Plant Ecology **164:** 235–248, 2002.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Tree competition and species coexistence in a warm-temperate old-growth evergreen broad-leaved forest in Japan

N. Nishimura[1,5,*], T. Hara[2], M. Miura[3], T. Manabe[4] and S. Yamamoto[3]
*[1]Laboratory of Applied Plant Ecology, Graduate School of Natural Science and Technology, Okayama University, Okayama, 700-8530, Japan; [2]The Institute of Low Temperature Science, Hokkaido University, Sapporo, 060-0819, Japan; [3]Laboratory of Forest Ecology and Physiology, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya, 464-8601, Japan; [4]Kitakyushu Museum and Institute of Natural History, Kitakyushu, 805-0061, Japan; [5]Current address: Bukkyo University Correspondence Division, Kyoto, 603-8301, Japan; *Author for correspondence*

Received 26 January 2001; accepted in revised form 23 August 2001

Key words: Diffusion model, Growth dynamics, Interspecific competition, One-sided competition, Species diversity, Tatera Forest Reserve

Abstract

The growth dynamics and mode of competition between adult trees $\geqslant$ 5.0 cm in diameter at breast height (DBH) of nine abundant tree species occupying ca. 85% of the total basal area were investigated in a 4 ha study plot (200 m × 200 m) of a warm-temperate old-growth evergreen broad-leaved forest in the Tatera Forest Reserve of Tsushima Island, southwestern Japan. In the plot, adult trees $\geqslant$ 5.0 cm DBH co-occurred with 35 woody plant species (except for woody vine species). The most dominant and largest species, *Castanopsis cuspidata* var. *sieboldii* exhibited a bimodal DBH distribution; it was found in both the upper and lower vertical layers. Other tree species had unimodal DBH distributions corresponding mostly to the lower vertical layer. We developed a model for individual growth incorporating both intra- and interspecific competition and degree of competitive asymmetry. One-sided interspecific competition was detected in 17 cases out of the 66 possible combinations on the scale of the 4 ha study plot. The direction of interspecific competition was generally one-sided from layer-I species to layer-II and III ones. The effects of two-sided competition were detected only in layer-II and III species. Only *Distylium racemosum* exhibited one-sided intraspecific competition. We also found 11 cases of positive interspecific relationships. Generally, competitive relationships prevailed over positive relationships between adult trees in this warm-temperate evergreen broad-leaved forest. Competition between adult trees $\geqslant$ 5.0 cm in DBH did not occur in the same vertical layer, but occurred only between trees in different vertical layers. This suggests that competition between adult trees $\geqslant$ 5.0 cm in DBH plays a key role in the variation in species coexistence between different vertical layers on the 4 ha scale of the warm-temperate evergreen broad-leaved forests. Moreover, it was found by comparing with three different forest types that interspecific competition is more intense in warm-temperate forests than in cool-temperate or sub-boreal forests. We conclude that, compared to cool-temperate or sub-boreal forests (which have little interspecific competition), warm-temperate forests support more complex interspecific relationships and species-specific habitat preferences that result in higher species diversity.

Introduction

Many studies have emphasized that life-history parameters (fecundity, recruitment, seedling establishment, mortality, longevity), environmental heterogeneity, and disturbance (e.g. gap dynamics) are important for the coexistence of different plant species (e.g. Grubb (1977); Nakashizuka et al. (1992); Rebertus and Veblen (1993); Manabe et al. (2000)). In particular, Grubb (1977) 'regeneration niche' hypothesis suggests that important niche differences among coexisting species are manifested only in the early stages of their life histories. However, these studies did not consider competitive interactions between canopy trees or adult plants.

On the other hand, competition between plants in crowded monospecific stands may be mainly for light, and may thus to be one-sided or asymmetric [see reviews by Weiner and Thomas (1986); Hara (1988); Weiner (1990)]. There have been only a few studies on competition and species coexistence based on the growth of individual trees in multi-species natural forests (Kohyama 1992, 1993; Hara et al. 1995; Kubota and Hara 1995). Assuming one-sided competition, Kohyama (1992, 1993) simulated the coexistence of three major tree species, *Distylium racemosum*, *Illicium anisatum* and *Eurya japonica*, in a warm-temperate rain forest. The three species occurred in different vertical layers, but he did not consider interspecific competition in the same vertical layers. In a cool-temperate forest, Hara et al. (1995) showed that competition between abundant tree species occurred locally between only a few specific species, and suggested that the process of species coexistence was related to the habitat preference of each species and landslide disturbance. They concluded that the ‘regeneration-disturbance’ hypothesis (Yamamoto et al. 1995) describes the main mechanism by which species coexist in cool-temperate forests. Kubota and Hara (1995, 1996a, 1996b) put forth the ‘boundary condition’ hypothesis to explain the pattern of for species coexistence in a sub-boreal forest: species persistence is largely due to species-specific processes of sapling recruitment (boundary conditions for adult tree growth dynamics), rather than to interspecific competition.

The vertical structure of warm-temperate evergreen broad-leaved forests is more developed than that of cool-temperate or sub-boreal forests, and interspecific relationships between species are assumed to be more complicated, although Kohyama (1992, 1993) considered only one-sided competition between species occupying different vertical layers for species coexistence. However, we should consider coexistence between various species in the same vertical layer as well as coexistence between species occupying different vertical layers.

We assumed that the stand structure, species composition, and mechanisms of species coexistence and diversity in warm-temperate evergreen broad-leaved forests are strongly related to the mode of competition between individual adult trees. In this paper we analysed the growth dynamics of individual adult trees ⩾ 5.0 cm in DBH (stem diameter at breast height) for the modes of intra- and inter-specific competition in a warm-temperate old-growth evergreen broad-leaved forest in southwestern Japan. We examined the effects of adult tree competition in the same vertical layers and between different vertical layers on the coexistence of species in this forest.

Methods

Study site

The Tatera Forest Reserve is located in the centre of the south Island of Tsushima (34°25′ N, 129°20′ E) between the Japanese Archipelago and the Korean Peninsula. The reserve, situated on a north-facing slope of Mt. Tatera, comprises about 10 ha and ranges in altitude from 120 m to 560 m above sea level. The topography is flat or gently sloping at low and middle altitudes, and steeper at high altitudes. According to data from the Izuhara Weather Station near the mountain (1981–1990), monthly-mean temperatures ranged from 26.4 °C in August to 4.7 °C in January, with an annual average of 15.3 °C. Monthly precipitation ranged from 46.2 mm in December to 409.4 mm in June, and the mean annual precipitation was 2140.2 mm. There were few reports of snowfall.

The reserve is a truly primary evergreen broad-leaved forest that has been free from human disturbance for centuries, because the mountain itself has been regarded as sacred by ancient religion. A forest on the lower part of the mountain (< 350 m above sea level) has been identified phytosociologically as Distylio-Quercetum salicinae (Itow et al. 1993). It has a general canopy of 20–30 m in height dominated by evergreen broad-leaved trees with DBH greater than 1 m. These trees include *Castanopsis cuspidata* var. *sieboldii*, *Distylium racemosum* and *Quercus salicina* (Yamamoto 1992). The forest on the upper part of the mountain is scrub dominated by *Quercus acuta* that grows only to 6–7 m in height due to strong winds and the rocky conditions.

