1. Changes in: A, B, mean; C, D, coefficient of variation (CV); and E, F, skewness of plant weight for variations in *b*/*a* [maximal photosynthetic rate per unit leaf area at infinity light intensity in eqn (2.10)]. *b*/*a*=2.0 (——), 2.9 (— —), 3.8 (- - -), 5.0 (·······), 6.3 (-·—·), 7.1 (--·-), 8.3 (---·--). Fixed values of other parameters are given in Table 3.1. A, C, E, Allometric parameter [eqn (2.6)] β=2; B, D, F, β=3.

Effects of variation in respiration rate

Effects of variation in respiration rate per unit leaf area, r_f, on the size-structure dynamics in terms of mean, CV and skewness are relatively small for β=2 (Fig. 3.2A, C, E), whilst those for β=3 are relatively large (Fig. 3.2B, D, F). Similar results were obtained for variation in maintenance respiration rate per unit weight, r_m, (Fig. 3.3) and growth respiration rate per unit weight, r_g: i.e. the statistics of plant weight distributions converge for β =2 (Fig. 3.3A, C, E) and diverge for β=3 (Fig. 3.3B, D, F) with time for different values of r_m, r_g and r_f. Effects of variation in r_f are relatively small compared with those for r_m and r_g (Figs. 3.2 and 3.3).

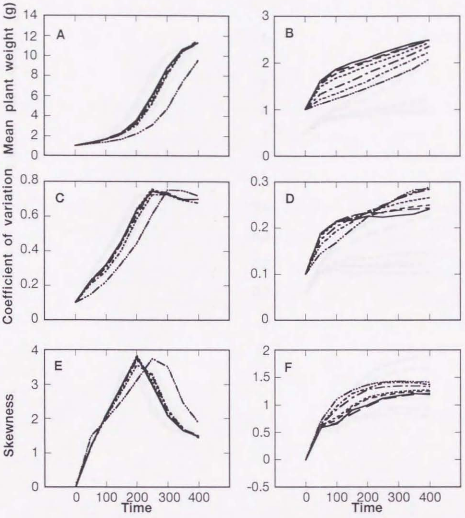

Fig. 3.2. Changes in: A, B, mean; C, D, coefficient of variation (CV); and E, F, skewness of plant weight for variations in r_f [respiration rate per unit leaf area in eqn (2.10)]. r_f=0.03 (——), 0.04 (— —), 0.06 (– – –), 0.1 (········), 0.3 (–·—·), 0.6 (–·–··), 1.0 (···–··). Fixed values of other parameters are given in Table 3.1. A, C, E, Allometric parameter [eqn (2.6)] β=2; B, D, F, β=3.

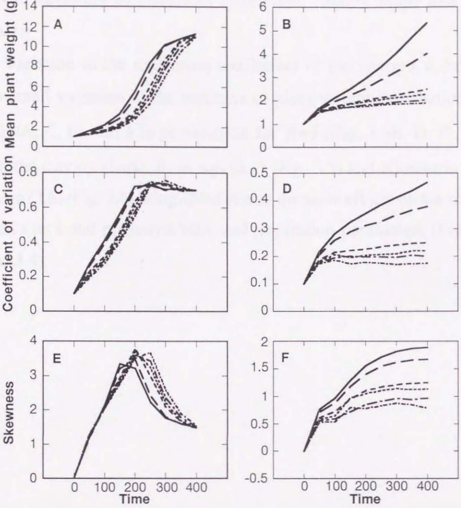

Fig. 3.3. Changes in: A, B, mean; C, D, coefficient of variation (CV); and E, F, skewness of plant weight for variations in r_m [maintenance respiration rate in eqn (2.11)]. r_m=0.02 (——), 0.03 (— —), 0.05 (- - -), 0.055 (·······), 0.06 (-- — --), 0.065 (—-—). Fixed values of other parameters are given in Table 3.1. A, C, E, Allometric parameter [eqn (2.11)] β=2; B, D, F, β=3.

Effects of variation in extinction coefficient, canopy shape and allometric parameter

Variation in the extinction coefficient of the canopy, *k*, brings about only a small variation in the statistics of plant weight distributions for β=2 (Fig. 3.4A, C, E), but a large variation for β=3 (Fig. 3.4B, D, F). Variations in both the canopy shape, θ, in eqn (3.1) (Fig. 3.5) and allometric parameter, α, in eqn (2.6) (Fig. 3.6) bring about almost the same effects on the size-structure dynamics as *k* and photosynthetic and respiration parameters (Figs. 3.1, 3.2, 3.3 and 3.4).

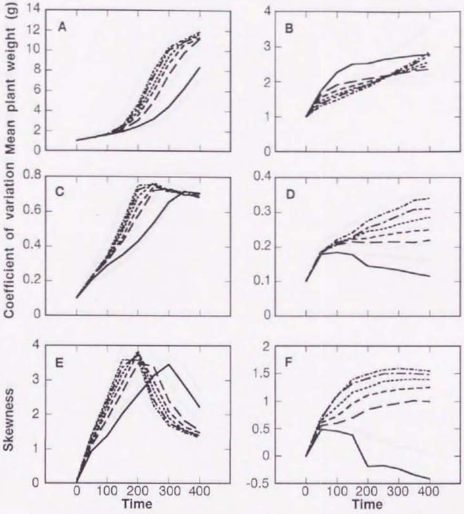

Fig. 3.4. Changes in: A, B, mean; C, D, coefficient of variation (CV); and E, F, skewness of plant weight for variations in k [light extinction coefficient in eqns (2.9) and (2.10)]. k=0.4 (——), 0.6 (— —), 0.7 (– – –), 0.8 (·······), 0.9 (-·—), 1.0 (-·-·-). Fixed values of other parameters are given in Table 3.1. A, C, E, Allometric parameter [eqn (2.6)] β=2; B, D, F, β=3.

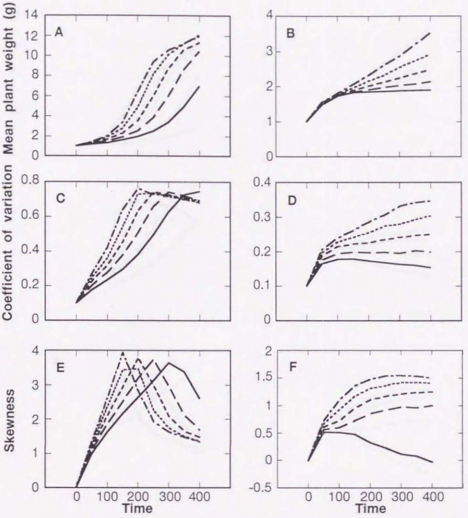

Fig. 3.5. Changes in: A, B, mean; C, D, coefficient of variation (CV); and E, F, skewness of plant weight for variations in θ [canopy shape parameter in eqns (3.1) and (3.2)]. θ=0.8 (——), 0.9 (— —), 1.0 (– – –), 1.1 (·······), 1.2 (–·—·). Fixed values of other parameters are given in Table 3.1. A, C, E, Allometric parameter [eqn (2.6)] β=2; B, D, F, β=3.

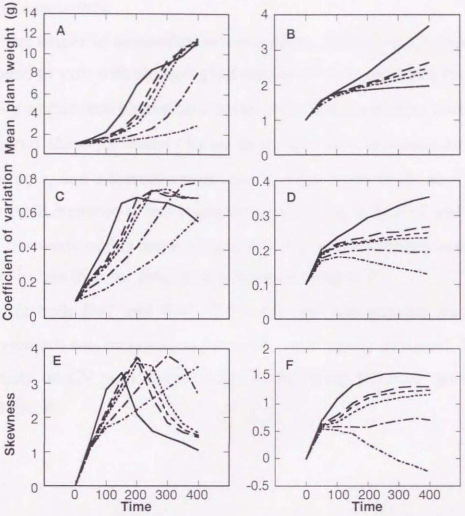

Fig. 3.6. Changes in: A, B, mean; C, D, coefficient of variation (CV); and E, F, skewness of plant weight for variations in α [allometric parameter in eqns (2.6) and (2.11)]. A, C, E, α=3.2 (——), 4.0 (— —), 4.2 (- - -), 4.4 (········), 5.2 (-·—·), 6.2 (-·-—·-·); B, D, F, α=2.7 (——), 3.5 (— —), 3.7 (- - -), 3.9 (········), 4.7 (-·—·), 5.7 (-·-—·-·), $\times 10^2$. Fixed values of other parameters are given in Table 3.1. A, C, E, Allometric parameter [eqn (2.6)] β=2; B, D, F, β=3.

Mode of competition

The degree of asymmetry in competition, defined as c_1/c_2 in eqn (2.17), was found to vary with physiological parameters: c_1/c_2 increases for both β=2 and β=3 as maximal photosynthetic rate (b/a), light extinction coefficient (k), and canopy shape parameter (θ) are increased, but it decreases for β=3 with increasing r_m and allometric parameter α (Fig. 3.7A, C, D, E, F). There is only a small response to leaf respiration rate (r_f) for both β=2 and β=3 (Fig. 3.7B). It is worth noting that in all graphs in Fig. 3.7, asymmetry in competition for β=3 is less than for β=2, as was found in Chapter 2.

For both β=2 and β=3, CV during the late growing stage (around t=300 onward) was increased as the initial stand density increased. The effects of density on CV were rather complicated during the early growing stage (Fig. 3.8A, B).

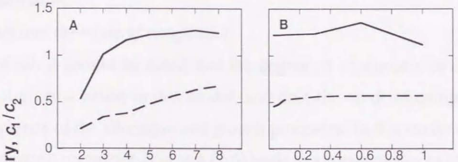

Fig. 3.7. Changes in the degree of asymmetry in competition defined as c_1/c_2 in eqn (2.17) with variations in: A, b/a [maximal photosynthetic rate per unit leaf area at infinity light intensity in eqn (2.10)]; B, r_f [respiration rate per unit leaf area in eqn (2.10)]; C, r_m [maintenance respiration rate in eqn (2.10)]; D, k [light extinction coefficient in eqns (2.9) and (2.10)]; E, θ [canopy shape parameter in eqn (3.1)]; and F, α [allometric parameter in eqns (2.6) and (2.11)]. c_1/c_2 is 0 for completely symmetric two-sided competition and $+\infty$ for completely asymmetric one-sided competition. Fixed values of other parameters for each case are given in Table 3.1. Allometric parameter [eqn (2.6)] β=2 (——) and β=3 (— —). F, α is $\times 10^0$ for β=2 and $\times 10^2$ for β=3.

3.3 Discussion

Stability and the mode of competition

First of all, it should be noted that the degree of asymmetry in competition was not given *a priori* in this model, and thus the mode of competition is a consequence of the allocation and growth processes. In this study, variation in the allometric parameter β in eqn (2.6) leads to various modes of competition. Therefore, the discussion made in this chapter is primarily based on the allometry and the allocation and growth processes, but not on the *a priori* mode of competition *per se*.

The results in Figs. 3.1 - 3.5 and 3.6 show that size-structure dynamics as $t \rightarrow \infty$ for β=2 (more asymmetric competition) are little affected by changing physiological parameters, whilst size-structure dynamics for β=3 (less asymmetric competition) show a divergent response. Therefore, a plant population undergoing strongly asymmetric competition is not so sensitive to fluctuations in environmental conditions which generate variations in physiological parameters, i.e. a stable system, whereas a plant population undergoing symmetric competition is highly sensitive to those fluctuations. Kohyama (1991) and Hara (1992) both showed that variation in recruitment rate (number of seedlings which enter the population per unit time) at time t, $R(t)$, affects only a little the shape of the stationary size distribution under one-sided competition (most asymmetric competition), whilst that under symmetric two-sided competition is greatly affected. These results were obtained by simulation (Kohyama ,1991) and theoretically (Hara, 1992), based on the continuity equation model with empirical functions obtained from rain forests (these empirical functions were also reproduced by the simulation model of Chapter 2).

In summary, a single-species plant population undergoing one-sided or strongly asymmetric competition, which is brought about by a small β around 2, is a stable system, little affected by variation in physiological parameters and in recruitment rate. A population undergoing symmetric competition, which is brought about by a large β around 3, is an unstable system with respect to variation in these parameters. It follows that growth and size-structure dynamics should be similar among different species with different physiological parameter values if these species have small β near 2 but that these should be different among different species if these species have large β near 3.

It is difficult to interprete these simulation results theoretically based on original model of Chapter 2. Based on approximate eqns (2.15), (2.16) and (2.17), only an intuitive explanation of the difference in sensitivity between one-sided competition and symmetric two-sided competition can be given by employing the same logic used by Hara (1992). Because $C(t,w)$ is a decreasing function of w, the effect of c_1 (one-sided competition) on ΔRGR in eqn (2.17) diminishes as w increases, and vanishes at $w=w_{\max}$ [i.e. $c_1C(t,w_{\max})=0$]. But the effect of c_2 (symmetric two-sided competition) remains the same over the whole range of w in eqn (2.17) (i.e. $c_2C(t,w_0)$=constant irrespective of w), suggesting that the effect of symmetric two-sided competition is relatively large *as a whole* compared with that of one-sided competition. Therefore, because variation in physiological parameters changes c_1 and c_2, symmetric two-sided competition is more likely to affect ΔRGR, then $G(t,w)$ and hence size-structure dynamics through a change in c_2 than one-sided competition is through a change in c_1 (Hara, 1992). The magnitude of the allometric parameter β determines the way how variation in physiological parameters affects the mode of competition and the size-structure dynamics. These processes are associated with the balance between respiration and photosynthesis of an individual. When β is large, cost due to maintenance respiration is relatively large for large individuals, generating a linear or concave $G(t,w)$ function which is associated with symmetric two-sided competition. When β is small, cost due to maintenance respiration is relatively small for large individuals, generating a convex $G(t,w)$ function which is associated with asymmetric or one-sided competition.

