J. Plant Res. **107** : 107-116, 1994

Journal of Plant Research

Invited Article

Size-Structure-Based Models of Forest Dynamics to Interpret Population- and Community-Level Mechanisms

Takashi Kohyama*

Center for Ecological Research, Kyoto University, Shimosakamoto, Otsu, 520-01 Japan

Functional size-structure-based models of forest tree population dynamics present a unifying explanation for population-level patterns and tree community organization. Density-dependent regulation can be explicitly replaced by the effect of size-structure-dependent suppression on demographic processes in functional size-structure models. This suppression effect sufficiently explains various patterns reported for crowded even-aged populations. Further, it stabilizes natural forest populations of overlapping generations at a stationary state with balanced recruitment and mortality. The spatial heterogeneity of light resources created by tree size structure offers an opportunity for multiple species to coexist by means of trade-offs between demographic parameters. The energy correlation of tree species diversity at a geographic scale is also attributable to the architectural feature of forests.

Key words: Coexistence — Density dependence — Gap dynamics — Metapopulation — One-sided competition — Size structure — Species diversity — Tree community — Tree population

Physiological attributes of a plant individual are strongly related to its developmental stage, or size. Individual size varies widely even between the same-aged plants due to the change in size growth rate with local site condition, the intensity of interaction between plants, and so on. Such size variability or plasticity of plants makes it difficult to describe the population-level dynamics (Harper 1977).

Plant population studies have, however, coped with this difficulty, and discovered patterns of density-dependent regulation of plant size growth particularly in the even-aged monocultures within a generation (Hozumi 1973, Harper 1977, Silvertown 1987). These density-dependent patterns are complex, and have prevented the inclusion of monoculture-level understandings into the dynamics of natural populations between generations and natural multi-species systems which are dealt with in plant community studies.

Terrestrial plants rely on solar energy for their photosynthesis. The vertical component of plant size distribution or the size hierarchy within a local stand largely affects the fate of each plant. To describe the dynamics of plant size distribution, we can employ mathematical models that allow both theoretical and numerical analyses. We can include such functional properties as the size-structure dependence of demographic behaviour into the model. This article reviews recent studies of functional size-structure models of terrestrial plants, which offer a new paradigm combining population- and community-level studies through functional constraints at the individual level.

I deal primarily with forest tree populations and communities throughout here, because the size-structured feature plays an emergent role particularly in forest ecosystems. Annual and herbaceous perennial systems develop size structure with each growing season, and the size-structure dependence does not last until the next season/until. A tree as a component of forest systems is an ecological life form characterized by cumulative development of three-dimensional architecture throughout its life. Such a life form is advantageous in exploiting light resources at the aboveground part. Newly-formed leaves can enjoy better-lit conditions as the surface of tree crown gains in height. Consequently, forests, where trees co-occur densely, maintain a stout above-ground architecture over seasons. The decline in light resources along a vertical profile is a stable characteristic of forests, and recruits need to grow up through this gradient. The shifting gap mosaic of stands initiated by the fall of large trees is then another characteristic of forests (Yamamoto 1992). It introduces temporal-horizontal variation in the vertical light gradient and chance opportunities for small individuals to receive more light resources. Thus the dynamics of forest tree populations depend strongly on the size distribution of all trees regardless of species, within a forest stand, and on the shifting mosaic among stands.

Tools of Modelling Size Distribution Dynamics

We can sufficiently describe the dynamics of size-structured tree populations by three demographic processes, i.e. size growth rate, survival rate (or mortality), and

---

* Recipient of the Botanical Society Award of Young Scientists, 1992.

recruitment rate. We derive the size growth rate from field censuses as an attribute of each tree, while survival and recruitment rates as population- or stand-level measures. These three fluxes are measurable by repeated censuses of marked trees in permanent plots.

The size projection matrix model (Lefkovitch 1965, Caswell 1989) has been applied to describe the size-structure dynamics of forest tree populations (Harcombe 1987). The projection matrix includes all the above three demographic processes. A merit of the projection matrix model, while outside the interest of this article, is that it is applicable not only to any arbitrary size class but to qualitative developmental stages. When a projection matrix does not change over time, a theoretical consequence of the matrix model is that the system converges to the state where the population size changes exponentially while keeping proportionally 'stable' (not stationary !) size distribution (Lefkovitch 1965). Some studies of forest tree populations have thus concluded the stability of 'climax' populations from near-zero intrinsic growth rate of simulated populations and the agreement between a simulated 'stable' distribution and an observed one (Hartshorn 1975, Lorimer and Frelich 1984, Harcombe 1987). However, these studies were carried out in forests which approximate to a steady state where demographic rates are strongly controlled by that crowded state. One can explicitly include a density-dependent depression effect into the projection matrix cells (e.g. Solbrig *et al.* 1988) ; but such a study has hardly been carried out for forest tree populations (Alvarez-Buylla 1994).

Another approach of modelling size structure dynamics is to apply the one-dimensional continuity equation of fluid dynamics with a mortality term (Sinko and Streifer 1967, VanSickle 1977, Metz and Diekmann 1986, Vance *et al.* 1988). To describe the dynamics of a distribution density function in terms of size, the equation requires continuous size-dependent functions of size growth rate and mortality. The recruitment process, which should be a function of size distribution of mother trees in a closed system, defines the lower boundary condition with respect to plant size. Compared with projection models which inevitably describe size and time in discrete units, the continuity equation model has the advantage of dealing with time and size as the continuous variables that they are. Convergence to the state of exponential population growth with 'stable' size distribution is a theoretical consequence of the continuity equation model with time-independent demographic functions (VanSickle 1977), just as it is in the discrete projection matrix model. We can extend the continuity equation model to include the effect of variability in size growth rate at the same tree size, by adding the diffusion term to the continuity equation (Suzuki 1966, Hara 1984a, b, Metz and Diekmann 1986). Hara (1984a) provides a good guide for derivation of growth, diffusion (ingrowth), and mortality functions of the diffusion equation from the field data. Continuous models have been applied to artificial forest stands (Umemura and Suzuki 1974) and natural rain forest stands (Nagano 1978, Kohyama 1987) where demographic functions were treated as time-dependent.