We sampled the area of evergreen broad-leaved forest dominated by *C. cuspidata* var. *sieboldii*, *Distylium racemosum* and *Quercus salicina* with a mature and homogeneous crown surface at the canopy. A study stand was chosen on a gentle slope (ca. 9° mean inclination), ca. 140–190 m above sea level at the northern foot of Mt. Tatera, according to the following criteria: (1) stand with trees > 1 m in DBH and >

25 m tall – which is our definition of ‘old-growth’; (2) no obvious altitudinal gradient within the stand; (3) no evidence of human disturbance.

Field measurements

A permanent 4 ha (200 m × 200 m) plot was set up within the study site in 1990. All live or dead woody stems $\geqslant$ 5.0 cm in DBH in the study plot (4570 living stems in total in 1990) were tagged and identified by species. Each was mapped to the nearest 0.1 m as x- and y-coordinates, and measured for DBH to the nearest 0.1 cm in 1990, 1992 and 1997. Tree height was recorded as a vertical canopy layer for each tree according to the crown position: layer I, upper-canopy layer; layer II, lower-canopy layer and $\geqslant$ 8 m tall; and layer III, < 8 m tall. The total number of live woody plant species $\geqslant$ 5.0 cm in DBH was 35 except for woody vine species. Nomenclature follows Ohwi and Kitagawa (1992).

The model and data analysis

Hara (1984) proposed a size-structured stochastic model (‘diffusion model’) to describe the growth dynamics of a single-species plant population:

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

where $f(t, x)$ is the size distribution function of size x at time t, and $G(t, x)$, $D(t, x)$ and $M(t, x)$ are the mean absolute growth rates, the variance of absolute growth rates, and the mortality rate of individuals of size x at t, respectively. The $G(t, x)$ and $M(t, x)$ functions represent averaged size-dependent species characteristics, whereas the $D(t, x)$ function represents variation in species characteristics caused by environmental heterogeneity, genetic variation, and variation in effect of the neighbourhood competition due to the spatial distribution of individuals. The recruitment rate (number of individuals entering the population per unit time through the minimum size of the population, $x_{\min}$), $R(t)$, gives a boundary condition for Equation (1).

Values of the $G(t, x)$, $D(t, x)$ and $M(t, x)$ can be estimated directly from DBH growth data for individual trees. In this paper, these functions were estimated for nine abundant species (> 100 individuals per 4 ha study plot) which occupied ca. 85% of the total basal area [sum of $(\pi/4)(\mathrm{DBH})^2$] in 1990, (number of trees in parentheses; see Figure 1): *D. racemosum* (1633), *Cleyera japonica* (756), *Camellia japonica* (574), *Symplocos lucida* (218), *C. cuspidata* var. *sieboldii* (152), *Eurya japonica* (145), *Dendropanax trifidus* (143), *Cinnamomum japonica* (116), *Neolitsea aciculata* (112). The trees of each species were divided into about 10 DBH-classes, each with at least 10 individuals. For each DBH-class, we calculated the means and variances of DBH increments from 1990 to 1997, and mortality rate (= number of dead stems in 7 years / number of initial live stems in 1990). These provide values of the $G(t, x)$, $D(t, x)$ and $M(t, x)$, respectively, when x is given as a midpoint value of each DBH-class at time t (= 1990).

Using a canopy photosynthesis model, Yokozawa and Hara (1992) theoretically derived a general function form of $G(t, x)$ of individual size (plant mass or stem diameter), x. Let $C(t, x)$ represent the total leaf area of individuals of size > x at time t expressed as

$$C(t,x) = \int_{x}^{x_{\max}} L(t,y)f(t,y)dy, \tag{2}$$

where $L(t, y)$ represents the leaf area of an individual of size y at t and $x_{\max}$ is the maximal size in the stand. The theoretical general function form of $G(t, x)$ is given as,

$$G(t,x) = x[a_0 - a_1 \ln x - c_1 C(t,x) - c_2 C(t,x_{\min})], \tag{3}$$

where $x_{\min}$ is the minimal size in the stand, and a_0, a_1, c_1 and c_2 are constants. The term $c_1 C(t, x)$ with $c_1 > 0$ in Equation (3) expresses the effect of suppression on the growth of individuals of size x due only to individuals of size > x. The ratio c_1/c_2 in Equation (3) defines the mode of competition for any size x such that $x_{\min} < x < x_{\max}$ as follows (Hara 1992; Yokozawa and Hara 1992): if $c_1 = 0$ and $c_2 > 0$, competition is two-sided and symmetric, where relative growth rate RGR [$=G(t, x)/x$], of every plant is equally suppressed by others (i.e. *both larger and smaller individuals*) due to stand crowdedness in terms of leaf area index given by $C(t, x_{\min})$; as c_2 (> 0) decreases towards 0 (c_1/c_2 increases towards infinity) with $c_1 > 0$, competition becomes more asymmetric (but still two-sided) and completely one-sided (i.e. suppression *only by larger individuals*) when $c_1 > 0$ and $c_2 = 0$ or $c_1 / c_2 \to +\infty$ (one-sided competition is the most extreme case of asymmetric competition); if $c_1 = c_2 = 0$, competition is absent. For $x = x_{\text{min}}$, one-sided competition is identical to symmetric competition in effect; for $x = x_{\text{max}}$, one-sided competition is identical to the absence of competition in effect. Note that the effect of asymmetric competition on RGR is size-dependent, while that of symmetric competition is size-independent. This definition fits various models of symmetric (simple 'two-sided' in some researchers' terminology), asymmetric and one-sided competition used by many researchers (e.g. Weiner (1990); Kohyama (1992, 1993); Wyszomirski (1992)).

Diffusion model for multi-species forest and regression analysis for the mode of competition

Equation (3) suggests that we can build the following linear regression model for the multi-species warm-temperate evergreen broad-leaved forest so as to examine both inter- and intraspecific competition for each of N species constituting the forest, k (= 1, 2, …, N):

$$G_k(t,x) = x\left[a_0 - \sum_{i=1}^{N} c_{1,i} C_i(t,x) - \sum_{i=1}^{N} c_{2,i} C_i(t,x_{\text{min}})\right], \tag{4}$$

where $C_i(t, x)$ is the total leaf area of individuals of species i at time t with DBH > x and $c_{1,i}$ and $c_{2,i}$ are constants. In the present model, the term '$-a_1 \ln x$' in brackets in Equation (3), which was originally introduced by Yokozawa and Hara (1992), was omitted, because there was a high correlation (> 0.99) between 'x' and '$x \ln x$' in the range of DBH used. Moreover, the term '$-a_1 \ln x$' represents a long-term effect (age effect) coupled with species-specific physiological and morphogenetical constraints. To evaluate precisely the effect of term '$-a_1 \ln x$', we need long-term data on growth of each individual tree. Instead, our present study deals with the instantaneous effects of competition at the present moment from neighbouring trees on a focal individual, apart from the effect of the term '$-a_1 \ln x$'.