Nutrient conditions and the mode of competition

For a given species, nitrogen concentration per unit leaf area or leaf weight, which depends on the nutrient level in the soil, is positively correlated with the maximal photosynthetic rate per unit leaf area at infinity light intensity, b/a (e.g. Nátr, 1975; Van Keulen and Seligman, 1987; Hirose and Werger, 1987). Therefore, by considering effects of variation in b/a, some inferences can be made on the effects of nutrient conditions in the soil on the mode of competition although no direct root competition was incorporated in the model but only a competition for light was dealt. In this model, variation of nutrient conditions and root competition for nutrients in the soil are reflected in the variation of b/a. Because the degree of asymmetry in competition (for light) decreases with decreasing b/a for both $\beta=2$ and $\beta=3$ (Fig. 3.7A), the reduced nutrient level, which leads to a decrease in b/a, brings about less asymmetric competition for light. Then, considering both competition for light and root competition as a whole, competition becomes symmetric two-sided under low-nutrient conditions because root competition is regarded as symmetric two-sided in most cases (e.g. see Weiner and Thomas, 1986; Weiner, 1990). This theoretical result conforms to the findings of Morris and Myerscough (1991) that the reduced nutrient level in the soil brought about higher β and more intense root competition (hence symmetric two-sided competition).

Hirose (1987, 1988a, b) proposed a model of plant growth as a function of nitrogen concentration in each organ of an individual for a single 'average' plant of a particular species. Therefore, dynamics at the population level were not considered in his model. Using a growth model, Hirose et al. (1989) showed that the relative growth rate (RGR) of two *Carex* species is more sensitive to proportional changes in photosynthetic nitrogen use efficiency than to changes in respiration coefficients. This is consistent with the above result that the effect of variation in leaf respiration rate on the size-structure dynamics is relatvely small (Fig. 3.2) as compared with that due to variation in photosynthetic parameters (Fig. 3.1).

Allometry and the mode of competition

In these simulations, CV during the later growing stage increased as initial stand density was increased for both β=2 (strongly asymmetric competition) and β=3 (near-symmetric competition) (Fig. 3.8). This is in accordance with the results of Bonan's (1991) spatial simulation model that the increase in CV with density is not direct evidence for asymmetric one-sided competition. But it should be noted that the canopy photosynthesis model in this chapter generates neither completely asymmetric one-sided competition nor completely symmetric two-sided competition (these two were assumed *a priori* in Bonan's (1991) model). Competition here is always a combination of the two extremes.

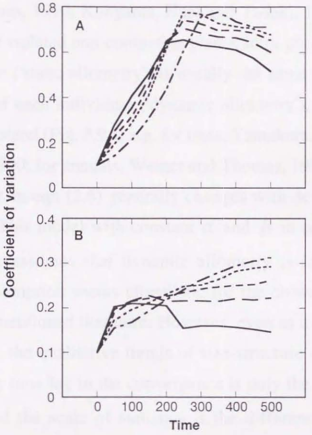

Fig. 3.8. Changes in coefficient of variation (CV) over time for different initial stand densities (m^{-2}): 200 (——), 300 (— —), 400 (- - -), 500 (……), 600 (- — -). A, Allometric parameter [eqn (2.6)] β=2; B, β=3. Fixed values of other parameters are given in Table 3.1.

Growth form or allometry is closely associated with the mode of competition in plant populations (Morris and Myerscough, 1985, 1987, 1991; Ellison and Rabinowitz, 1989; Geber, 1989; Thomas and Weiner, 1989; Weiner, Berntson and Thomas, 1990; Kohyama, Hara and Tadaki, 1990; Weiner and Thomas, 1992). For isolated non-competing plants, intra-population allometry at one point in time ('static allometry') is usually the same as the allometric growth trajectory of each individual ('dynamic allometry'), whilst these two differ in a crowded stand (Fig. 3.9A; e.g. for trees, Yamakura, 1985; Kohyama, Hara and Tadaki, 1990; for annuals, Weiner and Thomas, 1992). Moreover, in a crowded stand, α in eqn (2.6) generally changes with development of the stand (Fig. 3.9A). This model with constant α and β in eqn (2.6) over the stand development assumes that dynamic allometry is identical to static allometry. This assumption seems unrealistic for the crowded stands in the light of the above-mentioned literature. However, even as a changes over the stand development, the qualitative trends of size-structure dynamics remain the same (Fig. 3.6); time lag in the convergence is only the difference for β =2 (Fig. 3.6A), and the scale of statistics is the difference for β=3 (Fig. 3.6B).

Instead of a simple allometry given by eqn (2.6), curvilinear allometries on a log-log scale are often found between stem diameter and plant height and between plant height and plant weight in the crowded stands (Fig. 3.9B; e.g. Ogawa and Kira, 1977; Hara, 1986a; Kohyama, Hara and Tadaki, 1990; Weiner and Thomas, 1992). Roughly speaking, such a curvilinear allometry between plant height and plant weight can be regarded as consisting of two simple allometries: smaller α and larger β for larger individuals and larger α and smaller β for smaller individuals [Fig. 3.9B; e.g. see Figs. 1, 2 and 4 of Weiner and Thomas (1992)]. This suggests that such a plant stand may be regarded as consisting of two subpopulations: less asymmetrically competing large individuals and more asymmetrically competing small individuals.

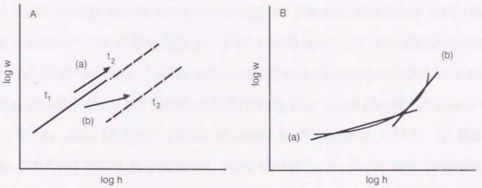

Fig. 3.9. A, If the allometric relationship between plant height, h, and plant weight, w, is given by $w = \alpha h^{\beta}$ with constant parameters, α and β [eqn (2.6)], intra-population allometry at one point in time ('static allometry' at time t_1 or t_2) is identical to the allometric growth trajectory of each individual along the arrow ('dynamic allometry') marked (a). If a changes with the stand development, static allometry at each point in time (t_1 and t_2) develops along the arrow marked (b) and is different from the dynamic allometry. In both cases, each plant grows in the direction of the arrow from time t_1 to t_2. B, curvilinear static allometry between h and w on a log-log scale is often found in crowded plant stands, where allometry can be approximated by two lines with different α and β values: (a) larger α and smaller β for smaller individuals and (b) smaller α and larger β for larger individuals.

Morris and Myerscough (1984) described two types of competition: 'altered-form competition' as a lowering of the self-thinning line (biomass-density trajectory on a log-log plot) in lower-nutrient stands (Furnas, 1981; Morris and Myerscough, 1985) and 'altered-speed competition' as a trajectory following substantially the same self-thinning line more slowly in lower-nutrient stands (White and Harper, 1970; Bazzaz and Harper, 1974). In the former case, as nutrient level is reduced, root:shoot ratio increases bringing about more intense root competition and then 'altered-form competition' emerges (Morris and Myerscough, 1985, 1991). It is very probable that 'altered-form competition' is associated with transition from a lower to a higher β (i.e. decrease in the degree of competitive asymmetry) and hence more variable size-structure dynamics as nutrient level is reduced (Morris and Myerscough (1991) found that β of *Ocimum basilicum* increased with reduced nutrient level). In 'altered-speed competition', this transition from a lower to a higher β may not occur when the nutrient level is reduced, and a rather stable size-structure is realized at a lower β (even with a variable α) with the time lag in the convergence being the only difference between variations in physiological parameter values (see Figs. 3.1-3.6A, C, E).

Plant community dynamics and the mode of competition

The parameter-sensitivity of the plant population in relation to the mode of competition (degree of asymmetry) or allometry (allocation-growth pattern) should be taken into account when we study the dynamics of multi-species plant communities. In mean-value-based models, competitive ability is asymmetrically hierarchical giving rise to transitive competition among species (e.g. Keddy and Shipley 1989; Tilman 1990). On the other hand, there have been arguments that competitive abilities of species are not strictly hierarchical, especially in grasslands (i.e. competition among species is non-transitive; e.g. Aarssen 1983, 1989; Wilson 1989; Taylor and Aarssen 1990; Glenn and

Collins 1990; Herben and Krahulec 1990; Herben et al. 1990; Hara 1993).

An inference about the mode of inter-specific competition can be made, although the model in this chapter dealt with only intra-specific competition: non-transitive competition may be associated with plant species of symmetric two-sided competition which are highly sensitive to changes in physiological parameters caused by environmental fluctuations.

Large effects of variation in physiological parameters under symmetric two-sided competition implies large fluctuations in individual growth, which give rise to the diffusion function term $D(t,w)$ together with eqn (2.1):

$$\frac{\partial f(t,w)}{\partial t}=\frac{\partial^2}{\partial w^2}\left[D(t,w)f(t,w)\right]-\frac{\partial}{\partial w}\left[G(t,w)f(t,w)\right]-M(t,w)f(t,w). \qquad (3.3)$$

Hara (1993) showed that inferior competitor species in terms of mean species traits such as $G(t,w)$, $M(t,w)$ and $R(t)$ functions can coexist with superior competitor species, if the $D(t,w)$ function of inferior competitor species is greater than that of superior competitor species. Therefore, it is very likely that the large $D(t,w)$ function, high parameter-sensitivity in symmetric two-sided competition, non-transitivity of competition among species, and species diversity are all closely associated with each other. Non-equilibrium theory for community dynamics (e.g. Huston, 1979) may be explained in this context.

Chapter 4

Foliage profile, size-structure and stem diameter - plant height relationship in plant populations

In most of the theoretical models for plant growth (e.g. Shugart, 1984; Botkin, 1993), a relationship between stem diameter (*D*) and plant height (*H*) has been assumed *a priori* as a species-specific characteristic. Also in the previous chapters, a simple allometry between plant weight and plant height was assumed. In this chapter, such an *a priori* assumption is not made. Instead, *D* and *H* are treated as two independent variables to investigate the effects on size structure, competition and *D*-*H* relationship of the vertical foliage profile of an individual plant and allocation pattern between *D* and *H* in crowded populations. The simulation study in this chapter is based on an extended version of the canopy photosynthesis model developed in Chapter 2 together with a two-dimensional continuity equation model.

4.1 Model

Time development of two-dimensional size distribution density

Let $f(t,D,H)$ be a distribution density of individuals of stem diameter *D* and plant height *H* per unit area at time *t*. Hara et al. (1990) and Hara, Kimura and Kikuzawa (1991) proposed a diffusion equation model to describe the dynamics of $f(t,D,H)$. This was an extended version of Hara's diffusion model for size-structured plant populations (Hara, 1984a, b) incorporating two kinds of size measure at the same time.

$$\begin{aligned}\frac{\partial f(t,D,H)}{\partial t} &= \frac{1}{2}\frac{\partial^2}{\partial D^2}\left[D_d(t,D,H)f(t,D,H)\right]+\frac{\partial^2}{\partial D\partial H}\left[D_{dh}(t,D,H)f(t,D,H)\right]\\ &+\frac{1}{2}\frac{\partial^2}{\partial H^2}\left[D_h(t,D,H)f(t,D,H)\right]-\frac{\partial}{\partial D}\left[G_d(t,D,H)f(t,D,H)\right],\\ &-\frac{\partial}{\partial H}\left[G_h(t,D,H)f(t,D,H)\right]-M(t,D,H)f(t,D,H) \qquad (4.1)\end{aligned}$$

The "diffusion" terms [the first, the second and the third terms in the right-hand side of eqn (4.1)] represent spatial heterogeneity and genetic variations in a population. In this thesis, I consider an even-aged plant population which grows in a homogeneous environment, where effects of the diffusion terms are assumed to be small. Moreover, for investigating biological meanings of the relationship between competition process and size structure dynamics, I focus mainly on the deterministic processes in this chapter. In the last subsection (pages 84-86), the effects of these diffusion terms are discussed. Here, the following two-dimensional continuity equation is adopted for the time development of distribution density, $f(t,D,H)$ as a basic equation:

$$\frac{\partial f(t,D,H)}{\partial t}=-\frac{\partial}{\partial D}\left[G_d(t,D,H)f(t,D,H)\right]-\frac{\partial}{\partial H}\left[G_h(t,D,H)f(t,D,H)\right]$$
$$-M(t,D,H)f(t,D,H), \qquad (4.2)$$

where $G_d(t,D,H)$ is the mean stem diameter growth rate (instantaneous mean of increments of stem diameter per unit time) of individuals of stem diameter D and plant height H at time t, and $G_h(t,D,H)$ is the mean height growth rate (instantaneous mean of increments of plant height per unit time) of individuals of stem diameter D and plant height H at time t. $M(t,D,H)$ is the mean mortality rate of individuals of stem diameter D and plant height H at time t (Hara, 1984a, 1988). The density (number of individuals per unit ground area) at time t, $\rho(t)$, is given by

$$\rho(t)=\int_0^{H_{\max}}\int_0^{D_{\max}} f(t,D,H)\mathrm{d}D\mathrm{d}H, \qquad (4.3)$$

where $D_{\max}$ and $H_{\max}$ are the maximal stem diameter and the maximal plant height, respectively.