Demographic functions change with time in crowded plant populations, but when we take into account the underlying processes of competition for light resources, we can express these functions in terms of the instantaneous size structure. Takada and Iwasa (1986) modelled the dynamics of size distribution for an even-aged population where the growth rate of a plant of a given size was suppressed by the one-sided integration of size distributions larger than that size. Kohyama (1989) introduced a one-sided competition index and simulated the stand development of a warm-temperate rain forest using the continuous model. As the data available were dbh (trunk diameter at breast height) censuses, Kohyama used cumulative basal area, which is the cumulative density of section area of trunks for trees larger than the size of the subject tree, as a one-sided competition index. The section area of a trunk is roughly proportional to the total leaf mass of a tree, which is supported by the pipe model theory (Shinozaki *et al.* 1964). Therefore, the cumulative basal area above a given size is roughly proportional to the leaf mass density above the tree of that size. Yokozawa and Hara (1992) simulated the change in plant weight distribution for an idealized model population. They incorporated into the continuity model the physiological parameters of individual processes, light absorption by upper leaves, and allometry between individual weight and height.

Two contrasting models, the discrete matrix model and the continuous diffusion model, describe the same process, and they should be mutually related. Actually, when we simulate size structure dynamics with continuous model in a digital computer, we need to approximate the continuous equations to discrete ones, differential to difference, and integration to summation. Takada and Hara (1994) made a notable contribution to this exercise. For the process of plant size projection (excluding reproduction), they proved the following : the forward and backward one-step projection matrix, i.e. a matrix where plants of a given size class can move to neighbouring smaller or larger class in a unit time step, corresponds to the diffusion equation (with size variance term) of the continuous model. They also showed that n-step matrix corresponds to the 2n-th-order expansion of the diffusion model. However, such a bilateral movement is not realistic for the life form of trees. For plants exclusively with positive growth rate, only the forward-direction projection occurs. They also analysed the case of forward projection, and showed that the one-step projection matrix corresponds to the continuity equation without the diffusion term, the two-step one to the diffusion equation, and three-step one to the 3rd-order expansion of diffusion equation. The number of steps depends on the resolution of observation, or the ratio of size class width to time interval. Usually, projection matrices of forest trees have forward one-step projections (Hartshorn 1975, Harcombe 1987), which are described sufficiently by the continuity equation. The positively skewed distribution of size growth rate in the same size class is generally observed in tree populations. To evaluate the effect of the skewness in growth rate distribution, we must apply the 3rd-order expansion of diffusion equation (Kohyama and Hara 1989). Takada and Hara further suggested that the scheme of difference approximation of the diffusion model should be different between the forward-type projections and bilateral-type projections. It is worth mentioning here the Takada-Hara scheme of the backward difference approximation of continuous models for tree populations corresponding to the forward projection matrices (Appendix).

Population Models and Stationary Distribution

The population-level consequence of the size-structure-dependent regulation of individual plant demography can be tested by size-structure-based models.

Yokozawa and Hara (1992) modelled the time course of an even-aged monoculture. Their model plants have conical distributions of leafy crowns, and every plant has the same lowest height of crown because of the pruning of lower leaves with negative net assimilation rate. They calculated gross assimilation and respiration of individual plants along a stand-level vertical light gradient, and derived individual growth rates depending on the vertical leaf distribution. Plants with negative net assimilation rate died. Simulation results reproduced well-documented population-level phenomena (Table 1).

Kohyama (1989, 1992b) employed a contrasting approach for simulating population development. He semi-empirically obtained size growth and mortality functions from data of repeated tree dbh censuses in natural rain forests. Growth rate in the same size class decreased linearly, and mortality increased linearly, as the cumulative basal area increased. The employment of these functions dependent on the cumulative basal area means that the model assumed completely one-sided competition for light without crown overlap. This one-sided-competition model successfully reproduced the time course of stand development (Kohyama 1989). The same model reproduced population-level phenomena (Kohyama 1992b, Table 1), just like the Yokozawa-Hara model with no crown stratification.

Analyses of the sensitivity of population-level responses to changing physiological parameters (Hara and Yokozawa, 1994) and changing spatial dispersion pattern of individuals (Hara and Wyszomirski, 1994) show that one-sided competition, or the dominating effect of crown hierarchy, diminishes effects of these variations.

The mixed-cohort simulation, based on the observed species-specific parameters of forest trees, gave significant results (Kohyama 1992b): fundamentally the same phenomena as occurred in single species cohorts were reproduced in terms of the summation of species, but not for each species cohort. The results agree with what Bazzaz and Harper (1976) found in mixture experiments of two winter annual species (Table 1).

All of these results suggest that (1) population-level patterns reported can be explained by a single individual-level mechanism, i.e. size-structure-dependent depression of growth and survival, and consequently, (2) the so-called 'population-level' patterns of density dependence are not single-species-level attributes but actually patterns of groups of individuals of similar life forms irrespective of differences between component species.