According to the pipe model theory of Shinozaki et al. (1964a, 1964b), $L(t, y)$ in Equation (2) can be assumed to be proportional to the square of DBH [or $(\text{DBH})^h$ with h around 2] for many tree species (Kohyama 1992). Species-specific effects of foliage structure and leaf area are included in $c_{1,i}$ and $c_{2,i}$. Furthermore, to consider spatial effects on individual growth (i.e. distant neighbours have smaller effects on the growth of a focal individual than close neighbours), the distance between individuals was also incorporated into the model. Thus, the $C_i(t, x)$ function in Equation (4) was given as,

$$C_i(t,x) = \sum_{i=1}^{m_i} \delta_{i,j} (y_{i,j})^2 (s_{i,j})^{-1} \tag{5}$$

$$(\text{if} \quad y_{i,j} > x, \delta_{i,j} = 1; \quad \text{if} \quad y_{i,j} \leqslant x, \delta_{i,j} = 0),$$

where $y_{i,j}$ denotes DBH of the jth individual of species i with m_i individuals and $s_{i,j}$ denotes the distance from the jth individual of species i to the focal individual species k with DBH x in a circular neighbourhood of radius r_{N} with the focal individual being at the centre. Thus, the term $c_{1,i} C_i(t, x)$ with $c_{1,i} > 0$ in Equation (4) expresses the effect of suppression on the growth of a focal tree of species k with DBH x due only to individual trees of species i with DBH > x present in the neighbourhood. The degree of the *competitive (suppressive) effect* of species i on species k is measured by $c_{1,i}$ (> 0, one-sided) and $c_{2,i}$ (> 0, symmetric). The *response* of species k is represented by $G_k(t, x)$. The *direction of the competitive effect* is from species i to species k, if $c_{1,i} > 0$ or $c_{2,i} > 0$ for $G_k(t, x)$. Moreover, if $c_{1,k} > 0$ or $c_{2,k} > 0$ holds for $G_i(t, x)$, the direction of interspecific competition is symmetric (two-sided); otherwise [if $c_{1,k} = 0$ and $c_{2,k} = 0$ for $G_i(t, x)$], the competitive direction is one-sided, only from species i to species k. If $c_{1,i} < 0$ or $c_{2,i} < 0$, interspecific relationship is positive (non-competitive): the individual RGR value for species k increases with the abundance of species i in the same neighbourhood. For $i = k$ (i.e. intraspecific competition), the competitive direction is identical to the competitive effect in the mode (symmetric, asymmetric or one-sided).

Equation (4) includes time t in the function $C_i(t, x)$ and $C_i(t, x_{\text{min}})$. To estimate the coefficients in Equation (4) from the 7-yr data (without following stand development over several hundred years!), it was assumed that the phase average (or ensemble average) is identical to the time average, as it is in thermal physics and statistical dynamics [e.g. see Kittel (1969)]. This assumption is reasonable, because the forest that we studied can be considered 'old-growth'. Thus, the forest is multi-aged, divides into grid cells in various conditions in terms of $C_i(t, x)$ and $C_i(t, x_{\min})$ ranging from a gap to a closed canopy, and presents various phases of stand development.

Multiple linear regression analysis was conducted for the DBH increment of each individual tree as the dependent variable [for $G_k(t, x)$] and 'x', '$x\ C_i(t, x)$' and '$x\ C_i(t, x_{\min})$' ($i = 1, 2, \ldots, N$) as the explanatory variables in Equation (4) for each of the nine abundant species (> 100 in tree number per 4 ha plot; see Figure 1) and for the other 26 species together (i.e. $N = 10$). The forward stepwise method (explanatory variables are entered or removed stepwise one at a time) was used. The values of the F-statistic to enter and to remove an explanatory variable were both set at 2. Individual trees within a $(200 - r_N) \times (200 - r_N)$ m square in the centre of the 4 ha study plot were used for calculation. Eighteen values of the neighbourhood radius r_N, 3, 4, 5, …, 20 m by 1 m, were used for the regression analysis to find the best value of r_N (in terms of the d.f.-adjusted R^2) for each species k. The remaining variation $(1 - R^2)$, which is not accounted for by Equation (4), is attributable to the $D(t, x)$ function. In terms of the regression analysis, the $G(t, x)$ and $D(t, x)$ functions represent the predicted value (Figure 2) and variance of residuals (see Figure 3), respectively (Hara 1984).

Instead of multiple linear regression analysis, discriminant analysis was also conducted for (DBH increment) = 0 or > 0 of each individual tree as the dependent variable, when the species has many individuals of (DBH increment) = 0. The same method as the above-mentioned multiple linear regression analysis was used.

Spatial association among tree species

We analysed the spatial association among nine tree species using Iwao's ω-index (Iwao 1977; Manabe et al. 2000). The ω-index reflects the degree of spatial correlation between species, and the index varies from 1 (completely overlapping), though 0 (independent occurrence) to −1 (complete exclusion). See Iwao (1977) for more details of the ω-index.

The ω-index was calculated for 20 m × 20 m quadrats as the unit size. This scale was chosen in accordance with our analysis of competitive relationships (the neighbourhood radius r_N was ca. 10 m in most cases). We conducted a randomization sampling test in order to determine whether spatial correlations between species A and species B are significantly different from random. We calculated the ω-index for the 800 possible combinations of the 100 quadrats of each of species A and species B, i.e. 2 reflections × 4 rotations × 10 x-shifts × 10 y-shifts of species A, keeping spatial pattern of species B fixed. If the observed ω-index was within either of the 5 % tails of the calculated ω-index distribution, the spatial correlation between species A and species B was assumed to be significantly different from random.

Results

Size structure, growth and mortality

The total basal area of woody stems $\geqslant$ 5 cm in DBH in the study plot was 63.5 m^2/ha in 1990, ca. 71.5% of which was occupied by the two dominant species, *C. cuspidata* var. *sieboldii* (39.3%) and *D. racemosum* (32.2%). The density of stems $\geqslant$ 5 cm in DBH in the plot was 1124 /ha, and *D. racemosum* was the most abundant species occupying 35.9% of stem density, *Cleyera japonica* was second (16.8%), and *Camellia japonica* was the third (12.6%) abundant species. The vertical structure of the stand was generally multi-layered (Table 1). Eight species had stems in all vertical layers, but only *E. japonica* lacked layer I. The most stems of *C. cuspidata* var. *sieboldii* belonged to layer I, and its DBH distribution was remarkably bimodal with 79.1% of stems $\geqslant$ 40 cm in DBH corresponding to layer I, and the rest < 40 cm in DBH corresponding to layers II and III (Figure 1). The other species had almost unimodal and inverse J-shaped DBH distributions. *D. racemosum* and *D. trifidus* had more of its stems in layer I and II, the rest species being mostly in layer II and III (Table 1). See Manabe et al. (2000) for detailed DBH statistics for all 35 tree and shrub species.