The function forms of $G_d(t,D,H)$, $G_h(t,D,H)$ and $M(t,D,H)$ are determined by the processes of competition between individuals. Here, competition only for light is considered assuming that nutrients and water in the soil are sufficient.

Leaf area density profile of an individual incorporating plant height and stem diameter

First, let consider an individual grown in isolation. Let $d(z)$ be a profile of stem diameter of an individual plant at height z above the ground. Here $d(z)$ is assumed to be given by the following function:

$$d(z) = D\left[1-\left(\frac{z}{H}\right)^{\eta}\right], \tag{4.4}$$

where D is the stem diameter at ground level (z=0) and H is the plant height. This function can represent various shapes of profile of stem diameter as illustrated in Fig.4.1A by changing the parameter η [Armstrong, 1990, 1993; but in these references the profile of a canopy was given by eqn (4.4)]. From the pipe model theory (Shinozaki et al. 1964a, b), the cross section of a stem at any height above ground is proportional to the accumulated weight of leaves existing above that height of a plant. Then there is a relationship between the vertical distribution of leaf area density, $f_{LA}(z,D,H)$, and the profile of stem diameter, $d(z)$, as

$$\theta\{d(z)\}^2 = \int_z^H f_{LA}(z',D,H)\mathrm{d}z', \tag{4.5}$$

where θ is a proportional constant. Differentiating both the sides of eqn (4.4) with respect to z together with eqn (4.3), we can obtain the function form of $f_{LA}(z,D,H)$:

$$f_{LA}(z,D,H)=2\theta\eta D^2\left[1-\left(\frac{z}{H}\right)^{\eta}\right]\frac{z^{\eta-1}}{H^{\eta}}. \tag{4.6}$$

The vertical distribution of leaf area density for several values of η (hereafter η is called as canopy shape parameter) are shown in Fig.4.1B. For $\eta=1$, the vertical distribution of leaf area density presents a conic canopy such as coniferous trees; for large value of η, it gives such a shape as broad-leaved trees (larger leaf mass in the upper layer than in the lower layer, and $\eta\to\infty$ gives a flat-topped canopy). In the same way as in previous chapters, it is further assumed that the foliage layer at height x from ground dies if the daily total net photosynthetic rate per unit leaf area at that height of an individual of stem diameter D and plant height H is negative because of self-shading within the crown of a plant.

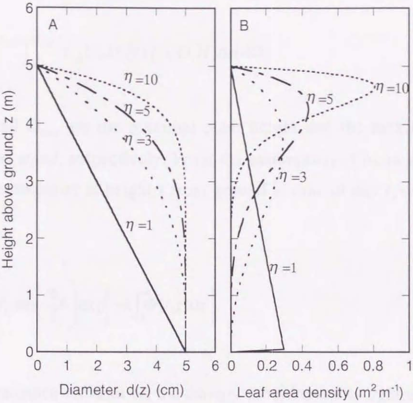

Fig. 4.1. A, stem diameter profiles of an individual plant grown in isolation of stem diameter at ground level D=5.0 cm and plant height H=5.0 m for several values of the parameter η in eqn (4.4). B, vertical foliage profiles of an individual of D=5.0 cm and H=5.0 m for several values of the parameter η in eqn (4.6).

Canopy photosynthetic process

As in previous chapters, it is assumed that plant foliage is homogeneously reducing the intensity of radiation by absorption according to Beer-Lambert's law and that radiation is vertically incident. This can only be an approximation for discretely and homogeneously located leaves, with transmittance=0 and reflectance=0, for non-vertical sky irradiance and for direct sunlight in sunflecks.

In a crowded stand, the mean vertical leaf area density at height x from ground on day t is given by

$$\Phi(t,x)=\int_0^{D_{\max}}\int_0^{H_{\max}} f_{LA}(x,D,H)f(t,D,H)\mathrm{d}H\mathrm{d}D, \tag{4.7}$$

where $H_{\max}$ and $D_{\max}$ are the maximal plant height and the maximal stem diameter in the stand, respectively. From the assumption of homogeneity of the stand, light intensity at height x from ground at time of day t_d on day t is given as

$$I(t,t_d,x)=I_0\sin\left(\frac{\pi t_d}{T_d}\right)\exp\left[-k\int_x^{\infty}\Phi(t,z)\mathrm{d}z\right], \tag{4.8}$$

where I_0 is irradiance incident on the canopy at midday; k is light extinction coefficient; T_d is daylength. Then daily mean net photosynthetic rate per unit leaf area at height x from ground in the stand on day t, $p_n(t,x)$, is given as

$$p_n(t,x)=\int_0^{T_d}\frac{bkI(t,t_d,x)}{1+akI(t,t_d,x)}\mathrm{d}t_d-r_f. \tag{4.9}$$

In this case, the foliage layer at height x from ground is assumed to die if $p_n(t,x)$ is negative, although, of course, height of leaf death is different in the crowded stand. Let $f_{LA}^{*}(t,x,D,H)$ represent $f_{LA}(x,D,H)$ in the crowded stand on day t and let $p_n^{*}(t,x)$, which is calculated using $f_{LA}^{*}(t,x,D,H)$, represent $p_n(t,x)$ in the crowded stand. Daily net photosynthetic rate of an individual of stem diameter D and plant height H in the stand on day t is obtained by

$$P_n^{*}(t,D,H)=\frac{1}{1+r_g}\left[u\int_0^{H}p_n^{*}(t,x)f_{LA}^{*}(t,x,D,H)\mathrm{d}x-r_m\alpha D^2H\right], \tag{4.10}$$

where u, r_g, r_m, are conversion factor, growth respiration rate per unit weight, maintenance respiration rate per unit weight for non-photosynthetic organs, respectively. The first term in the parentheses of eqn (4.10) gives net photosynthetic production per day by leaves of an individual of stem diameter D and plant height H. The second term represents the weight loss by respiration of non-photosynthetic organs assumed as $\alpha D^2 H$.

Allocation process of an individual

It is assumed that plants allocate net photosynthetic gain per unit time to the growth of both stem diameter and plant height. The mechanisms of allocation pattern may be quite different among species. Here, let consider three types of relationship between the increment of stem diameter per unit time, ΔD, and the increment of plant height, ΔH,

$$\text{size-independent allocation: } \frac{\Delta H}{\Delta D} = \beta; \tag{4.11a}$$

$$H\text{-dependent allocation: } \frac{\Delta H}{\Delta D} = \beta \exp[-\gamma H], \tag{4.11b}$$

and

$$\text{competition-dependent allocation: } \frac{\Delta H}{\Delta D} = \beta \exp[\gamma C(t, D, H)], \tag{4.11c}$$

where β and γ are positive parameters. Equation (4.11a) stands for a size-independent allocation pattern irrespective of individual size. Equation (4.11b) as H-dependent allocation pattern allows an individual to give more allocation to height growth than to stem diameter growth if the individual has small plant height. The competition function, $C(t,D,H)$, in eqn (4.11c) is defined as in eqn (2.16)

$$C(t,D,H)=\int_{D}^{D_{\max}}\mathrm{d}D'\int_{H}^{H_{\max}}\mathrm{d}H'\left[\int_{0}^{H'}f_{LA}^{*}(t,x,D',H')\mathrm{d}x\right]. \tag{4.12}$$

This gives the accumulated leaf area of individuals larger than stem diameter D and plant height H at time t, and is a monotonically decreasing function of D and H. Therefore, for eqn(4.11c) as competition-dependent allocation pattern, a small suppressed individual gives more allocation to height growth than to stem diameter growth through eqn (4.12).

Here it is assumed that the total plant weight of an individual of stem diameter D and plant height H is given by

$$w_{\mathrm{total}}=\alpha D^{2}H+\frac{L(t,D,H)}{s}, \tag{4.13}$$

where $L(t,D,H)$ is total leaf area on day t and s is specific leaf area of an individual of D and H. $L(t,D,H)$ is given as

$$L(t,D,H)=\int_{0}^{H}f_{LA}^{*}(t,x,D,H)\mathrm{d}x. \tag{4.14}$$

The first and the second terms of eqn (4.13) give the weights of non-photosynthetic organs and leaves, respectively. When stem diameter and plant height increase by ΔD and ΔH for an individual of stem diameter D and plant height H per unit time, total plant weight w_{total} increase by $\Delta w_{\mathrm{total}}$, which corresponds to net photosynthetic rate given by eqn (4.10):

$$\begin{aligned}P_{n}^{*}(t,D,H)=\Delta w_{\mathrm{total}}=\alpha(D+\Delta D)^{2}(H+\Delta H)+\frac{L(t,D+\Delta D,H+\Delta H)}{s}\\-\left[\alpha D^{2}H+\frac{L(t,D,H)}{s}\right],\end{aligned} \tag{4.15}$$

where s is assumed to be time-independent. From eqns (4.10), (4.11), (4.13) - (4.15), we can obtain the increments of stem diameter, ΔD, and of plant height, ΔH, per unit time for individuals of D and H, which represent $G_d(t,D,H)$ and $G_h(t,D,H)$, respectively.

Mortality process

As in previous chapters, it was assumed for simplicity that mortality rate of an individual is set at unity only when the daily net photosynthetic rate of an individual is negative. Then, the distribution density of the individuals decays exponentially for fixed D and H with a time constant of one day. Therefore, the function form of $M(t,D,H)$ is assumed as

$$M(t,D,H)=0, \qquad (P_n^*(t,D,H)\geq 0); \tag{4.16a}$$

$$=1, \qquad (P_n^*(t,D,H)<0). \tag{4.16b}$$

The lack of a diffusion term means that once a size class is eliminated it cannot be restored.

Initial and boundary conditions

From the above formulations the dynamics of size structure of a plant stand can be described based on eqn (4.2) together with initial and boundary conditions given as:

initial condition,

$$f(0,D,H)=\frac{N_0}{\left(\sqrt{2\pi}\right)^2\sigma_D\sigma_H}\exp\left[-\frac{\left(D-\overline{D_0}\right)^2}{2\sigma_D}-\frac{\left(H-\overline{H_0}\right)^2}{2\sigma_H}\right]; \tag{4.17}$$

boundary conditions,

$$f(t,0,H)=f(t,D,0)=0. \tag{4.18}$$

Parameter N_0 represents the initial density at t=0; s_D and s_H are the standard deviations of stem diameter and plant height, respectively; $\overline{D_0}$ and $\overline{H_0}$ are the initial mean stem diameter and the initial mean plant height of the stand, respectively.

Simulation methods

The two-dimensional Lax-Wendroff method was employed for numerically solving the partial differential equation, eqn (4.2) (e.g. Smith, 1985). Integration involved in eqns (4.7) - (4.10), (4.12) and (4.14) was performed by the spline integration method (e.g. Davis and Rabinowitz, 1984). Intervals for discretization were 0.2 cm for stem diameter D, 0.2 m for plant height H and one day for time t. Physiological parameters involved in eqns (4.8) - (4.10) are presented in Table 4.1. Initial density N_0 was 5.0 m^{-2}, and initial mean stem diameter and initial plant height were 5.0 cm and 5.0 m, respectively. The standard deviations of initial stem diameter and plant height distributions were 1.5 cm and 1.5 m, respectively. These parameters were fixed for each simulation set.

Table 4.1. *Parameter values used for simulations in Chapter 4*

Parameter	Unit	Definition
α=10.0	($gcm^{-2}m^{-1}$)	Allometric parameter: eqns (4.10), (4.13), (4.15)
θ=0.03	(m^2cm^{-2})	Parameter for leaf area distribution: eqns (4.5), (4.6)
u=0.65	($g\ g_{CO_2}^{-1}$)	Conversion factor: eqn (4.10)
k=0.4		Light extinction coefficient: eqns (4.8), (4.9)
a=0.01	($W^{-1}m^2$)	Parameters for light-photosynthetic rate curve: eqn (4.9)
b=0.05	($g_{CO_2}W^{-1}h^{-1}$)	
I_0=250.0	(Wm^{-2})	Irradiance incident on the canopy at midday: eqn (4.8)
T_d=14.0	(hour)	Daylength: eqn (4.8)
r_f=0.6	($g_{CO_2}m^{-2}d^{-1}$)	Respiration rate of leaves: eqn (4.9)
r_m=0.001	($gg^{-1}d^{-1}$)	Maintenance respiration rate: eqn (4.10)
r_g=0.3	(gg^{-1})	Growth respiration rate: eqn (4.10)
s=0.03	(m^2g^{-1})	Specific leaf area: eqns (4.13), (4.15)

Simulations were carried out by changing the canopy shape of an individual, [i.e. the value of canopy shape parameter, η, in eqns (4.4) and (4.6)] and the allocation ratio of the growth rate of stem diameter and plant height of an individual [i.e. the parameter values of β and γ in eqns (4.11a)-(4.11c)] for each allocation pattern, size-dependent, H-dependent and competition-dependent. Simulation set are summarized in Table 4.2.