Studies with size-structure models have not yet perfectly reproduced reported patterns in crowded cohorts over time (Table 1). Yokozawa and Hara (1992) and Kohyama (1992b) simulated the convergent upper boundary line with self-thinning on the density-yield coordinates, but slopes of these thinning lines did not fit to the $-2/3$ rule of self-thinning (Yoda *et al.* 1963, Westoby 1984, but see critical reviews e.g. Weller 1987, Lonsdale 1990). Two models have simulated dynamics in only one size dimension. A simple explanation of the $-2/3$ rule of self-thinning is that the stand canopy develops vertically maintaining a state of full coverage of leaf density over a projected area (Yoda *et al.* 1963, Westoby 1984). Therefore, two-dimensional expansion of the size-distribution model (such as trunk diameter and tree height) is necessary to reproduce this pattern. Similarly, the shift of cohort-level allometries with stand development (e.g. Kohyama *et al.* 1990) should be tested in two-dimensional size-distribution model (Table 1). Such an expansion of continual diffusion model is easily derived (Suzuki 1966), and there is no substantial difficulty in possible two-size-dimensional simulations. Thus we can expect to get results of such simulations in the near future.

On the other hand, the effect of local-crowding which changes the spatial dispersion pattern through self-thinning is difficult to simulate in size-structure-based models (Table 1). Individual-based simulation models (e.g. Firbank and Watkinson 1985) are more appropriate. However, the inclusion of patch-level spatial heterogeneity into the size-structure model as an alternative model has been carried out as is seen later.

By applying the same framework of a one-sided-competition model (Kohyama 1989, 1992b), we can describe the dynamics of tree populations of overlapping generations, as in natural forest stands. The observed recruitment rate decreases with stand crowding, and we again obtain a size-structure-dependent function of recruitment rate (Kohyama 1991). The simulation of a functional size-structure model including the recruitment process converged to unique stationary (not 'stable') size distributions, where recruitment and growth were balanced by mortality. The agreement of the simulated stationary distribution to the observed distribution in primary forest stands was satisfactory in two simulations of different rain forests. The all-species-averaged data of dynamics were fitted to the demographic function in simulations. Variance in growth rate of a given size, which may reflect the species differences, had little effect on simulation results. Therefore, these results suggest the prevailing importance of

Table 1. Density-dependent patterns reported for even-aged stands, and reproduction by size-structure-dependent model of a mono-storied cohort (Yokozawa and Hara 1992)[1] and that of multi-storied cohort (Kohyama 1992b)[2]

Patterns successfully reproduced by models

Hyperbolic density-yield relationship (Shinozaki and Kira 1956, Watkinson 1980)[1,2]

Upper yield bouneary by self-thinning (Yoda *et al.* 1963, Westoby 1984)[1,2]

Decreasing size variability with self-thinning (Kohyama and Fujita 1981, Weiner and Thomas 1986)[1,2]

Decreasing skewness of size distribution with self-thinning (Koyama and Kira 1956, Ford 1975)[1,2]

Density-yield patterns only irrespective of species in multi-species system (Bazzaz and Harper 1976)[2]

Patterns not yet reproduced by models

The density-yield line of self-thinning with slope around −0.5 (Yoda *et al.* 1963, Westoby 1984)

Change with time in stand-level allometries, e.g. trunk diameter versus tree height (Kohyama *et al.* 1990)

Change in spatial dispersion pattern with time (Kohyama and Fujita 1981)

the size-structure-dependent regulation on the average growth rate level.

Sensitivity analysis showed that changing recruitment rates had little effect on the stationary size structure in the one-sided-competition model, but the effect was remarkable in an alternative two-sided-competition model of growth rate suppression (Kohyama 1991). Hara (1992) analytically confirmed this stabilizing effect of one-sided competition and little contribution of variance term under the regulation of one-sided competition.

The stationary-state forest simulated by Kohyama (1991) has no spatial heterogeneity due to gap dynamics (Yamamoto 1992). To include the spatial mosaic of stands which reflects processes of gap formation and succeeding stand regeneration, it is useful to introduce the idea of the demography of a metapopulation, i.e. the 'population' composed of local populations as units (Roughgarden and Iwasa 1986, Gilpin and Hanski 1991, Alvarez-Buylla and García-Barrios 1993). The usual dynamic models of age-structured populations can be applicable to stand age distribution (Fig. 1a). The age of a stand does not correspond to the age of trees therein because there usually exists trees which survive gap formation and recruitment proceeds in stands of any age.