The directly estimated $G(t, x)$ for DBH (= x) differed significantly among the nine abundant tree species (ANCOVA with the covariate $\ln x$, $P < 10^{-6}$; Figure 2. There were significant differences in the $G(t, x)$ function between *C. cuspidata* var. *sieboldii* and the other species, but there was no significant difference between other combinations (Scheffé test, Table 2). The $G(t, x) - \sqrt{D(t, x)}$ relationship also differed significantly among the nine abundant tree species (ANCOVA, $P < 0.01$; Figure 3). The $G(t, x) - \sqrt{\mathrm{D}(t, x)}$ relationship including all the nine species was concave rather than linear {second-order polynomial regression analysis, $\sqrt{D(t, x)} = (-0.0687 \pm 0.0169)\ [G(t, x)]^2 + (0.9389 \pm 0.0789)\ G(t, x) +$

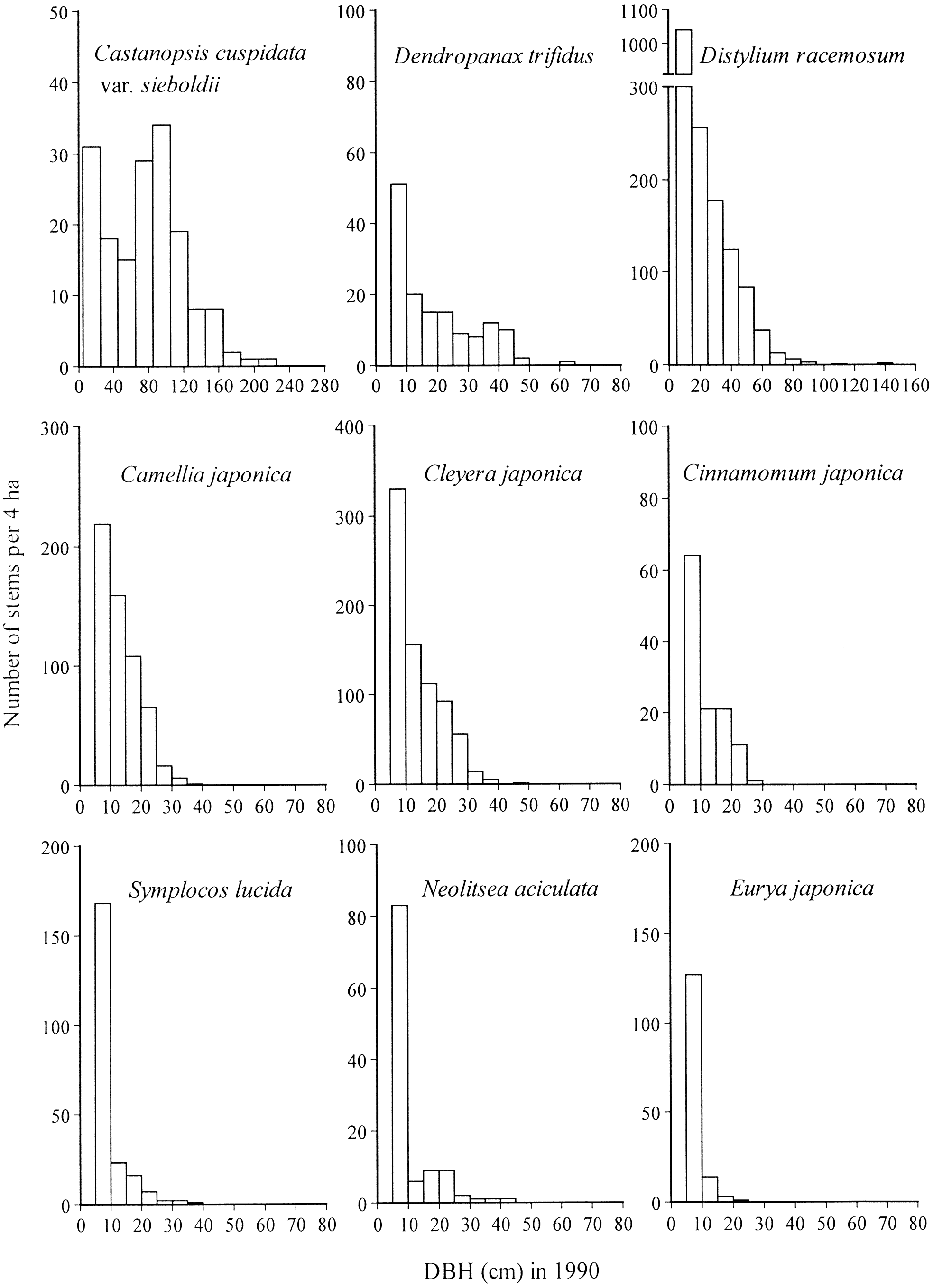


Figure 1. Frequency distributions of DBH of the nine abundant species in 1990.

(0.1783 ± 0.0570) [(estimate ± SE), $n = 74$, $R = 0.9358$, $P < 10^{-6}$]; see Figure 3}, suggesting that tree competition was one-sided or asymmetric in these species. There were significant differences in the $G(t, x) - \sqrt{D(t, x)}$ relationship between *C. cuspidata* var. *sieboldii* and the other species, *D. trifidus* and *Cleyera japonica*, and *Cleyera japonica* and *Cinnamomum japonica*, but there was no significant difference between other combinations (Scheffé test, Table 2). The number of all stems ⩾ 5 cm in DBH in the study plot decreased from 4494 in 1990 to 4198 in 1997 except for recruits. Thus, the overall mortality rate per