Table 4.2. *Simulation cases in Chapter 4*

Case	Canopy type	Allocation pattern	Parameter values
case 1	broad-leaved	size-independent $\frac{\Delta H}{\Delta D} = \beta$	η=5.0, β=0.6
case 2	coniferous		η=1.0, β=0.6
case 3	broad-leaved	*H*-dependent $\frac{\Delta H}{\Delta D} = \beta \exp[-\gamma H]$	η=5.0, β=5.0, γ=0.3
case 4	coniferous		η=1.0, β=5.0, γ=0.3
case 5	broad-leaved	competition-dependent $\frac{\Delta H}{\Delta D} = \beta \exp[\gamma C(t,D,H)]$	η=5.0, β=0.6, γ=0.5
case 6	coniferous		η=1.0, β=0.6, γ=0.5

4.2 Simulation results

For cases 1, 3 and 5, the mean stem diameter - mean plant height trajectory with time was curvilinear, while for cases 2, 4 and 6, it was approximately linear (Fig. 4.2). This means that as the canopy shape parameter η increases, the mean D - mean H trajectory becomes curvilinear irrespective of allocation pattern. All the time courses of the statistics of simulated distributions were distinctly separated by the canopy shape parameter η, while only small differences were found between allocation patterns (Fig. 4.3). Leaf area index and population density of the stand for η=5 began to decrease at earlier time than for η=1 due to severe self-thinning (Fig. 4.3A, B). For the value of η=5, coefficient of variation and skewness of weight increased in early stage and then decreased as time passed (Fig. 4.3C, D).

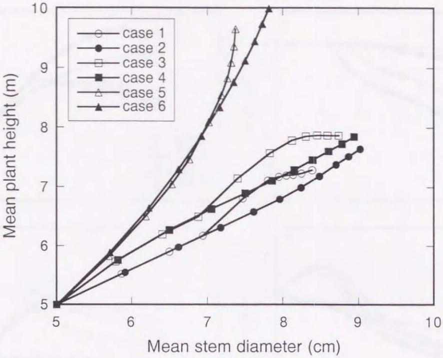

Fig. 4.2. The relationships between mean stem diameter and mean plant height of the simulated stands. Case 1 (○) corresponds to broad-leaved type plants with size-independent allocation pattern for the value of β=0.6 in eqn (4.11a); case 2 (●), to coniferous type plants with size-independent allocation pattern for the value of β=0.6 in eqn (4.11a); case 3 (□), to broad-leaved type plants with *H*-dependent allocation pattern for the values of β=5.0, γ=0.3 in eqn (4.11b); case 4 (■), to coniferous type plants with *H*-dependent allocation pattern for the values of β=5.0, γ=0.3 in eqn (4.11b); case 5 (△), to broad-leaved type plants with competition-function dependent allocation pattern for the values of β=0.6, γ=0.5 in eqn (4.11c); case 6 (▲), to coniferous type plants with competition-function dependent allocation pattern for the values of β=0.6, γ=0.5 in eqn (4.11c).

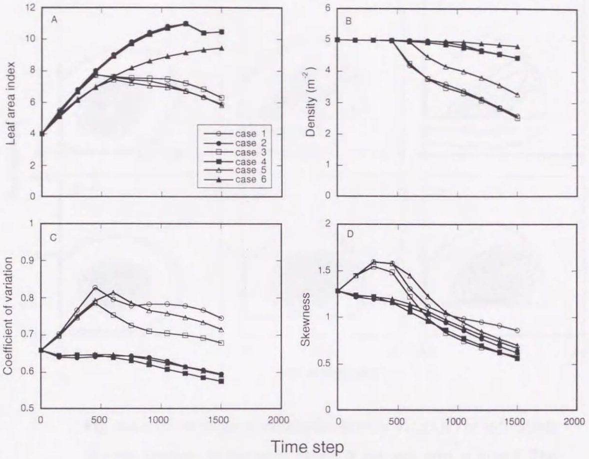

Fig. 4.3. Simulated changes over time in: A, leaf area index; B, density of the stand; C, coefficient of variation of plant weight distribution; D, skewness of plant weight distribution. Key as Fig. 4.2.

The contour maps of distribution density, $f(t,D,H)$, for the three cases of allocation pattern show that height distributions for η=5 were bimodal and that those for η=1 were unimodal irrespective of allocation pattern (Figs 4.4, 4.5 and 4.6). On the other hand, diameter distributions were unimodal for all the cases. The contour maps of distribution density of net photosynthetic rate, $P_n^*(t,D,H)$, (Figs 4.7, 4.8 and 4.9) show that in the case of η=5 for all the allocation patterns, there were maximum values in the net photosynthetic rate of individuals of small height and large diameter (Fig. 4.7A, 4.8A and 4.9A) giving rise to height bimodal distributions.

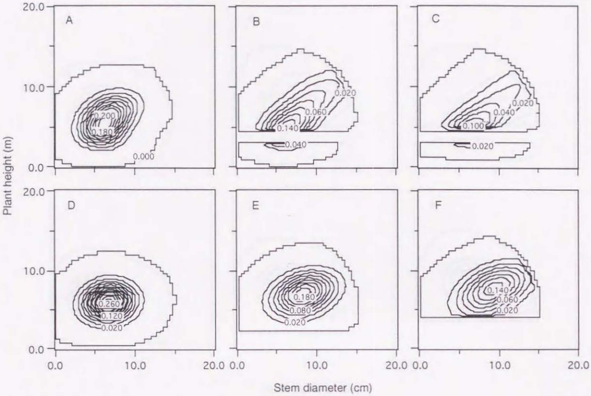

Fig. 4.4. Contour maps of distribution density $f(t,D,H)$ of individuals of stem diameter D and plant height H per unit area at time t. The quantity, $f(t,D,H)\mathrm{d}D\mathrm{d}H$, represents the number of individuals of $D \in [D, D+\Delta D]$ and $H \in [H, H+\Delta H]$ per unit area (unit of $f(t,D,H)$ is [(number of plants) cm^{-1} m^{-1} m^{-2}]). For case 1, A, the distribution density at time step t=300 days; B, at t=900 days; C, at t=1500 days. For case 2, D, at t=300 days; E, at t=900 days; F at t=1500 days. For case 1, there is bimodality in height distributions (B and C), although stem diameter distribution is unimodal. Numerals in the figures denote the value of distribution density.

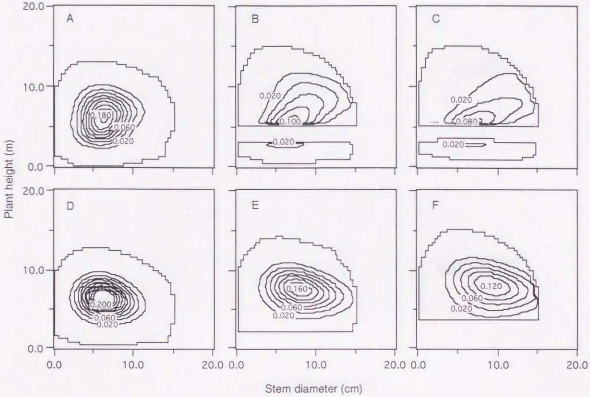

Fig. 4.5. As in Fig. 4.4. A, B and C for case 3; D, E and F for case 4. For case 3, there is bimodality in height distributions (B and C), although stem diameter distribution is unimodal. Numerals in the figures denote the value of distribution density.

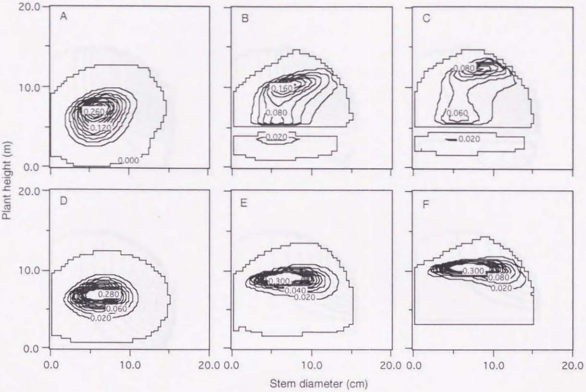

Fig. 4.6. As in Fig. 4.4. A, B and C for case 5; D, E and F for case 6. For case 5, there is bimodality in height distributions (B and C), although stem diameter distribution is unimodal. Numerals in the figures denote the value of distribution density.

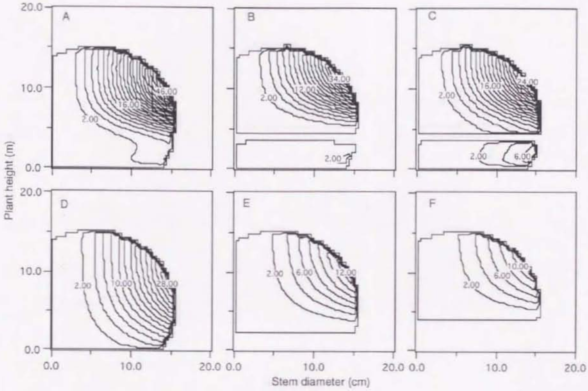

Fig. 4.7. Contour maps of net photosynthetic rate distribution, $P_n^*(t, D, H)$ (g day^{-1}), of an individual of stem diameter, D, and plant height, H. For case 1, A, the net photosynthetic rate distribution at time step t=300 days; B, at t=900 days; C at t=1500 days. For case 2, D, at t=300 days; E, at t=900 days; F at t=1500 days. For case 1, there are maximum values in the net photosynthetic rate of individuals of small height and large diameter (B and C), giving rise to height bimodal distributions. Numerals in the figures denote the value of net photosynthetic rate.

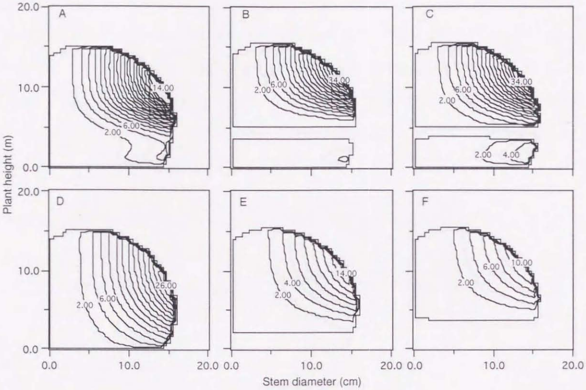

Fig. 4.8. As in Fig. 4.7. A, B and C for case 3; D, E and F for case 4. For case 3, there are maximum values in the net photosynthetic rate of individuals of small height and large diameter (B and C), giving rise to height bimodal distributions. Numerals in the figures denote the value of net photosynthetic rate.

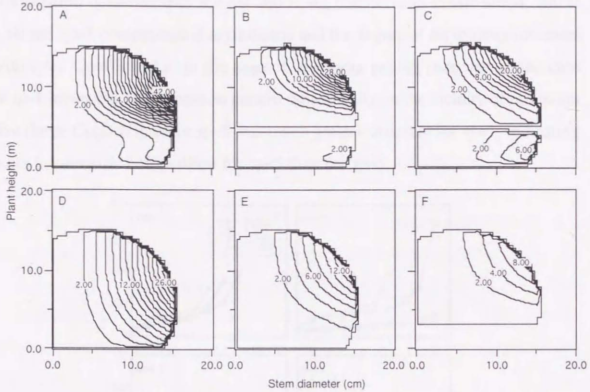

Fig. 4.9. As in Fig.4.7. A, B and C for case 5; D, E and F for case 6. For case 5, there are maximum values in the net photosynthetic rate of individuals of small height and large diameter (B and C), giving rise to height bimodal distributions. Numerals in the figures denote the value of net photosynthetic rate.

ΔRGR is defined as a difference between RGR (relative growth rate of plant weight) in an isolated condition and RGR in a crowded condition for an individual of plant height H and stem diameter D. The relationship between the competition function, $C(t,D,H)$, [eqn (4.11)] and ΔRGR at $t \rightarrow \infty$ as (Fig. 4.10) can be approximated by.

$$\Delta\text{RGR} = c_1 C(t,D,H) + c_2 C(t,D_{\min},H_{\min}), \tag{4.19}$$

where $D_{\min}$ and $H_{\min}$ are the minimal stem diameter and the minimal plant height in the stand, respectively; c_1 and c_2 are constants. If $c_1=0$ and $c_2>0$, competition is symmetric; if $c_1>0$ and $c_2=0$, competition is one-sided; and if $c_1>0$ and $c_2>0$, competition is asymmetric and the degree of asymmetry increases with c_1/c_2. Coefficient c_1 in the case of $\eta=5$ was greater than that in the case of $\eta=1$ irrespective of allocation pattern. Specifically, in the vicinity of minimum size [large $C(t,D,H)$], c_1 for $\eta=5$ was much greater than that for $\eta=1$, indicating more asymmetric competition for $\eta=5$ than for $\eta=1$.