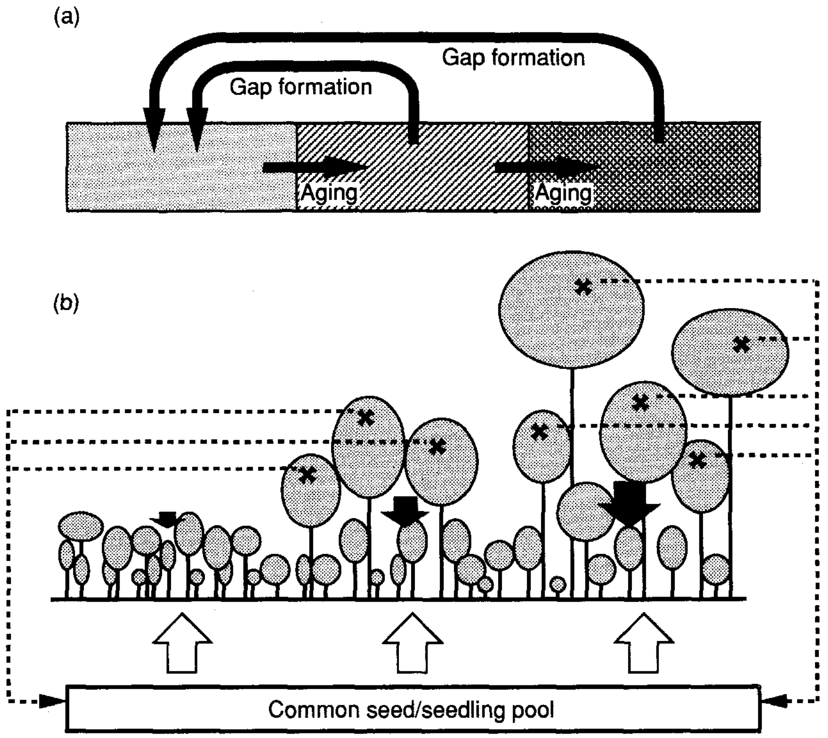

Fig. 1. Diagram of gap-dynamic size-structured model of forest trees (Kohyama 1993a). (a) Submodel of stand 'demography', or the dynamics of stand age distribution ; where dead stands immediately reborn to form gap stands. (b) Submodel of tree size distribution; where size-structure-dependent suppression occurs locally, i.e. in stand-age-specific manner (solid downward arrows), while the potential recruitment rate is the function of the density of seed trees (cross-marked) in a whole forest (open upward arrows).

So, besides the submodel of stand age distribution, we need another submodel describing the size distribution of trees in each stand (Fig. 2b). For the second submodel, we can employ the continuous model of age-size-structured populations (Sinko and Streifer 1967, Metz and Diekmann 1986, Vance *et al*. 1988). Kohyama (1993a) presented the size-structure model of tree populations in gap-dynamic forests, based on this idea of coupling stand demography and the dynamics of individual size structure in each stand. The simulation results for species-averaged system reproduced the gap-dynamic state of a warm-temperate rain forest. Now the convergent unique equilibrium is such that both stand age structure and tree size structure at each stand are maintained at the stationary state. The simulated size distributions fit well to the observed distributions in gaps and closed stands. We can also apply such a metapopulation model with size-structured local populations to the landscape-level dynamics of forests.

Community Models and Conditions for Species Coexistence

Kohyama (1992a) explicitly extended the functional size-structured model to a multi-species system. There, suppression intensity by larger trees in terms of light interception is proportional to individual basal area irrespective of species, or it does not include a species-to-species-specific competition coefficient. Usually, there exists a convergence in allometries among coexisting forest tree species (Ogawa and Kira 1977). The assumption of the model means that allometry between trunk diameter and tree height and that between trunk area and leaf mass are not significantly different between co-occurring tree species. Tree growth rate is suppressed by cumulative basal area of larger trees, and recruitment rate is suppressed by total basal area.

Two kinds of model simulation were carried out based on the estimated parameters from the repeated census data in a warm-temperate rain forest: one used an open reproduction system allowing the system-independent potential recruitment for each species, and the second used a closed system where the recruitment of each species relied exclusively on the population within the model system. The open-system simulation successfully reproduced secondary succession over time and attained a stationary state of a multi-species system after several hundred years. The closed-system simulation also converged to an equilibrium coexistence between species within a limited range of species parameters; however, it took a quite long time (more than 10,000 years) to attain to a state of stable coexistence (Kohyama 1992a).

The gap-dynamic version of the size-structured multi-species model, which employed an entirely closed reproduction system at a whole forest level (Fig. 1), again simulated convergence to stable coexistence. Compared with a gap-averaged model, the inclusion of a gap mosaic extended the possibilities of coexistence and shortened the time for convergence to equilibrium to around a few thousand years (Kohyama 1993a).

For a closed multi-species system in models, a stronger species in terms of any one parameter of demographic processes exclude lesser species, when other parameters are retained the same between species. Then, Kohyama (1993a) tested every possible pair of parameters with counter effect in two-species systems in models. In the gap-averaged model, only the trade-off between potential maximum size and potential per-capita rate of recruitment had a region of stable coexistence (Fig. 2). By contrast, in the gap-dynamic model, the range of coexistence was wider in the same trade-off, and further, every trade-off relationship between parameters (except those with the parameter of susceptibility to suppression of recruitment rate) had the range of coexistence. It is easy to understand these results: species stratification is a necessary condition for size-structured but gap-averaged systems, but it is not necessary in horizontally heterogeneous gap-mosaic systems. The trade-off between maximum size and reproduction rate reflects the fundamental constraint in allocation between vegetative and reproductive growth, found in any kind of organism. In gap-dynamic forests, less tolerant species can coexist with more tolerant species with slower potential size growth rate at the same stratum by segregation into local stands at different regeneration stages. This trade-off between tolerance and potential growth rate is also a consequence of physiological processes.

Patch dynamics in a mosaic landscape cannot itself facilitate coexistence of many species, when populations are not size-structured (Levin 1976). Multi-site mosaic models without size structure for each site have been applied to theoretical community studies. Factors which allow several species to coexist have been identified as the temporal fluctuation in establishment in vacant sites (Chesson and Warner 1981, Ågran and Fagerström 1984, Shmida and Ellner 1984), the local segregation of species due to the prevailing establishment success nearby adults (Shmida and Ellner 1984), and conversely, reciprocal replacement, or the tendency of avoiding within-species regeneration in a given site (Whittaker and Levin 1977).

Tilman (1982) theoretically examined resource-population systems. He showed that differences in efficiency of use of resources between species play an important role in community organization. At most *n* species can coexist when *n* resources are subject to competition. He also showed that environments with lower rates of supply of resources will support more plant species through finer segregation in spatial heterogeneity in supply ratio of plural resources, which is called the 'resource-ratio hypothesis'. Tilman (1988) simulated size-structured terrestrial plant systems, where light (along a vertical gradient) and soil nitrogen were the resources of interest. He gave results, however, along his resource-ratio hypothesis and did not suggest the possibility that the light resource alone can promote multiple-species coexistence.