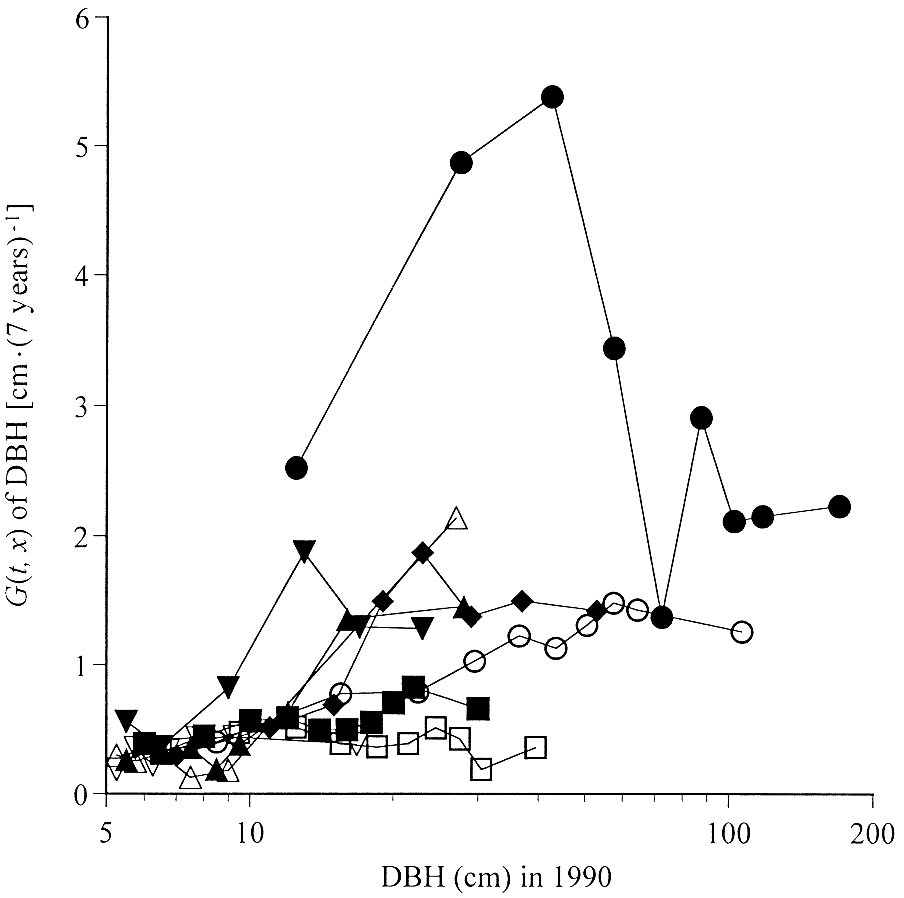


Figure 2. The relationship between DBH in 1990 (log scale) and mean absolute growth rate $G(t, x)$ of DBH from 1990 to 1997 for nine abundant tree species. ●: *C. cuspidata* var. *sieboldii*, ◆: *D. trifidus*, ○: *D. racemosum*, ■: *Camellia japonica*, □: *Cleyera japonica*, ▼: *Cinnamomum japonica*, △: *N. aciculata*, ▲: *S. lucida*, ▽: *E. japonica*.

year was 0.97%. The directly estimated $M(t, x)$ function for DBH differed significantly among the nine species (ANCOVA for arcsine$\sqrt{}$-transformed mortality rate with the covariate ln x, $P < 0.01$; Figure 4). There was a significant difference in the $M(t, x)$ function of DBH only between *D. racemosum* and *Cinnamomum japonica* (Scheffé test, Table 2).

Growth and the mode of tree competition

To estimate the theoretical general function form of $G(t, x)$ from the field data, we attempted three transformations of the dependent variable, DBH increment (ξ), so that the errors (residuals) had constant variances (see Figure 3 for untransformed cases): $\ln(1 + \xi)$, $\sqrt{\xi}$, and $\sqrt{\xi+1}$ (Freedman-Tukey transformation). The homogeneity of residual variances was examined using residual-predicted value scatter plots and the Bartlett χ^2 test, and the best transformation was chosen (but actually, the statistical results were similar among transformations). In all the regressions, the Durbin-Watson statistic and the serial correlation of residuals were close to 2 and 0, respectively, implying little autocorrelation between residuals. The normality of residuals was checked with normal plots. Outliers were also checked using residual-deleted residual plots and Cook's distances, and extreme outliers were excluded from the regression analysis. None of these residual analysis indicated inadequacy of the regression model, Equation (4). High correlations (> 0.9) were found between $xC_i(t, x)$ and $xC_i(t, x_{\min})$ [i.e. $xC_i(t, x) \approx xC_i(t, x_{\min})$ or $x \approx x_{\min}$] in several cases (i.e. one-sided competition was identical to symmetric competition in effect). For these cases, we conducted regressions in which one of the high-correlation variables was discarded, in order to avoid an unstable estimation due to multicollinearity. In the other cases, the correlation between the explanatory

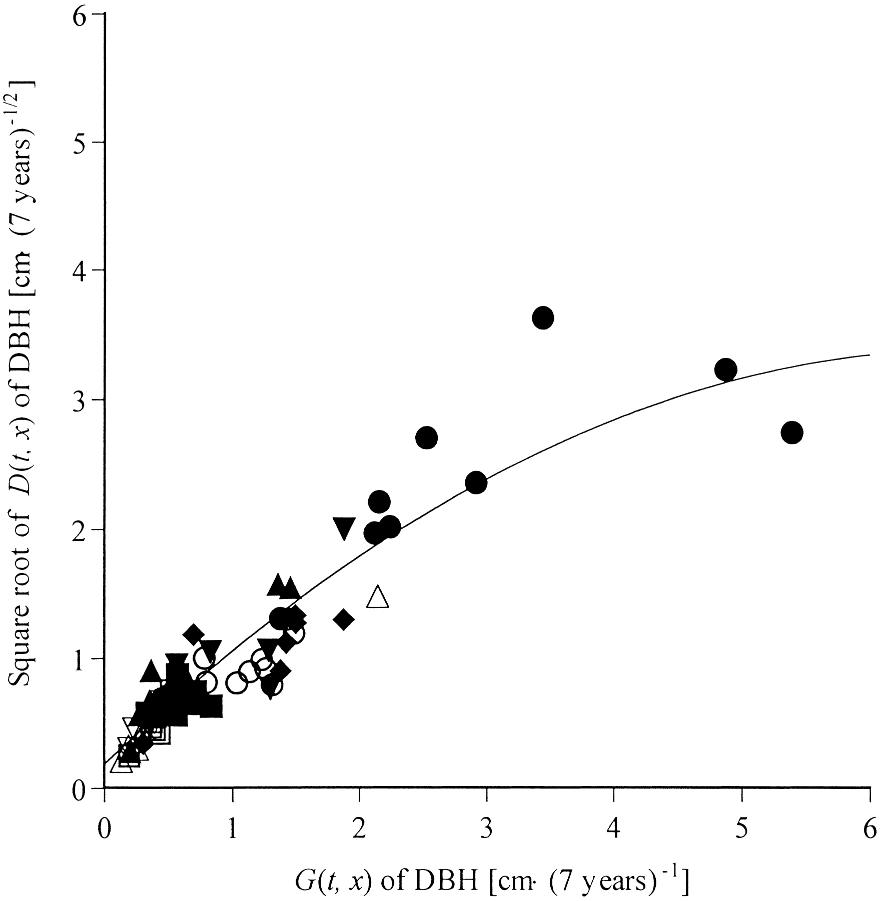


Figure 3. The relationship between mean absolute growth rate $G(t, x)$ of DBH from 1990 to 1997 and square root of the variance in absolute growth rate $D(t, x)$ of DBH for nine abundant tree species. Symbols are as in Figure 2.

variables was usually less than 0.7, and multicollinearity was not detected. For each species k (= 1, 2, …, 10), one to six explanatory variables out of 23 were entered into the regression model and were significant [$P < 10^{-3}$ except for CIJ ($P < 0.01$); Table 3).