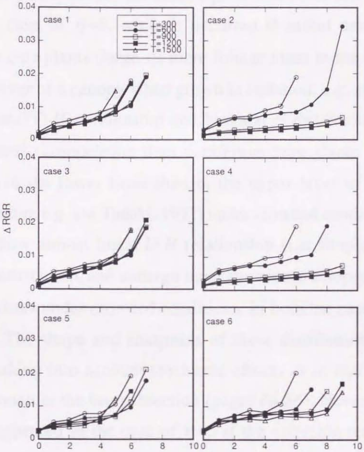

Fig. 4.10. Relationships between the competition function, $C(t,D,H)$, and ΔRGR. ΔRGR is defined by a difference between RGR (relative growth rate of plant weight) in an isolated condition and RGR in a crowded condition for an individual of plant height H and stem diameter D.

4.3 Discussion

The simulation model showed that the vertical foliage profile of an individual plant grown in isolation (i.e. species-specific branching pattern and canopy morphology) has a great effect on the growth dynamics and *D*-*H* relationship of crowded populations (note that the actual canopy shape of an individual in a crowded stand is produced by self-pruning from the canopy shape of an isolated single plant, but for the results presented here, self-pruning did not occur in the case of η=5, while it occurred if initial density was high). Broad-leaved type plants (large η; more foliage mass in the upper layer than in the lower layer of a canopy when grown in isolation; e.g. see Tadaki, 1977) show curvilinear *D*-*H* relationship and bimodal *H* distribution, and undergo more asymmetric competition than coniferous type plants (small η; more foliage mass in the lower layer than in the upper layer of a canopy when grown in isolation; e.g. see Tadaki, 1977) under crowded conditions. Coniferous type plants show almost linear *D*-*H* relationship (i.e. simple allometry) and unimodal *H* distribution, and undergo more symmetric competition than broad-leaved type plants under crowded conditions. In both the cases *D* distribution is unimodal. The shape and sharpness of these distribution densities were changed by taking into account stochastic effects as in eqn (4.1). This case will be performed in the last subsection (pages 84-86). Nevertheless, bimodal distribution appeared in the case of η=5 if the diffusion terms were small, although large diffusion terms extinguished the bimodality. The value of η for an individual plant [eqns (4.4), (4.6); foliage profile parameter of an individual canopy representing a species-specific branching pattern and canopy morphology when grown in isolation] governs size structure (bimodal or unimodal), the mode of competition, *D*-*H* relationship and mean *D* - mean *H* trajectory with time under crowded conditions. The allocation pattern between *D* and *H* (size-independent, *H*-dependent, and competition-dependent) affects these features only a little. If a change in canopy morphology occurs from one type to the other under crowded conditions, changes in growth dynamics, *D-H* relationship and the mode of competition will also occur. Curvilinear *D-H* relationship is associated with bimodal plant height distribution, whereas almost linear *D-H* relationship is associated with unimodal height distribution. The former can be seen also in several annual forbs (*Impatiens pallida*, *Tagetes patula*, *Polygonum pensylvanicum*, *Kochia scoparia*) presented by Weiner and Thomas (1992) and Weiner and Fishman (1994). As in Kohyama et al. (1990) for trees, Weiner and Thomas (1992) and Weiner and Fishman (1994) also concluded that the curvilinear *D-H* relationship of these annual plants is brought about by asymmetric competition for light.

These simulation results can explain many actual data. In a nearly even-aged natural stand of *Betula ermanii* (a broad-leaved tree; Fig. 4.11; Kikuzawa, 1988; Hara et al., 1990), *H* distribution showed clear bimodality and *D* distribution showed unimodality in the early growing stage and slight bimodality only in the later growing stage (Fig. 4.11), which can be regarded as a result of 3-5 year difference at the initial stage of invasion (Hara et al. 1990, 1991). In an even-aged plantation of *Abies sachalinensis* (a conifer; Fig. 4.12; Hara, 1985), both *D* and *H* show unimodal distributions.

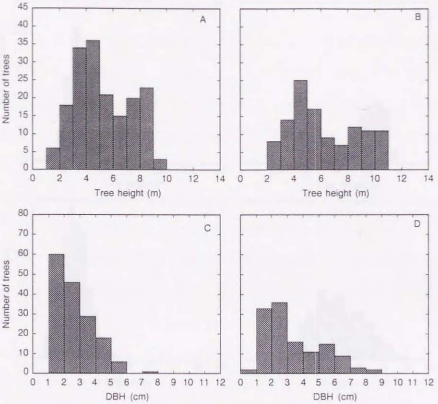

Fig. 4.11. Frequency distributions of tree height and stem diameter at breast height (DBH) in a *Betula ermanii* natural stand in 1983 (7-12 years old; A and C) and in 1987 (11-16 years old; B and D) [redrawn from Kikuzawa (1988) and Hara et al. (1990)].

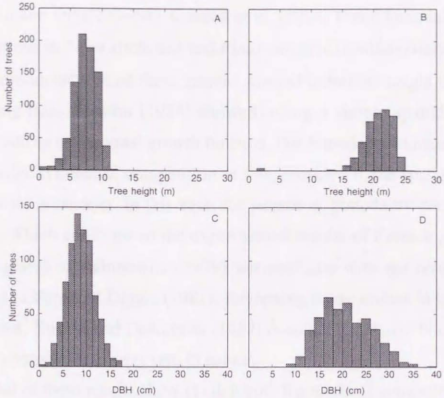

Fig. 4.12. Frequency distributions of tree height and stem diameter at breast height (DBH) in an *Abies sachalinensis* plantation in 1948 (20 years old; A and C) and in 1978 (50 years old; B and D) [recalculated and redrawn from Hara (1985)].

The equation, $1/H = 1/aD^b + 1/H_{\max}$, was applied to oak forests dominated by *Castanopsis cuspidata*, *Quercus acutissima* etc. (Ogawa and Kira, 1977) and to *Abies veitchii* and *A. mariesii* (conifers) stands (Kohyama et al., 1990). However, the regression result of the former is much more curvilinear than the results of the latter. *Betula ermanii* of Hara et al. (1990) also showed significantly curvilinear *D-H* relationships. Ford (1975) and Ford and Diggle (1981) argued that competition for light is asymmetric (or one-sided) and brings about size bimodality as density increases. However, clear bimodality was found only in plant heights of several annual forbs (*Tagetes patula*, *Tagetes erecta*, *Sinapis alba* and *Lycopersicon esculentum*) in Ford (1975) and Ford and Diggle (1981). Cannell et al. (1984) found bimodal tree height distributions in *Picea sitchensis* and *Pinus contorta* (conifers) only when dead trees were included, and these species showed unimodal height distributions for living trees. Huston (1986) showed, using a simple spatial simulation model with an exponential growth function, that bimodality in mass can appear even under symmetric competition at low densities if the spatial pattern of individuals is random. In this case, the degree of bimodality decreased with density, which conforms to the experimental results of *Festuca paradoxa* (a prairie grass) of Rabinowitz (1979) but contrasts with the results of Ford (1975) and Ford and Diggle (1981). Reviewing many studies in both animals and plants, Huston and DeAngelis (1987) concluded that size bimodality due only to competition is very rare in nature.

All of these results show (1) that both the mode of competition and size structure (bimodal or unimodal) are determined by the type of canopy structure and (2) that clear bimodality appears mostly in plant height of broad-leaved species under crowded conditions, although log-transformed mass, but not untransformed mass, showed bimodality in several cases (e.g. Ford, 1975). These results can be explained by the theoretical model in this chapter. A simple view of the competition-allometry relationship that competition determines allometry should be reevaluated incorporating the foliage profile of an individual.

The bimodal height distribution of broad-leaved type plants, irrespective of allocation pattern between *D* and *H*, suggests a separation of vertical space for upper and lower canopy layers (i.e. multi-layered canopy). It will be easy for another species to occupy the middle sparse layer in broad-leaved type plants. In coniferous type plants, however, it will be difficult for another species to invade if competition is strongly asymmetric, because the canopy is occupied by a single coniferous species as suggested by unimodal height distribution (i.e. mono-layered canopy). Therefore, it is hypothesized that species coexistence in broad-leaved type plants is mainly by way of separation of vertical space and that species coexistence in coniferous type plants is due to symmetric competition in a single canopy layer (see Discussion of Chapter 3; Hara and Wyszomirski, 1994). The former represents niche separation under strongly asymmetric competition (or one-sided competition) and conforms to Kohyama's (1993) "forest architecture hypothesis" for a warm-temperate rain forest. The latter is supported by the results of Hara et al. (1994) for the coexistence of *Abies veitchii* and *A. mariesii* in a subalpine coniferous forest. It should be noted that even in broad-leaved type plants, species coexistence in the same vertical layer is possible if competition is symmetric, although it is unstable.

Effects of diffusion terms

Here, it is showed that effects of diffusion terms on the distribution density $f(t,D,H)$ of individuals of stem diameter D and plant height H per unit area at time t. The time development of $f(t,D,H)$ is governed by the equation [the same as eqn (4.1) without cross-correlation term]:

$$\begin{aligned}\frac{\partial f(t,D,H)}{\partial t} &= \frac{1}{2}\frac{\partial^2}{\partial D^2}\left[D_d(t,D,H)f(t,D,H)\right]+\frac{1}{2}\frac{\partial^2}{\partial H^2}\left[D_h(t,D,H)f(t,D,H)\right]\\ &-\frac{\partial}{\partial D}\left[G_d(t,D,H)f(t,D,H)\right]-\frac{\partial}{\partial H}\left[G_h(t,D,H)f(t,D,H)\right]-M(t,D,H)f(t,D,H),\end{aligned} \tag{4.19}$$

where D_d and D_h are diffusion coefficients representing the variance of growth rates (variance of increments per unit time) of stem diameter D and plant height H at time t. Here, it is assumed that both the diffusion coefficients are constant and the covariance of D and H is zero.

In Fig. 4.13, bimodality of height distribution appears for both the cases of η=5.0 (broad-leaved type plants) as in the case without the diffusion terms, although the absolute value of distribution densities decreases as the diffusion terms become large. When $D_d=D_h=10^{-2}$, distribution densities converge to zero by t=900 days. The sharpness of distribution density decreases as the diffusion terms become large.

In Fig. 4.14, there is little change in the shape of distribution densities for η=1.0 (coniferous type plants) even when the diffusion terms are added, although it becomes gentler than without the diffusion terms.

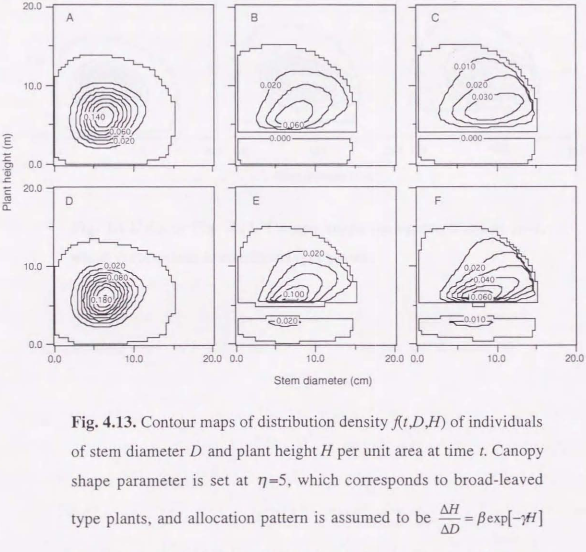

Fig. 4.13. Contour maps of distribution density $f(t,D,H)$ of individuals of stem diameter D and plant height H per unit area at time t. Canopy shape parameter is set at η=5, which corresponds to broad-leaved type plants, and allocation pattern is assumed to be $\frac{\Delta H}{\Delta D}=\beta\exp[-\gamma H]$ for the value of β=5.0 and γ=0.3. A, the distribution density at t=300 days; B, at t=900 days; C, at t=1500 days for the value of $D_d=D_h=10^{-3}$. D, at t=300 days; E, at t=900 days; F at t=1500 days for the value of $D_d=D_h=10^{-4}$.

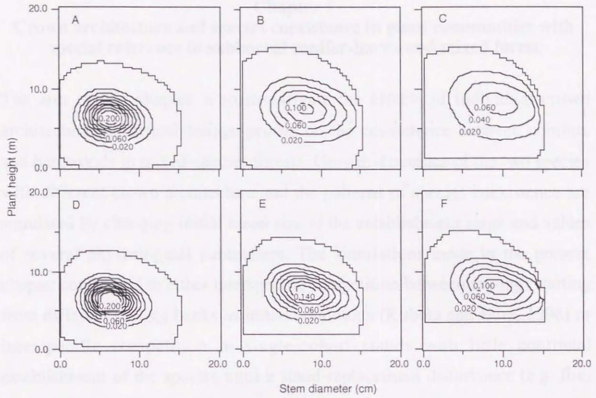

Fig. 4.14. As in Fig. 4.13. Canopy shape parameter is set at η=1, which corresponds to coniferous type plants.

Chapter 5
Crown architecture and species coexistence in plant communities with special reference to subboreal conifer-hardwood mixed forest

The aim of this chapter is to investigate the effects of individual crown architecture as vertical foliage profile on the coexistence between conifers and hardwoods in mixed-species forests. Growth dynamics of the two species with different crown architecture and the patterns of species coexistence are simulated by changing initial mean size at the establishment stage and values of several physiological parameters. The simulations made in the present chapter correspond to either interspecific competition between saplings starting from different sapling banks as initial conditions (Kubota and Hara, 1996) or interspecific competition in single-cohort stands with little continual establishment of the species until a stand-replacement disturbance (e.g. fire; Youngblood, 1995). Therefore, recruitment processes are not incorporated in the model of this chapter.