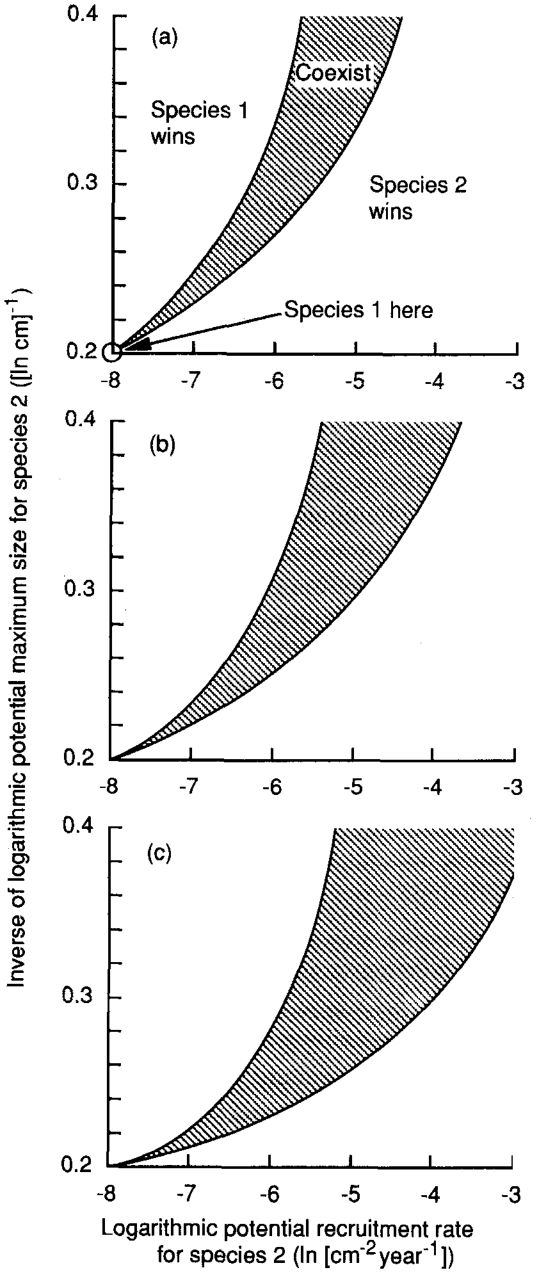

Fig. 2. Dependence of the stable equilibrium state of two-species sysyem on two model parameters in the gap-averaged size-structured model. Other model parameters are identical between two species. Lateral and vertical axes give increasing per-capita recruitment rate and the decreasing potential maximum size for species 2, respectively, keeping the trait of species 1 on the left-bottom corner. The intrinsic rate of relative size growth (for trees at 2.718 cm dbh) is respectively 0.03, 0.04 and 0.05 cm cm^{-1} year^{-1} for (a), (b) and (c). The model and other parameters in Kohyama (1993a, Table 2).

Table 2 summarizes the results of competition models of closed systems of sessile organisms in stable environments. We can see that the persistent size structure plays a fundamentally important role in the organization of forest tree communities. A gap mosaic is important, however, because it allows more possibilities for species to coexist. Tree size structure in local stands and shifting mosaic of stands in a forest create spatial heterogeneity in the essential light resources. Therefore, the conclusion of size-distribution-mediated coexistence can be classified to be a variant of the spatial heterogeneity theory of coexistence (Levin 1976, Tilman 1982, 1988). However, the case of a forest system is unique because that tree populations create a structural pattern of resource heterogeneity in space. Hence, to emphasize the essential role of forest architecture in the coexistence of tree species, Kohyama (1993a) proposed the 'forest architecture hypothesis'.

In the coexistence of tree species, Hara (1993) pointed out the importance of the diffusion term, i.e. the variance in size growth rate among trees of identical size at the same time. He applied the gap-averaged version of the multi-species model of Kohyama (1992a), and found that inferior species in terms of susceptibility to suppression can coexist with superior species when the variance term of inferior species is sufficiently larger. Hara carried out simulation for 1,500 years which were usually one-order shorter than the time system requires to attain to a steady state in my simulation results (Kohyama 1992a, 1993a). He tested only for the trade-off between suppression susceptibility and growth-rate variance. Thus, we need further analyses to answer how differences among species in the variance of size growth rate contributes to the coexistence of plant species.

It is still worth evaluating the preliminary results of Hara (1993) in relation to those of other studies. Begon and Wall (1987) analysed an abstract (i.e. not size-structured) two-species competition model which took into account the within-species variation in population growth rate. They found stable coexistence mediated by the variation. Within-species variation in their model can be realized in a size-structured model through either the variation between individuals of different sizes (Kohyama 1992a) or the variation between individuals of the same size (Hara 1993). We have not yet measured any species with obviously wider variance in size growth rate than other coexisting species (Kohyama and Hara 1989, Kohyama 1992a), although we can expect that pioneer species will have wider variation along a light regime than non-pioneers. The shifting gap mosaic of forests allows pioneers to coexist with non-pioneers (Kohyama 1993a). Coexistence between species with different variances in growth rate, suggested from the gap-averaged diffusion model (Hara 1993), possibly support the gap-mosaic-mediated coexistence of pioneers and non-pioneers, concluded from the explicit gap-dynamic model (Kohyama 1993b).