Based on the results of multiple linear regression and discriminant analysis (significant coefficients, $c_{1,i}$ and $c_{2,i}$ at $P < 0.05$), Figure 5 summarizes the competitive (suppressive) effect and direction ($c_{1,i}$, $c_{2,i} > 0$) and the positive effect and direction ($c_{1,i}$, $c_{2,i} < 0$) amongst the trees of the nine abundant species and the other 26 species combined. The value of r_N that gave the greatest d.f.-adjusted R^2-value was employed for each species in Figure 5 [d.f.-adjusted $R^2 = 1 - \{(1 - r^2)(n-1)/(n-q-1)\}$; n, sample size; q, number of explanatory variables of the regression equation; r, multiple correlation coefficient]. Only *D. racemosum* showed one-sided intraspecific competition Figure 5. Interspecific competition was detected in 16 cases out of the 66 possible combinations. The direction of interspecific competition was generally one-sided by layer-I species toward layer-II and III ones: by *C. cuspidata* var. *sieboldii* toward *Camellia japonica*, *Cleyera japonica*, *Cinnamomum japonica* and *E. japonica*; by *D. racemosum* toward *Camellia japonica* and *Cleyera japonica*; by *D. trifidus* toward *S. lucida*. The effect of two-sided competition was detected only in layer-II and III species: *Camellia japonica* and *N. aciculata*; *Cleyera japonica* and layer-II and III trees of *D. racemosum*. A positive relationship was found in 11 cases. Therefore, competitive relationships ($c_{1,i}$, $c_{2,i} > 0$) prevailed over positive ones ($c_{1,i}$, $c_{2,i} < 0$) in the study plot.

Spatial association among tree species

Spatial correlations between species were significant in 10 pairs out of the 36 possible combinations (Ta-

Table 1. The proportion (%) of stems (DBH ⩾ 5 cm) belonging to each vertical layer of nine abundant species in the 4 ha study plot. Each vertical layer was classified according to crown position and tree height as follows. Layer I: canopy layer; layer II: below canopy and ⩾ 8 m tall; layer III < 8 m tall.

Species	Species code	Layer		
		I	II	III
Layer-I species				
Castanopsis cuspidata var. *sieboldii*	CAC	80.7	7.8	11.5
Dendropanax trifidus	DET	30.1	42.6	27.3
Distylium racemosum	DIR	28.7	31.3	40.0
Layer-II species				
Camellia japonica	CAJ	3.0	47.5	49.5
Cleyera japonica	CLJ	10.7	37.2	52.1
Cinnamomum japonica	CIJ	4.2	35.6	60.2
Layer-III species				
Symplocos lucida	SYL	4.1	25.6	70.3
Neolitsea aciculata	NEA	7.1	20.6	72.3
Eurya japonica	EUJ	0.0	11.7	88.3

ble 4). Negative spatial associations were generally detected between layer-I species and layer-II and III ones: *D. racemosum* vs. *Camellia japonica*, *Cleyera japonica*, *Cinnamomum japonica* and *N. aciculata*; *D. trifidus* vs. *E. japonica*. Only one pairs of layer-I species showed a negative spatial association: *C. cuspidata* var. *sieboldii* vs. *D. racemosum*. Positive spatial associations were generally found between layer-II and/or III species: *Camellia japonica* vs. *Cleyera japonica* and *Cinnamomum japonica*; *Cleyera japonica* and *S. lucida* vs. *E. japonica*; *Cinnamomum japonica* vs. *N. aciculate*.

Discussion

Competition between trees of warm-temperate evergreen broad-leaved forest

Interspecific competitive (suppressive) relationships between trees ⩾ 5 cm in DBH were more common than interspecific positive ones on the scale of the 4 ha study plot in the warm-temperate evergreen broad-leaved forest (Figure 5). The growth of the layer-I species, *C. cuspidata* var. *sieboldii*, was never affected by other species, and the $G(t, x)$ values for this species directly estimated from the field data were significantly higher than those of other species (Figure 2). Our result suggests that bimodality of DBH distribution of *C. cuspidata* var. *sieboldii* (Figure 1) is caused by regeneration characteristics of the species, rather than by competition (Yokozawa and Hara 1995). Results for the most dominant species, *Fagus crenata*, in a cool-temperate forest were similar (Hara et al. 1995). The growth of layer-I individuals of the two layer-I species, *D. racemosum* and *D. trifidus*, was never affected by other species, but, that of layer-II and III individuals was affected by the layer-II and III species, which was also supported by the higher mortality rate $M(t, x)$ of smaller sized individuals (Figure 4). The competitive effect of the layer-I species on the layer-II species was one-sided, but that on layer-III species was scarce. The effect of one-sided interspecific competition is supported by the concave-curve $G(t, x) - \sqrt{D(t, x)}$ relationship (Hara et al. 1991). Interspecific competition occurred also between the layer-II and III species. Interspecific competition among the same layer species was rare. Positive relationships were generally found among the layer-II species, but were not found among the layer-I species or the layer-III species.

The analysis of spatial association showed that the layer-I species tended to occur at different sites, whereas the layer-II and III species tended to occur at the same sites. The layer-II and III species tended to occur at sites where the layer-I species were scarce.

In summary, each layer-I species had a species-specific habitat preference, and did not compete with one another. The layer-II and III species did not compete with each other in the same layer except for one case, although they tended to co-occur. They also showed positive relationships (Figure 5). The positive relationship suggests that these species have similar habitat preferences (similar favourable environmental

Table 2. Statistical results in probabilities for post hoc tests of the relationship between DBH in 1990 and $G(t, x)$, between $G(t, x)$ and $D(t, x)$, and between DBH in 1990 and $M(t, x)$ among the nine tree species (***, $P < 0.001$; *, $P < 0.05$; blank, not significant by Scheffé test). See Table 1 for species codes.

Species code	DBH in 1990 vs. $G(t, x)$									$G(t, x)$ vs. $D(t, x)$									DBH in 1990 vs. $M(t, x)$								
	CAC	DET	DIR	CAJ	CLJ	CIJ	SYL	NEA	EUJ	CAC	DET	DIR	CAJ	CLJ	CIJ	SYL	NEA	EUJ	CAC	DET	DIR	CAJ	CLJ	CIJ	SYL	NEA	EUJ
CAC																											
DET	***									***																	
DIR	***									***																	
CAJ	***									***																	
CLJ	***									***	*																
CIJ	***									***				*							*						
SYL	***									***																	
NEA	***									***																	
EUJ	***									***																	