5.1 Model and simulation

Diffusion model and canopy photosynthesis model for a plant community

Consider a multi-species plant community where each individual is growing under homogeneous environmental and competitive conditions. Let $f_i(t,x)$ denote the distribution density of the i-th species' individuals (i=1, 2,..., n) of plant size x (mass, stem diameter or plant height) at time t in a community with n species. With the inter- and/or intra-specific interactions, its distribution density varies with time. For even-aged monocultures (n=1), in Chapter 2, the general $G_i(t,x)$ function is derived based on a canopy photosynthesis model, which was derived from the canopy photosynthetic processes of competing individuals. Kohyama (1992) used the folowing model for a n-species plant community:

$$\frac{\partial f_i(t,x)}{\partial t}=\frac{1}{2}\frac{\partial^2}{\partial x^2}\left[D_i(t,x)f_i(t,x)\right]-\frac{\partial}{\partial x}\left[G_i(t,x)f_i(t,x)\right]-M_i(t,x)f_i(t,x),$$
$$(i=1,2,\ldots,n). \qquad (5.1)$$

Subscript i denotes each species i. The $D_i(t,x)$, $G_i(t,x)$ and $M_i(t,x)$ functions are the variance of absolute growth rate, the mean absolute growth rate and the mortality rate of individuals of plant size x of species i at time t, respectively.

Let $\Phi_i(t,z)$ be an averaged vertical foliage density profile within the stand at height z above ground of species i at time t:

$$\Phi_i(t,z)=\int_0^\infty f_{LA,i}(t,z,x)f_i(t,x)\mathrm{d}x, \qquad (5.2)$$

where $f_{LA,i}(t,z,x)$ is the vertical distribution density of leaf area of an individual of size x at height z above ground for species i and $f_i(t,x)$ is the distribution density of individuals of size x of species i at time t. From the Beer-Lambert law, light intensity at height z above ground at time of day t_d on day t is given by

$$I(t,t_d,z)=I_0\sin\left(\frac{\pi t_d}{T_d}\right)\exp\left[-\sum_{i=1}^{n}\int_z^\infty k_i\Phi_i(t,y)\mathrm{d}y\right], \qquad (5.3)$$

where I_0 is the irradiance incident on the canopy at midday, k_i is the light extinction coefficient in the canopy of species i. In eqn (5.3), we assume that the plant foliage reduces homogeneously the intensity of radiation without reflectance or transmittance by leaves as in previous chapters. Then, the averaged daily net photosynthetic rate per unit leaf area of species i at height z above ground in the stand on day t, $p_{n,i}(t,z)$, is given by

$$p_{n,i}(t,z)=\int_0^{T_d}\frac{b_i k_i I(t,t_d,z)}{1+a_i k_i I(t,t_d,z)}\mathrm{d}t_d-r_f, \tag{5.4}$$

where a_i and b_i are parameters of the light-photosynthetic rate curve of species i and r_f is the respiration rate per unit leaf area (the same for every species in the simulations). It is approximated that the light-photosynthetic rate curve by a rectangular hyperbola, where b_i and b_i/a_i represent the slope at the origin and the asymptotic value of the curve, respectively. Then, the averaged daily net photosynthetic rate of an individual of size x of species i at time t, which is equivalent to the $G_i(t,x)$ function, is given by

$$\begin{aligned}G_i(t,x)&=\frac{1}{1+r_g}\left[u\int_0^{H(x)}f_{LA,i}(t,z,x)p_{n,i}(t,z)\mathrm{d}z-r_m w_{\mathrm{non}}\right]\\&=\frac{1}{1+r_g}\left[u\int_0^{H(x)}f_{LA,i}(t,z,x)\left(\int_0^{T_d}\frac{b_i k_i I(t,t_d,z)}{1+a_i k_i I(t,t_d,z)}\mathrm{d}t_d-r_f\right)\mathrm{d}z-r_m w_{\mathrm{non}}\right],\end{aligned} \tag{5.5}$$

where u is the conversion coefficient, r_m is the respiration rate of non-photosynthetic organs, r_g is the growth respiration rate (these parameter values were the same for every species in the simulations), w_{non} is the mass of non-photosynthetic organs. $H(x)$ represents the plant height of an individual of size x (mass, stem diameter or plant height). In the model, only light competition is considered for intra- and inter-specific interactions between individuals.

As in previous chapters, it is assumed for simplicity that the mortality rate of an individual of size x of species i at time t, $M_i(t,x)$, is set at unity only when the daily net photosynthetic rate of an individual of species i, $G_i(t,x)$, is negative. The function form of $M_i(t,x)$ is then given by

$$\begin{aligned} M_i(t,x) &= 0, \qquad (G_i(t,x) \geq 0); \\ &= 1, \qquad (G_i(t,x) < 0). \end{aligned} \tag{5.6}$$

Then, from eqn (5.1), the size distribution density of individuals of species i decays exponentially with a time constant of one day.

Allometry and crown shape of an isolated plant

As in Chapter 4, it is assumed that the stem diameter profile at height z above the ground, $d(z)$, of an individual of plant height H and stem diameter D is given as (4.4). Moreover, it is assumed that plants allocate net photosynthetic gain per unit time to the growth of both stem diameter and plant height. The mechanisms of allocation patterns may be quite different among species. However, in Chapter 4, it was shown theoretically that the difference in the allocation patterns (constant, size-dependent or competition-dependent) affects the size-structure dynamics of a population only a little. Therefore, here, only the H-dependent relationship between the increment of stem diameter per unit time, ΔD, and the increment of plant height, ΔH, is used, that is the same as eqn (4.11b).

$$\frac{\Delta H}{\Delta D} = \beta \exp[-\gamma H], \tag{5.7}$$

where β and γ are positive constants. Eqn (5.7) allows an individual plant to give more allocation to height growth than to stem diameter growth if the individual has a small plant height under suppressed conditions. Integrating eqn (5.7), we obtain the relationship between plant height, H, and stem diameter, D,

$$D = \frac{1}{\beta\gamma}\left[\exp(\gamma H) - 1\right]. \tag{5.8}$$

Equation (5.8) describes how the stem diameter, D, depends on plant height, H in each individual plant. It should be noted that the growth rates of plant height and stem diameter in the derivative form [eqn (4.11b), (5.7)] adopted in Chapter 4 depends on time, while its integral form [eqn (5.8)] is independent of time. Therefore, the allometry of each individual is unchanged throughout the time course of its growth. Then plant height, H, is taken as an independent variable using the relationship between D and H as eqn (5.8).

The mass of non-photosynthetic organs, w_{non} in eqn (5.5), is thus given as

$$w_{\mathrm{non}} = \alpha D^2 H = \frac{\alpha}{\beta^2\gamma^2}\left[\exp(\gamma H) - 1\right]^2 H, \tag{5.9}$$

where α is a positive constant.

Thus, the vertical distribution of leaf area density, $f_{LA}(z,H)$, of an isolated individual having a stem diameter profile given by eqn (4.4) is derived from the same theory as used in Chapter 4 (the pipe model theory):

$$f_{LA}(z,H) = 2\theta\eta\left\{\frac{1}{\beta\gamma}\left[\exp(\gamma H) - 1\right]\right\}^2\left[1 - \left(\frac{z}{H}\right)^{\eta}\right]\frac{z^{\eta-1}}{H^{\eta}}, \tag{5.10}$$

where θ is a positive constant. As in Chapter 4, for η=1, the vertical distribution of leaf area density presents a conic crown shape such as coniferous trees; larger values of η give spheroidal crown shapes such as broad-leaved trees (hardwoods) having larger leaf mass in the upper layer than in the lower layer, and $\eta \to +\infty$ gives a flat-topped crown (see Fig. 4.1 of Chapter 4). It is further assumed that the foliage layer at any height above ground dies if the average daily net photosynthetic rate per unit leaf area at that height, eqn (5.4), is negative because of shading within the stand. Then, the vertical distribution of leaf area density can vary with development of the stand. Therefore, we represent the vertical distribution of leaf area is explicitly represented as $f_{LA}(t,z,H)$.

Simulation method

In this chapter, the diffusion term [the first term in the right-hand side of eqn (5.1)], which represents the effects of spatial heterogeneity and genetic variations on the growth and size-structure dynamics of a population, is neglected because it is considered that the population which grows in homogeneous conditions, where effects of the diffusion terms are assumed to be small, and only biological meanings of the relationship between competition processes and community dynamics is investigated. The presence of the diffusion terms makes the domain of species coexistence larger than the case of no diffusion terms (Hara 1993; see also Chapter 4). Therefore, I use a continuity equation for time development of a plant population of each species. Hereafter, I deal with the system of a continuity equation model for two-species plant communities [n=2 in eqn (5.1) with $D_i(t,x)=0$] together with the canopy photosynthesis model, eqns (5.2)-(5.5), (plant height, H, is adopted as plant size x)

$$\frac{\partial f_i(t,H)}{\partial t} = -\frac{\partial}{\partial H}\left[G_i(t,H)f_i(t,H)\right] - M_i(t,H)f_i(t,H);\ (i=1,\ 2), \qquad (5.11)$$

where $f_i(t,H)$ denotes the distribution density of plant height H of species i at time t. The lack of the diffusion terms means that once a size class is eliminated it cannot be restored.

The population density of species i at time t (the number of individuals of species i per unit ground area in the stand) is given by

$$\rho_i(t) = \int_{H_{\min}}^{H_{\max}} f_i(t,H)\mathrm{d}H; \ (i=1,\,2), \tag{5.12}$$

where $H_{\min}$ and $H_{\max}$ are the minimal and maximal plant height in the stand, respectively.

As an initial condition, the following Gaussian function is used:

$$f_i(0,H) = \frac{N_{i,0}}{\sqrt{2\pi}\sigma_{i,H}} \exp\left[-\frac{\left(H-\overline{H_{i,0}}\right)^2}{2\sigma_{i,H}}\right]; \ (i=1,\,2), \tag{5.13}$$

and a boundary condition:

$$f_i(t,0) = 0; \ (i=1,\,2), \tag{5.14}$$

where $N_{i,0}$, $\overline{H_{i,0}}$ and $\sigma_{i,H}$ represent the initial population density, the initial mean plant height and the standard deviation of plant height of species i, respectively. Recruitment processes are not incorporated and the effects of the growth dynamics of either saplings starting from different sapling banks (initial conditions) or trees in single-cohort stands with little continual establishment on the pattern of species coexistence are investigated.

The system of non-linear partial differential equations are solved numerically by using the Lax-Wendroff scheme (e.g. Smith, 1985). Integrations involved in eqns (5.2)-(5.4) were performed by the spline integration method as the same as in previous chapters. Intervals for discretization were 0.2 m for plant height H and one time unit (day) for time t. Simulations were carried out by changing the following parameter values for two fixed values of the crown shape parameter, $\eta=1.0$ (conic crown shape) and $\eta=5.0$ (spheroidal crown shape): extinction coefficient (k_i), slope of light-photosynthetic rate curve at the origin (b_i) with the fixed value of the ratio $b_i/a_i=2$, initial mean plant height ($\overline{H_{i,0}}$), initial standard deviation ($\sigma_{i,H}$). When changing parameter values for one species, those values of the other species were set at the 'standard values' given in Table 5.1. Simulations were conducted over the time interval from 0 to 500 time units (days).

Table 5.1. *Standard values of parameters used for simulations of Chapter 5. When changing parameter values of one species, those of the other species are fixed at the values listed below*

Parameter	unit	Definition
$\alpha=5.0$	($\mathrm{gcm^{-2}m^{-1}}$)	Allometric parameter: eqn (5.9)
$\theta=0.04$	($\mathrm{m^{2}cm^{-2}}$)	Parameter for leaf area distribution: eqns (5.10)
$u=0.65$	($\mathrm{g\ g_{CO_2}^{-1}}$)	Conversion factor: eqn (5.5)
$k=0.6$		Lght extinction coefficient in the canopy: eqns (5.3), (5.4), (5.5)
$a=0.075$	($\mathrm{W^{-1}m^{2}}$)	Parameters for light-photosynthetic rate curve: eqns (5.4), (5.5)
$b=0.15$	($\mathrm{g_{CO_2}W^{-1}h^{-1}}$)	
$I_0=250.0$	($\mathrm{Wm^{-2}}$)	Irradiance incident on the canopy at midday: eqn (5.3)
$T_d=14.0$	(hour)	Daylength: eqn (5.3)
$r_f=0.6$	($\mathrm{g_{CO_2}m^{-2}d^{-1}}$)	Respiration rate of leaves: eqns (5.4), (5.5)
$r_m=0.001$	($\mathrm{gg^{-1}d^{-1}}$)	Maintenance respiration rate: eqn (5.5)
$r_g=0.3$	($\mathrm{gg^{-1}}$)	Growth respiration rate: eqn (5.5)

5.2 Simulation results

For investigating the coexistence between the two species, it is defined that the 'state' of species *i* as follows: *species* i *survives if* $\rho_i(t=500) \geq 0.1 \times N_{i,0}$; *otherwise, species* i *is excluded by interspecific competition*, where $\rho_i(t=500)$ is the population density of species *i* at *t*=500 time units (days) and $N_{i,0}$ is the initial population density of species *i* at *t*=0. In the present study, recruitment processes were not incorporated. Thus the two species will die out eventually as time tends to infinity (*t*=ca. 1000 time units in these simulations). To assess the outcome of interspecific competition (survive or excluded), the results of the state of the two species at *t*=500 time units is given (almost the same results were obtained also at *t*=ca. 800 time units). The species with conic and spheroidal crowns in the model were assumed to be a conifer and a hardwood, respectively. Hereafter the species with a conic crown is called as a conifer and the one with a spheroidal crown as a hardwood.