Botkin *et al.* (1972) proposed an individual-based simulation model of multi-species forest systems. Since then, this model has been revised and used to describe dynamics in various forests (Shugart 1984, Huston *et al.* 1988, Botkin 1992, Urban and Shugart 1992). As these so-called 'gap models' (Shugart 1984) simulate the fate of each individual, the usual spatial scale of simulation is in

Table 2. Consequences of competition models for sessile perennial organisms without temporal fluctuation factor

	Gap-averaged	Gap-dynamic
Size-averaged	No coexistence*	No coexistence*
Size-structured	Coexistence by stratification	Coexistence by various trade-offs

* Only in particular case when the ratio of per-capita reproductive rate to mortality is identical between species, 'meta-stable' (*sensu* Levin 1976) coexistence occurs.

a patch of limited area, or in a gap surrounded by the background forest. The assumptions and the modelling scheme of gap models are fundamentally the same as my size-structure-based multi-species model (Kohyama 1992a, b, 1993a). Therefore, a difficult but possible simulation study with a closed-system individual-based model should reach the same conclusions as of the forest architecture hypothesis, though it has not yet been carried out. The same difficulty in otherwise more realistic gap models prevents straightforward extension of individual-based simulation to gap dynamics and landscape-level dynamics. For this kind of extension, it is necessary to employ a hierarchical procedure to relate fine-scaled gap models to broader-scaled models (Horn *et al.* 1989, Shugart *et al.* 1992). An advantage of the simpler size-distribution-based model is the capacity of straightforward extension to metapopulation-level without worrying about the total number of individuals in simulation (Kohyama 1993a).

Tree Species Diversity and the Forest Architecture Hypothesis

The forest architecture hypothesis can explain to a fair extent the geographic pattern of tree species diversity (Kohyama 1993b). Recent extensive investigations (Adams and Woodward 1989, Currie 1991, Rohde 1992) show that the prime determinant of tree species diversity is available environmental energy which also determines primary productivity. As Whittaker (1972) and Begon *et al.* (1986) describe, environments with high light energy supply will offer a wider range of light gradient, thus support more tree species in a vertical profile of forest. However, this explanation is insufficient because of a critical drawback, or 'a further consequence', 'that the tallest species must be able to operate over the whole range of light intensities, as they grow up from ground level to the upper canopy' (Begon *et al.* 1986, p. 793). The functional size-structure models have enabled us to overcome this drawback (Kohyama 1992a, 1993a).

The functional size-structure-based multi-species model suggests that (1) larger or taller forest can support more species; (2) the higher are all demographic rates, the faster the whole system attains a stable equilibrium; and (3) systems with higher tree growth rate relative to other demographic rates can support more species. These facilitative factors work multiplicatively in high energy environments such as tropical lowland rain forests.

The coexistence condition analysis showed that the larger the size differences are, the easier it is for species to coexist (Kohyama 1993a, Fig. 2). Taller stature and a less asymptotic curve of tree height against trunk diameter in tropical rain forests than other types of forests (Kira 1978) provide wider opportunities for tree species to coexist by means of stratification.

If a high energy environment accelerates all demographic parameters at the same magnitude, a clear consequence is that the system will converge to a stable equilibrium faster, while the possibility of coexistence at equilibrium is the same as in the slower system. Actually, it is more probable that trees grow faster compared with other demographic rates in more productive tropical rain forests (Kohyama 1993b). When only the potential size growth rate of trees is increased, the size-structure model suggests that the range of coexistence becomes wider (Fig. 2).

There exists a general tendency that tropical rain forests have one-order higher tree species richness than extra-tropical forests. It is difficult to explain this by any one resource axis. However, taking into consideration the correlated increase of high stature and primary productivity along the energy gradient, it is possible to explain an order difference of diversity from the forest architecture hypothesis. The reason why the energy correlation of diversity is only clear in forest trees among plant life forms (Grubb 1987) can be also answered by the persistently size-structured feature of forest communities.

In conclusion, the condition that the size structure of plant populations determines the spatial distribution of available light resources effectively explains various patterns at both the population and community levels. We can draw a positive view in the synthesis of plant ecological studies such that the physiology-based description of species traits will directly facilitate the understanding of populations and communities, by means of the size-structure-based modelling.

I thank Takenori Takada, Toshihiko Hara, Tohru Nakashizuka, Shin-ichi Yamamoto, Tamiji Inoue and Peter Bellingham for invaluable discussions and suggestions. I acknowledge the Faculty of Education of Kagoshima University: my essential findings based on the size-structure model emerged when I was there.

References

Ågren, G.I. and Fagerström, T. 1984. Limiting dissimilarity in plants: randomness prevents exclusion of species with similar competitive abilities. Oikos **43**: 369-375.

Alvarez-Buylla, E.R. 1994. Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. Am. Nat. **143**, 155-191.

Alvarez-Buylla, E. and García-Barrios, R. 1993. Models of patch dynamics in tropical forests. Trends Ecol. Evol. **8**: 201-204.

Bazzaz, F.A. and Harper, J.L. 1976. Relationship between plant and weight and numbers in mixed populations of *Sinapis alba* (L.). Rabenh. and *Lepidium sativum* L. J. Appl. Ecol. **13**: 211-216.

Begon, M., Harper, J.L., Townsend, C.R. 1986. Ecology: Individuals, Populations and Communities. Blackwell Sci. Publ., Oxford.

Begon, M. and Wall, R. 1987. Individual variation and competitor coexistence: a model. Funct. Ecol. **1**: 237-241.

Botkin, D.B. 1992. The Ecology of Forests: Theory and Evidence. Oxford Univ. Press, Oxford.

Botkin, D.B., Janak, J.F. and Wallis, J.R. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. **60**: 849-873.

Caswell, H. 1989. Matrix Population Model: Construction, Analysis and Interpretation. 328 pp. Sinauer Ass., Massachusetts.

Chesson, P.L. and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. **117**: 923-943.

Firbank, L.G. and Watkinson, A.R. 1985. A model of interference within plant monocultures. J. Theor. Biol. **116**: 291-311.

Ford, E.D. 1975. Competition and stand structure in some even-aged plant monocultures. J. Ecol. **63**: 311-333.

Gilpin, M. and Hanski, I., ed. 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. Biol. J. Linnean Soc. **42**: 1-336.