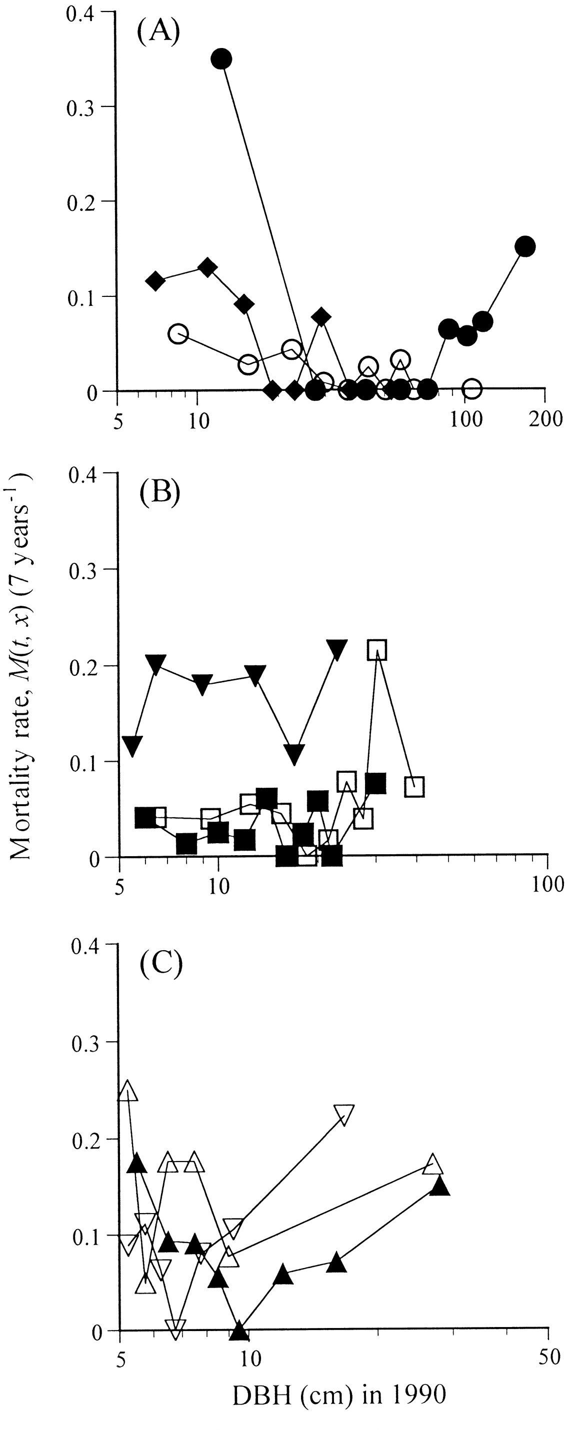


Figure 4. The relationship between DBH in 1990 and observed 7-year mortality rates $M(t, x)$ from 1990 to 1997 for nine abundant tree species. Symbols are as in Figure 2.

conditions for the species), where tree densities are not so high as to encourage competition. The layer-II species generally got the competitive effect from the

Table 3. Statistical results of multiple linear regression analysis for Equation (4). See Table 1 for species codes. The value of r_N that gave the greatest d.f.-adjusted R^2-value of the final model was employed for each species.

Species code	Layer	Sample size	r_N(m)	d.f.-adjusted R^2	P
CAC	I,II,III	93	10	0.21	$< 10^{-3}$
DET	I	27	8	0.10	$< 10^{-4}$
	II,III	49	11	0.26	$< 10^{-6}$
DIR	I	308	10	0.73	$< 10^{-6}$
	II,III	475	10	0.49	$< 10^{-5}$
CAJ	I,II,III	289	6	0.14	$< 10^{-5}$
CLJ	I,II,III	203	10	0.14	$< 10^{-5}$
CIJ	I,II,III	57	11	0.18	< 0.01
SYL	I,II,III	72	9	0.52	$< 10^{-5}$
NEA	I,II,III	39	8	0.48	$< 10^{-4}$
EUJ	I,II,III	43	11	0.31	$< 10^{-3}$
OTH	I,II,III	226	12	0.21	$< 10^{-6}$

layer-I and III species. One-sided interspecific competition from layer-I to layer-II species may be for light as has been pointed out in many studies (e.g. Kohyama (1992, 1993)). In our study, we detected interspecific competition by layer-III species toward layer-II species, which has been reported for natural forests only rarely. This finding suggests that belowground competition (Weiner 1990) is important for layer-II and III species. On a scale of the 4 ha study plot in the warm-temperate evergreen broad-leaved forest, interspecific competition did not occur in the same vertical layer (due to habitat segregation in layer-I and to positive relationships in layer-II and III), but did occur between species in different vertical layers. This suggests that interspecific competition between adult trees $\geqslant$ 5.0 cm in DBH plays an important role in the variation in species coexistence between different vertical layers.

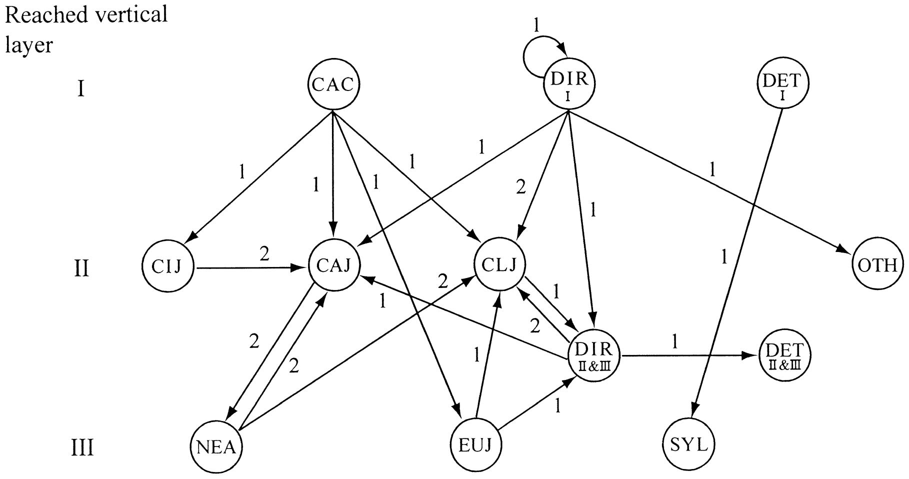
Interspecific competition and species coexistence of warm-temperate evergreen broad-leaved forest

Our results are noteworthy, because many researchers have suggested or emphasized that competition between plants in crowded monospecific stands is intense and either one-sided or asymmetric [e.g. Takada and Iwasa (1986); Weiner and Thomas (1986); Kohyama (1992, 1993); see also reviews by Hara (1988); Weiner (1990)]. Assuming one-sided competition, Kohyama (1992, 1993) simulated the coexistence of three major species in a warm-temperate rain forest, *D. racemosum*, *Illicium anisatum*, and *E. japonica*. These three species occurred in different vertical layers, and Kohyama's assumption did not consider interspecific competition in the same vertical layer.

On the other hand, in a cool-temperate forest, interspecific competition was detected only between a few specific species, and positive interspecific relationships prevailed over competitive relationships (Hara et al. 1995). Therefore, Hara et al. (1995) concluded that interspecific competition between adult trees played only a small role in the variation in species coexistence and that species-specific habitat preference played a key role as suggested by the strong positive relationship between species. In a sub-boreal forest, symmetric competition was far more common than one-sided or asymmetric competition, although statistical evidence for any competitive effects was rather weak (Kubota and Hara 1995). Therefore, Kubota and Hara (1995, 1996a, 1996b) proposed the boundary condition hypothesis for species coexistence in the sub-boreal forest that the persistence of each component species is ascribed largely to the different recruitment processes of saplings (boundary conditions for adult tree growth dynamics) and only a little to interspecific adult tree competition.