Figures 5.1 and 5.2 show phase diagrams for species coexistence between conifers and hardwoods at *t*=500 time units. In Fig. 5.1, the parameter values of hardwoods were changed with those of a conifer kept at the standard values (Table 5.1). There was a domain of coexistence for the lower values of the extinction coefficient (k_i) and the slope of light-photosynthetic rate curve at the origin (b_i), and the domain area of coexistence decreased with an increasing initial mean plant height of hardwoods. For the other parameter sets, only the hardwoods survived and the conifer was excluded. In Fig. 5.2, the parameter values of conifers were changed with those of a hardwood kept at the standard values (Table 5.1). There is a domain of coexistence for the higher values of the extinction coefficient and the slope of light-photosynthetic rate curve at the origin for conifers. For lower initial mean plant heights (i.e. hardwoods in the upper canopy layer and a conifer in the lower canopy layer) and higher initial mean plant heights (i.e. a conifer in the upper canopy layer and hardwoods in the lower canopy layer), the domain area of coexistence became large.

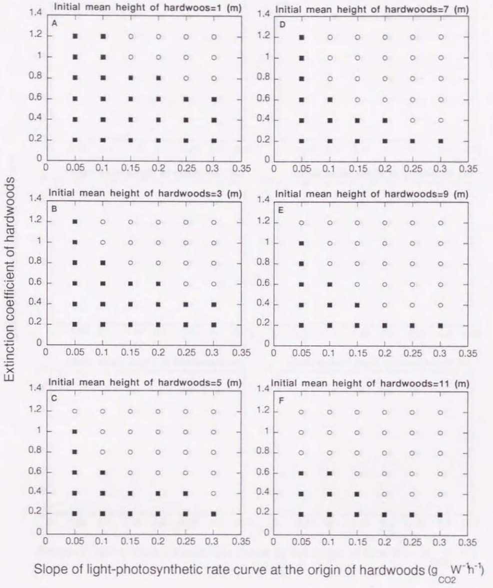

Fig. 5.1. Phase diagram of coexistence between species with a spheroidal crown (hardwoods) and those with a conic crown (conifers). The parameter values of hardwoods were changed, while those of a conifer were fixed at the standard values given in Table 5.1. ○, only hardwoods survived; ■, hardwoods coexisted with a conifer.

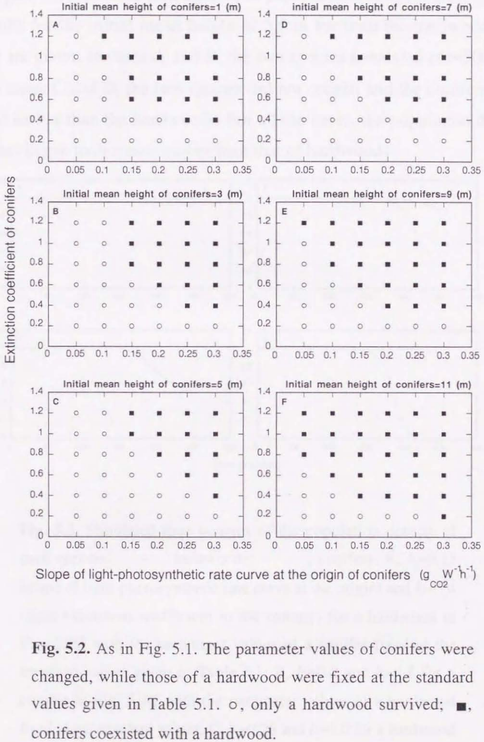

Fig. 5.2. As in Fig. 5.1. The parameter values of conifers were changed, while those of a hardwood were fixed at the standard values given in Table 5.1. ○, only a hardwood survived; ■, conifers coexisted with a hardwood.

Figure 5.3 shows the time courses of population density for each species. The results for the initial mean height of 5.0 m for both the hardwoods and conifers are given. In cases A and B, the two species coexisted at t=500 time units. In cases C and D, the two species did not coexist and the conifers were excluded earlier than the hardwoods. For all the cases, the population density of conifers began to decrease earlier than that of hardwoods.

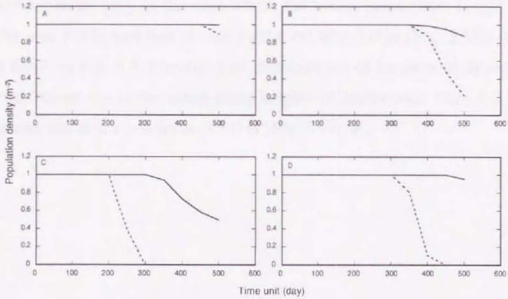

Fig. 5.3. Simulated time courses of the population density of each species. —— , hardwoods; ------ , conifers. A, b_i=0.15 (slope of light-photosynthetic rate curve at the origin) and k_i=0.4 (light extinction coefficient in the canopy) for a hardwood in Fig. 5.2C with the parameter values of a conifer fixed at the standard values given in Table 5.1; B, b_i=0.2 and k_i=0.8 for a conifer in Fig. 5.3C with the parameter values of a hardwood fixed at the standard values; C, b_i=0.25 and k_i=1.0 for a hardwood in Fig. 5.2C with the parameter values of a conifer fixed at the standard values; D, b_i=0.1 and k_i=0.4 for a conifer in Fig. 5.3C with the parameter values of a hardwood fixed at the standard values.

For the case of coexistence, size structures are shown for each species in Figs 5.4 and 5.5. In Fig. 5.4, size distribution of hardwoods became positively skewed, and the vertical layers of conifers and hardwoods were separated with an increasing difference in the initial mean size. However, in Fig. 5.5, size distribution of conifers was positively skewed, and the vertical layer was not separated in all the cases. In Fig. 5.4, a bimodal size distribution of a conifer appeared only in the case where the initial mean plant height of the conifer was 5.0 m and that of the hardwood was 7.0 m (Fig. 5.5D). On the other hand, in Fig. 5.5, bimodal size distributions of hardwoods appeared in the case where the initial mean plant heights of hardwoods were 1.0 m and 3.0 m and that of the conifer was 5.0 m (Fig. 5.5A, B).

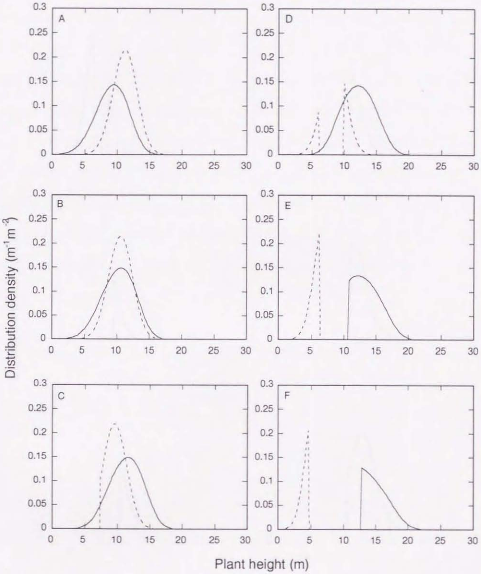

Fig. 5.4. Simulated plant height distribution densities for the coexisting species at t=500 time units (days) where the initial mean plant height of hardwoods was changed (———) with that of conifers (--------) kept at 5.0 m. For the hardwoods, b_i=0.15 and k_i=0.4; the parameter values of the conifers were fixed at the standard values given in Table 5.1. The initial mean plant height of hardwoods was set at: A, 1.0 m; B, 3.0 m; C, 5.0 m; D, 7.0 m; E, 9.0 m; F, 11.0 m.

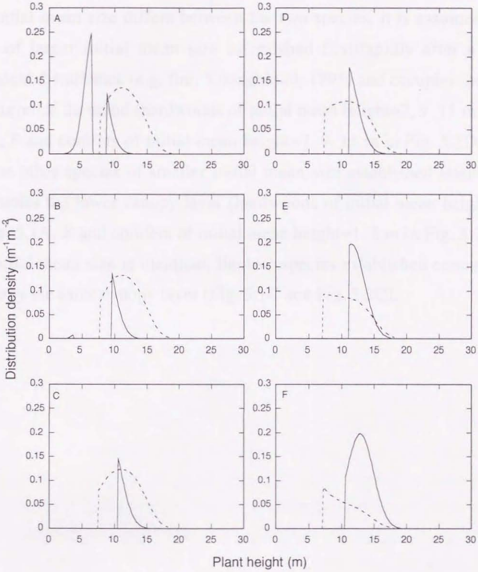

Fig. 5.5. As in Fig. 5.4. In this case, the initial mean plant height of conifers (--------) was changed with that of hardwoods (———) kept at 5.0 m. For the conifers, b_i=0.2 and k_i=0.8; the parameter values of hardwoods were fixed at the standard values given in Table 5.1. The initial mean plant height of conifers was set at: A, 1.0 m; B, 3.0 m; C, 5.0 m; D, 7.0 m; E, 9.0 m; F, 11.0 m.

5.3 Discussion

If the initial mean size differs between the two species, it is assumed that a species of larger initial mean size established first/rapidly after a stand-replacement disturbance (e.g. fire; Youngblood, 1995) and occupies the upper canopy layer of the stand (hardwoods of initial mean height=7, 9, 11 m in Fig. 5.1D, E, F and conifers of initial mean height=7, 9, 11 m in Fig. 5.2D, E, F), while the other species of smaller initial mean size established later/slowly and occupies the lower canopy layer (hardwoods of initial mean height=1, 3 m in Fig. 5.1A, B and conifers of initial mean height=1, 3 m in Fig. 5.2A, B). If the initial mean size is identical, the two species established concurrently and occupy the same canopy layer (Fig. 5.1C and Fig. 5.2C).

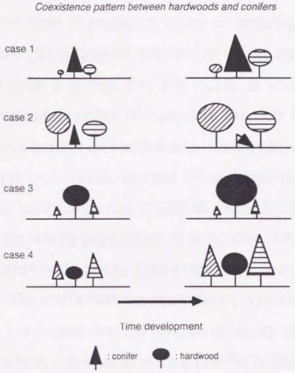

Fig. 5.6. Schematic diagrams for the coexistence between two species having conic (conifer) and spheroidal (hardwood) crown shapes. Case 1, hardwoods with various physiological parameter values can establish later/slowly in the lower canopy layer even if a conifer with the fixed parameter values established first/rapidly and overtops the hardwoods; case 2, a conifer with the fixed physiological parameter values can rarely establish later/slowly in the lower canopy layer if hardwoods with various physiological parameter values established first/rapidly and overtop the conifer; case 3, smallest-sized conifers with various physiological parameter values can persist well in the lowermost layer even if a hardwood with the fixed physiological parameter values established first/rapidly and overtops the conifers; case 4, a hardwood with the fixed physiological parameter values can establish later/slowly in the lower canopy layer even if conifers with various physiological parameter values established first/rapidly and overtop the hardwood.

In the simulations of Fig. 5.1, conifer's parameter values were fixed, while those of hardwoods were changed, in order to investigate how many hardwoods having distinct physiological parameter values can coexist with the conifer in the upper (case 1 in Fig. 5.6; Fig. 5.1A, B where hardwood's initial size < conifer's initial size) or lower (case 2 in Fig. 5.6; Fig. 5.1D, E, F where conifer's initial size < hardwood's initial size) canopy layer. The domain of coexistence between the two species in case 1 was larger than that in case 2, indicating that various hardwoods can establish later/slowly even if they are overtopped by a conifer which established first/rapidly. This suggests that the species diversity of hardwoods can be high even in the lower canopy layer overtopped by a conifer. The result that the coexistence domain in case 2 was smaller than that in case 1 indicates that the species diversity of hardwoods in the upper canopy layer, which can coexist with a conifer in the lower canopy layer, is limited. As the contrapositive proposition, if various hardwoods established first/rapidly and occupy the upper canopy layer, a conifer can rarely establish later/slowly in the lower canopy layer, namely, if the species diversity of hardwoods is high in the upper canopy layer, that of conifers is low in the lower canopy layer.