Grubb, P.J. 1987. Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. *In* J.H.R. Gee and P.S. Giller, ed., The Organization of Communities, Past and Present, Blackwell Sci. Publ., Oxford, pp. 99-118.

Hara, T. 1984a. A stochastic model and the moment dynamics of the growth and size distribution in plant populations. J. Theor. Biol. **109**: 173-190.

Hara, T. 1984b. Dynamics of stand structure in plant monocultures. J. Theor. Biol. **110**: 223-239.

Hara, T. 1992. Effects of the mode of competition on stationary size distribution in plant populations. Ann. Bot. **69**: 509-513.

Hara, T. 1993. Effects of variation in individual growth on plant species coexistence. J. Vegetation Sci. **4**: 409-416.

Hara, T. and Yokozawa, M. 1994. Effects of variation in physiological traits on size-structure dynamics in plant populations. Ann. Bot. **73**: 39-51.

Hara, T. and Wyszomirski, T. 1994. Competitive asymmetry reduces spatial effect on size-structure dynamics in plant populations. Ann. Bot. **73**, in press.

Harcombe, P.A. 1987. Tree life tables. BioScience **37**: 557-568.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London.

Hartshorn, G.S. 1965. A matrix model of tree population dynamics. *In* F.B. Golley and E. Medina, ed., Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research, Springer-Verlag, New York, pp. 41-51.

Horn, H.S., Shugart, H.H. and Urban, D.L. 1989. Simulators as models of forest dynamics. In J. Roughgarden, R.M. May and S.A. Levin, ed., Perspectives in Ecological Theory, Princeton Univ. Press, Princeton, pp. 256-267.

Hozumi, K. 1973. Interactions among higher plants. Kyoritsu Shuppan, Tokyo (in Japanese).

Huston, M., DeAngelis, D. and Post, W. 1988. New computer models unify ecological theory. BioScience **38**: 682-691.

Kira, T. 1978. Community architecture and organic matter dynamics in tropical lowland rain forests of southeast Asia with special reference to Pasoh forest, West Malaysia. *In* P.B. Tomlinson and M.H. Zimmermann, ed., Tropical Trees as Living Systems, Cambridge Univ. Press, Cambridge, pp. 561-590.

Kira, T., Ogawa, H. and Sakazaki, N. 1953. Intraspecific competition among higher plants. I. Competition-yield-density interrelationships in regularly dispersed populations. J. Inst. Polytech. Osaka City Univ. Ser. **D4**: 1-15.

Kohyama, T. 1987. Stand dynamics in a primary warm-temperate rain forests of southern Japan. Bot. Mag. Tokyo **100**: 305-317.

Kohyama, T. 1989. Simulation of the structural development of warm-temperate rain forest stands. Ann. Bot. **63**: 625-654.

Kohyama, T. 1991. Simulating stationary size distribution of trees in rain forests. Ann. Bot. **68**: 173-180.

Kohyama, T. 1992a. Size-structured multi-species model of rain forest trees. Funct. Ecol. **6** 3: 206-212.

Kohyama, T. 1992b. Density-size dynamics of trees simulated by a one-sided multi-species model of rain forest stands. Ann. Bot. **70**: 451-460.

Kohyama, T. 1993a. Size-structured tree populations in gap-dynamic forest: the forest architecture hypothesis for the stable coexistence of species. J. Ecol. **81**: 131-143.

Kohyama, T. 1993b. Why so many tree species can coexist in tropical rain forests? Kagaku **63**: 768-776 (in Japanese).

Kohyama, T. and Fujita, N. 1981. Studies on the Abies population of Mt. Shimagare I. Survivorship curve. Bot. Mag. Tokyo **94**: 55-68.

Kohyama, T. and Hara, T. 1989. Frequency distribution of tree growth rate in natural forest stands. Ann. Bot. **64**: 47-57.

Kohyama, T., Hara, T. and Tadaki, Y. 1990. Patterns of trunk diameter, tree height and crown depth in crowded Abies stands. Ann. Bot. **65**: 567-574.

Koyama, H. and Kira, T. 1956. Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. J. Inst. Polytech. Osaka City Univ. Ser. **D7**: 73-94.

Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. Biometrics **21**: 1-18.

Levin, S.A. 1976. Population dynamic models in heterogeneous environments. Ann. Rev. Ecol. Syst. **7**: 287-310.

Lonsdale, W.L. 1990. The self-thinning rule: dead or alive? Ecology **71**: 1373-1388.

Lorimer, C.G. and Frelich, L.E. 1984. A simulation of equilibrium diameter distributions of sugar maple (*Acer sacharum*). Bull. Torrey Bot. Club **111**: 193-199.

Metz, J.A.J. and Diekmann, O., ed. 1986. The Dynamics of Physiologically Structured Populations, Lecture Notes in Biomathematics 68. Springer-Verlag, Berlin.

Nagano, M. 1978. Dynamics of stand development. *In* T. Kira, Y. Ono and T. Hosokawa, ed., Biological Production in a Warm-Temperate Evergreen Oak Forest of Japan, JIBP Synthesis 18, Univ. Tokyo Press, Tokyo, pp. 21-32.

Ogawa, F. and Kira, T. 1977. Methods of estimating forest biomass. *In* T. Shidei and T. Kira, Primary Productivity of Japanese Forests, JIBP Synthesis 16, Univ. Tokyo Press, Tokyo, pp. 15-25.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary case. Oikos **65**: 514-527.

Roughgarden, J. and Iwasa, Y. 1986. Dynamics of a metapopulation with space-limited subpopulations. Theor. Popul. Biol. **29**: 235-261.