In the simulations of Fig. 5.2, hardwood's parameter values were fixed, while those of conifers were changed, to investigate how many conifers having distinct physiological parameter values can coexist with the hardwood in the upper (case 3 in Fig. 5.6; Fig. 5.2A, B where conifer's initial size < hardwood's initial size) or lower (case 4 in Fig. 5.6; Fig. 5.2D, E, F where hardwood's initial size < conifer's initial size) canopy layers. In case 3, the coexistence domain became larger with a decreased initial mean size of the conifer. This indicates that the smallest-sized conifers can persist well in the lowermost canopy layer when overtopped by a hardwood. This suggests a waiting strategy of conifers in the understorey of a crowded stand, which was found by Kubota, Konno and Hiura (1994) in a sub-boreal conifer-hardwood mixed-species forest in Hokkaido, northern Japan. In case 4, a larger coexistence domain was realized with an increase in the conifer's initial size. This suggests that even if various conifers established first/rapidly and occupy the upper canopy layer, a hardwood can establish later/slowly in the lower canopy layer.

Case 2 predicts that the species diversity of harwoods which established first/rapidly and occupy the upper canopy layer limits the number of conifer species which can establish later/slowly. In contrast, case 4 predicts that the species diversity of conifers which established first/rapidly and occupy the upper canopy layer does not affect the number of hardwood species which can establish later/slowly. Youngblood (1995) found two types of community dynamics after stand-replacement disturbance in single-cohort conifer-hardwood mixed-species forests at the intermediate-successional stage in interior Alaska, although no discernible difference in associated vegetation or site characteristics was detected between the stands of these two types: in stands of type 1, hardwoods and conifers establish concurrently or conifers establish first/rapidly followed by hardwoods; in stands of type 2, hardwoods establish first/rapidly followed by conifers. In stands of type 1, little suppression in height growth was found for both the conifer (*Picea glauca*) and hardwoods (*Betula papyrifera* and *Populus tremuloides*). On the contrary, in stands of type 2, height growth of the conifer was suppressed by the hardwoods. Youngblood (1995) thus predicted that the stands of type 1 would be eventually dominated by *P. glauca* as described for late-successional *P. glauca* stands in boreal forest (Van Cleve and Viereck, 1981) and that in the stands of type 2 *P. glauca* would never be dominant without reaching up to the top canopy. Therefore, the community dynamics of type 2 stands in Youngblood (1995) is explained by our theoretical prediction, case 2 or case 3, and that of type 1 by case 1 or case 4.

In the present chapter, the species with conic and spheroidal crowns were assumed to be a conifer and a hardwood in a boreal or sub-boreal mixed-species forest, respectively. It is showed that the size-structure dynamics of individuals of conifers and hardwoods changed with both initial mean size (height) and physiological parameters (Figs. 5.4, 5.5). The initial size distribution assumed in the model corresponds to the structural attributes of seedling or sapling banks after natural disturbances such as fire and wind, and the differences in physiological parameter values represent the functional diversity of species. Investigating the effects of initial mean size and physiological traits of the two species on community dynamics, it is derived that the four predictions for the coexistence pattern between conifers and hardwoods either at the sapling stage or in single-cohort stands without continual establishment of the species (Fig. 5.6). The combination of initial sizes at the establishment stage of the two species with different crown architecture affected the segregation of vertical positions in the canopy between the two species. The species coexistence pattern of conifer-hardwood forests is governed by functional relationships between species-specific crown architecture, physiological traits and establishment timing (in terms of initial size in the model).

In the sub-boreal conifer-hardwood mixed-species forest of Kubota and Hara (1995, 1996), the upper canopy layer [layer I and II in Kubota and Hara (1995)] was occupied by three conifers (*Picea glehnii*, *P. yezoensis* and *Abies sachalinensis*) and one hardwood (*Betula ermanii*) and the lower canopy layer [layer III and IV in Kubota and Hara (1996)] was occupied by the same three conifers and three hardwoods (*B. ermanii*, *Sorbus commixta* and *Acer ukurunduense*). The community structure of this sub-boreal forest is explained by our theoretical predictions that the species diversity of hardwoods in the lower canopy layer can be high even if the species diversity of conifers in the upper canopy layer is high and that the low species diversity of hardwoods in the upper canopy layer supports the high species diversity of conifers in the lower canopy layer.

Many studies have investigated mainly species-specific physiological traits (shade tolerance, maximum size, photosynthetic rate, etc.) for species coexistence focusing on the trade-offs between the species. The present study showed that not only the species-specific physiological traits but also the crown architecture is important for the pattern of species coexistence. Even for the same combination of physiological parameter values, the pattern of species coexistence differs depending on the crown architecture. Therefore, the crown architecture should be included for the study of species coexistence, especially in conifer-hardwood mixed-species forests.

Chapter 6
Conclusion

First, I summarize the results of the preceding chapters and address the applications and further investigations using the models in this thesis.

In Chapter 2, a dynamic model for growth and mortality of individual plants in a stand was developed, based on the process of canopy photosynthesis, and assuming an allometric relationship between plant height and weight, i.e. allocation-growth pattern of plant height and stem diameter. Functions $G(t,x)$, for the mean growth rate of individuals of size x at time t, and $M(t,x)$, for the mortality rate of individuals of size x at time t, were developed from this model and used in simulations. The dynamics of size structure were simulated, combining the continuity equation model, a simple version of the diffusion model, with these functions. Simulations reproduced several well-documented phenomena: (1) size variability in terms of coefficient of variation and skewness of plant weight increases at first with stand development and then stabilises or decreases with an onset of intensive self-thinning; (2) during the course of self-thinning, there is a power relationship between density and biomass per unit ground area, irrespective of the initial density and of the allocation-growth pattern in terms of the allometric parameter relating plant height and weight. The following were further shown by simulation: (i) competition between individuals in a crowded stand is never completely one-sided but always asymmetrically two-sided, even though competition is only for light; (ii) plants of 'height-growth' type exhibit a greater asymmetry in competition than plants of 'diameter-growth' type; (iii) the effect of competition on the growth of individuals in a crowded stand converges to a stationary state, even when the stand structure still changes greatly. All of these theoretical results can explain recent empirical results obtained from several natural plant communities. Finally, a new, general functional form for $G(t,x)$ in a crowded stand was proposed based on these theoretical results, instead of *a priori* or empirical growth and competition functions.

In Chapter 3, sensitivity analysis was conducted, based on the canopy photosynthesis and continuity equation models which were developed in Chapter 2, to investigate effects of variation in physiological parameters (maximal photosynthetic rate per unit leaf area, respiration rate per unit leaf area, maintenance respiration rate per unit weight, growth respiration rate per unit weight, light extinction coefficient of the canopy, etc.) on the size-structure dynamics in plant populations. As the degree of asymmetry in competition between individuals increased, effects of variation in physiological parameters diminished. Therefore, a population undergoing one-sided competition (the most asymmetric competition) is a stable system, little affected by temporal and spatial variations in the environmental conditions which lead to variation in physiological parameters, whereas a population undergoing symmetric two-sided competition is sensitive to these fluctuations. It was also shown by simulation that the degree of asymmetry in competition decreases (through effects on canopy photosynthesis) as nutrient level in the soil is reduced. It was suggested that symmetric two-sided competition is associated with non-transitivity of competition between species (i.e. frequent reversals of rank order of species), and hence with species diversity. Several other ecological phenomena were discussed in relation to allometry (i.e. allocation-growth pattern) and the degree of asymmetry in competition.

In Chapter 4, the relationships between vertical foliage profile of an individual plant, competition between individuals, size structure and allocation pattern between stem diameter (*D*) and plant height (*H*) were investigated using canopy photosynthesis and two-dimensional continuity equation models including *D* and *H* as two independent variables. Broad-leaved type plants (more foliage mass in the upper layer than in the lower layer of the canopy of an individual when grown in isolation) showed curvilinear *D*-*H* relationship and bimodal *H* distribution, and underwent more asymmetric competition than coniferous type plants (more foliage mass in the lower layer than in the upper layer of the canopy of an individual when grown in isolation) under crowded conditions. Coniferous type plants showed almost linear *D-H* relationship (i.e. simple allometry) and unimodal *H* distribution, and underwent more symmetric competition than broad-leaved type plants under crowded conditions. However, in both the cases *D* distributions were unimodal. Allocation patterns between *D* and *H* affected these features only a little. These simulation results can explain many actual data already published. The value of η for an individual plant (foliage profile parameter of an individual canopy representing a species-specific branching pattern and canopy morphology when grown in isolation) governed size structure (bimodal or unimodal), the mode of competition, *D-H* relationship and mean *D* - mean *H* trajectory with time under crowded conditions. Therefore, a simple view of the competition-allometry relationship that competition determines allometry should be reevaluated incorporating the foliage profile of an individual. These theoretical results should also be important when studying species coexistence. The canopy tends to be multi-layered in broad-leaved type plants and mono-layered in coniferous type plants. Therefore, it was hypothesized that species coexistence in the former is mainly by way of separation of vertical space (i.e. niche separation under strongly asymmetric competition) and that species coexistence in the latter is due to nearly symmetric competition in a single canopy layer.

In Chapter 5, the relationships between crown architecture and species coexistence were studied using the continuity equation model and the canopy photosynthesis model for multi-species plant communities. The model in this chapter dealt with two species having different crown shapes (conic and spheroidal), for various initial mean sizes at the establishment stage and physiological parameter values (photosynthetic rate, etc.). The species with conic and spheroidal crowns in the model were assumed to be conifers and hardwoods in boreal or sub-boreal forests, respectively. Recruitment processes were not incorporated in the model, and thus simulations were made for the effects on the pattern of species coexistence of either sapling competition starting from different sapling banks or competition in single-cohort stands with little continual establishment of the species until a stand-replacement disturbance. The following predictions were derived: (1) hardwoods can establish later/slowly in the lower canopy layer even if they are overtopped by a conifer which established first/rapidly; (2) if hardwoods established first/rapidly and occupy the upper canopy layer, a conifer can rarely establish later/slowly in the lower canopy layer; (3) smallest-sized conifers can persist well in the lowermost canopy layer overtopped by a hardwood, suggesting a waiting strategy of conifers, saplings in the understorey of a crowded stand; (4) even if conifers established first/rapidly and occupy the upper canopy layer, a hardwood can establish later/slowly in the lower canopy layer. Therefore, the species diversity of hardwoods which established first/rapidly and occupy the upper canopy layer limits the number of conifer species which can establish later/slowly. In contrast, the species diversity of conifers which established first/rapidly and occupy the upper canopy layer does not affect the number of hardwood species which can establish later/slowly. The combination of initial sizes of a conifer and a hardwood at the establishment stage (i.e. establishment timing) affects the segregation of vertical positions in the canopy between the two species with different crown shape, and not only species-specific physiological traits but also crown architecture greatly affects the coexistence pattern between conifers and hardwoods. The theoretical predictions obtained here can explain several phenomena found in single-cohort conifer-hardwood mixed-species forests, pointing to the significance of crown architecture for species coexistence.

Applications of the models and further investigations

The dynamic size-structured models (i.e. dynamic canopy photosynthesis models together with continuity equation) developed in this thesis simulated various behaviours of plant communities, i.e. self-thinning, competition and species coexistence, etc. The models are not empirical but mechanistic incorporating several physiological processes, i.e. canopy architecture, light-photosynthesis response, leaf respiration, and growth respiration, etc. With the models, effects of physiological variations brought about by environmental changes (e.g. global climate change, etc.) on size structure and species coexistence will be predicted theoretically.

From the results of simulations in this study, I proposed a general growth equation in a crowded stand, eqn (2.18). This equation has a simple structure and the competition function $C(t,x)$ [in eqn (2.18)] is easily determined from actual data. This equation has been extended to multi-species plant communities and clonal plants to investigate size-structure dynamics, competition modes and species coexistence conditions in natural plant communities. Using this equation, Hara, Nishimura and Yamamoto (1995) and Kubota and Hara (1995) investigated the mechanisms of species coexistence in a cool-temperate forest and in a subboreal forest, respectively; Suzuki (1994) investigated shoot competition processes of the clonal plant, *Polygonum cuspidatum*, in Mt. Fuji; Kikuzawa and Umeki (1996) investigated the relationship between competition mode and foliage structure in artificial populations of the two useful species for forestry, *Betula ermanii* and *Picea abies.*

I showed that canopy architecture is especially important for the dynamics of plant communities under light competition. Therefore, further investigations concerning canopy architecture are needed from the viewpoint of genetic character, evolution and development of individuals for ecological processes in natural plant communities. Moreover, direct implementation of not only aboveground competition processes but underground competition processes to the models is also needed in the future.

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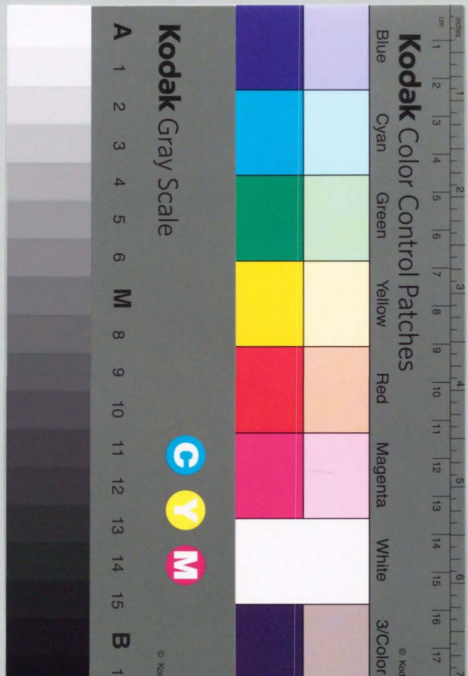
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