Shinozaki, K. and Kira, T. 1956. Intraspecific competition among higher plants VII. Logistic theory of the C-D effect. Journal of the Inst. Polytech. Osaka City Univ. Ser. **D7**: 35-72.

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. 1964. A quantitative analysis of plant form-the pipe model theory I. Basic analyses. Jpn. J. Ecol. **14**: 97-105.

Shmida, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. Vegetatio **58**: 29-55.

Shugart, H.H. 1984. A Theory of Forest Dynamics. Springer-Verlag, New York.

Shugart, H.H., Smith, T.M. and Post, W.M. 1992. The potential for application of individual-based simulation models for assessing the effects of global change. Ann. Rev. Ecol. Syst. **23**: 15-38.

Silvertown, J.W. 1987. Introduction to Plant Population Ecology, 2nd ed. Longman, Essex.

Sinko, J.W. and Streifer, W. 1967. A new model for age-size structure of a population. Ecology **48**: 910-918.

Solbrig, O.T., Sarandón, R. and Bossert, W. 1988. A density-dependent growth model of a perennial herb, *Viola fimbriatula*. Am. Nat. **131**: 385-400.

Suzuki, T. 1966. Forest transition as stochastic process I. J. Jpn. For. Soc. **48**: 436-439 (in Japanese).

Takada, T. and Hara, T. 1994. The relationship between the transition matrix model and the diffusion model. J. Math. Biol., in press.

Takada, T. and Iwasa, Y. 1986. Size distribution dynamics of plants with interaction by shading. Ecol. Modell. **33**: 173-184.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton Univ. Press, Princeton.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton Univ. Press, Princeton.

Umemura, T. and Suzuki, T. 1974. Forest transition as a stochastic process V. J. Jpn. For. Soc. **56**: 195-204 (in Japanese).

Urban, D.L. and Shugart, H.H. 1992. Individual-based models of forest succession. *In* D.C. Glenn-Lewin, R.K. Peet and T.T. Veblen, ed., Plant Succession: Theory and Prediction, Chapman and Hall, London, pp. 249-292.

Vance, R.R., Newman, W.I. and Sulsky, D. 1988. The demographic meanings of the classical population growth models of ecology. Theor. Popul. Biol. **33**: 199-225.

VanSickle, J. 1977. Analysis of a distributed-parameter population model based on physiological age. J. Theor. Biol. **64**: 571-586.

Watkinson, A.R. 1980. Density-dependence in single-species populations of plants. J. Theor. Biol. **83**: 345-357.

Weiner, J. and Thomas, S.C. 1986. Size variability and competition in plant monocultures. Oikos **47**: 211-222.

Weller, D.E. 1987. A reevaluation of the −3/2 power rule of plant self-thinning. Ecol. Monogr. **57**: 23-43.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. **14**: 167-225.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon **21**: 213-251.

Whittaker, R.H. and Levin, S.A. 1977. The role of mosaic phenomena in natural communities. Theor. Popul. Biol. **12**: 117-139.

Yamamoto, S. 1992. The gap theory in forest dynamics. Bot. Mag. Tokyo **105**: 375-383.

Yoda, K., Kira, T., Ogawa, H. and Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka City Univ. **14**: 107-129.

Yokozawa, M and Hara, T. 1992. A canopy photosynthesis model for the dynamics of size structure and self-thinning in plant populations. Ann. Bot. **70**: 305-316.

(*Received October 20, 1993: Accepted January 17, 1994*)

Appendix. Continuous size-structure models and Takada-Hara (1994) schemes of discrete approximation for tree populations (recruitment process as a boundary condition excluded)

Definition of symbols (units)

t, Δt	Time and a small time interval (year)
x, Δx	Plant size and a small size interval (cm)
$f(t, x)$	Distribution density function of size x at time t ($\mathrm{cm}^{-1}\ \mathrm{m}^{-2}$)
$G(t, x)$	Mean growth rate of size x at time t ($\mathrm{cm\ year}^{-1}$)
$D(t, x)$	Variance of growth rate at size x at time t ($\mathrm{cm}^2\ \mathrm{year}^{-1}$)
$M(t, x)$	Mortality at size x at time t (year^{-1})

Continuity equation corresponding to the forward one-step projection matrix

(1) Basic equation

$$\frac{\partial f(t, x)}{\partial t} = -\frac{\partial[G(t, x)f(t, x)]}{\partial x} - M(t, x)f(t, x)$$

(2) Difference approximation

$$f(t+\Delta t, x) - f(t, x) = -\frac{G(t, x)f(t, x) - G(t, x-\Delta x)f(t, x-\Delta x)}{\Delta x}\Delta t - M(t, x)f(t, x)\Delta t$$

Diffusion equation corresponding to the forward two-step projection matrix

(1) Basic equation

$$\frac{\partial f(t, x)}{\partial t} = \frac{1}{2}\frac{\partial^2[D(t,x)f(t, x)]}{\partial x^2} - \frac{\partial[G(t, x)f(t, x)]}{\partial x} - M(t, x)f(t, x)$$

(2) Difference approximation

$$f(t+\Delta t, x) - f(t, x) = \frac{1}{2}\frac{D(t, x)f(t, x) - 2D(t, x-\Delta x)f(t, x-\Delta x) + D(t, x-2\Delta x)f(t, x-2\Delta x)}{(\Delta x)^2}\Delta t$$

$$-\frac{3}{2}\frac{G(t, x)f(t, x) - G(t, x-\Delta x)f(t, x-\Delta x)}{\Delta x}\Delta t + \frac{1}{2}\frac{G(t, x-\Delta x)f(t, x-\Delta x) - G(t, x-2\Delta x)f(t, x-2\Delta x)}{\Delta x}\Delta t - M(t, x)f(t, x)\Delta t$$