Our results support Kohyama's assumption (Kohyama 1992, 1993) that competition between species in different vertical layers is one-sided in the warm-temperate evergreen broad-leaved forest. Moreover, our results showed that competition did not occur between species in the same vertical layer. The maintenance mechanism of species diversity seems to be different between warm-temperate and cool-temperate (or sub-boreal) forests. The intensity of interspecific competition tends to increase from cool-temperate (or sub-boreal) to warm-temperate forests, only

(a) Competitive (suppressive) relationship



(b) Positive relationship

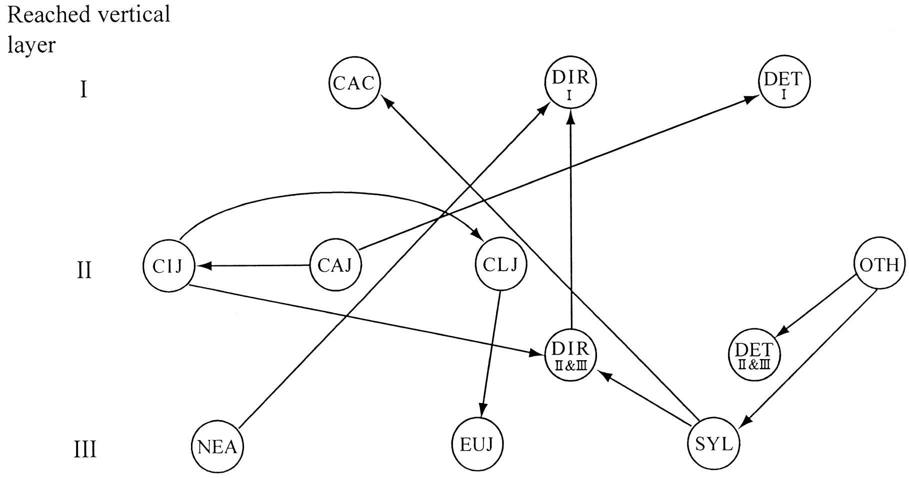


Figure 5. (**a**) Competitive (suppressive) and (**b**) positive relationships between trees $\geqslant$ 5 cm in DBH for the nine abundant species and all the other 26 species. Diagrams are based on the results of multiple linear regression of the theoretical general function form of $G_k(t, x)$, Equation (4). In the competitive relationship (a), 'species $i \longrightarrow$ species k' represents that species i suppresses the individual DBH growth of species k according to Equation (4) [i.e. $c_{1,i}$, > 0 or $c_{2,i} > 0$ for $G_k(t, x)$]. '1' at the arrow in (a) indicates a one-sided competitive effect (i.e. $c_{1,i}$, > 0 and $c_{2,i} = 0$ in Equation (4) significant at $P < 0.05$), and '2' at the arrow in (a) indicates a symmetric competitive effect (i.e. $c_{1,i}$, = 0 and $c_{2,i} > 0$ in Equation (4) significant at $P < 0.05$). In the positive relationship (b), 'species $i \longrightarrow$ species k' represents that the individual DBH growth rate of species k increases with the abundance of species i [i.e. $c_{1,i}$, < 0 or $c_{2,i} < 0$ for $G_k(t, x)$ in Equation (4)]. In (b), all the arrows indicate $c_{2,i} < 0$ in Equation (4) (significant at $P < 0.05$). See Table 1 for species code. OTH = other species combined.

between different vertical layers. In the same vertical layers, interspecific competition is scarce both in warm-temperate and cool-temperate (or sub-boreal) forests. The positive relationship tends to decrease from cool-temperate (or sub-boreal) to warm-temperate forests. We conclude that in warm-temperate forests, interspecific relationships are more complex, causing higher species diversity, than in cool-temperate or sub-boreal forests (interspecific competition and species-specific habitat preference in warm-temperate forests, as compared with almost only species-

Table 4. Spatial associations among nine tree species using ω-index on a 20 m × 20 m scale. See Table 1 for species codes. Values of ω-index with asterisks are statistically significant by randomization sampling test (*, $P < 0.05$; **, $P < 0.01$).

Species code	ω-index								
	CAC	DET	DIR	CAJ	CLJ	CIJ	SYL	NEA	EUJ
CAC									
DET	0.143								
DIR	–0.073*	–0.074							
CAJ	0.190	0.137	–0.247**						
CLJ	0.016	–0.058	–0.063*	0.209*					
CIJ	0.096	–0.201	–0.153*	0.230*	0.065				
SYL	0.113	0.076	0.096	0.009	0.049	0.118			
NEA	–0.080	–0.083	–0.146*	0.065	0.035	0.055	0.001		
EUJ	0.068	–0.257*	–0.046	0.099	0.245*	0.054	0.264*	0.020	

specific habitat preference in cool-temperate or sub-boreal forests).

Acknowledgements

Field assistance was provided by Satoshi Ito, Tomoshi Ohkawa, Tamotsu Sato, Hiroyuki Tanouchi, and some members of the Laboratory of Forest Ecology and Physiology of Nagoya University whose help is greatly acknowledged. We thank the Tsushima District Forest Office for permitting this study, and Shuzo Itow for his advice. This study was partly supported by Grants-in-Aid for Bio Cosmos Project from the Ministry of Agriculture, Fishery and Forestry, of Japan.

References

Grubb P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107–145.

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

Hara T. 1988. Dynamics of size structure in plant populations. Trends Ecol. Evol. 3: 129–133.

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

Hara T., Kimura M. and Kikuzawa K. 1991. Growth patterns of tree height and stem diameter in populations of *Abies veitchii, A. mariesii and Betula ermanii*. J. Ecol. 79: 1085–1098.

Hara T., Nishimura N. and Yamamoto S. 1995. Tree competition and species coexistence in a cool-temperate old-growth forest in southwestern Japan. J. Veg. Sci. 6: 565–574.

Itow S., Nakanishi H. and Kawasato H. 1993. Studies in the evergreen broad-leaved forest of Tatera Forest Reserve, Tsushima, Japan III. Phytosociology. Bull. Faculty of Liberal Arts, Nagasaki Univ. Nat. Sci. 33: 111–121.

Iwao S. 1977. Analysis of spatial association between two species based on the interspecies mean crowding. Res. Pop. Ecol. 18: 243–260.

Kittel C. 1969. Thermal Physics. Wiley & Sons, New York.

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

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

Kubota Y. and Hara T. 1995. Tree competition and species coexistence in a sub-boreal forest, northern Japan. Ann. Bot. 76: 503–512.

Kubota Y. and Hara T. 1996a. Allometry and competition between saplings of *Picea jezoensis* and *Abies sachalinensis* in a sub-boreal coniferous forest, northern Japan. Ann. Bot. 77: 529–537.

Kubota Y. and Hara T. 1996b. Recruitment processes and species coexistence in a sub-boreal forest in northern Japan. Ann. Bot. 78: 741–748.

Manabe T., Nishimura N., Miura M. and Yamamoto S. 2000. Population structure and spatial patterns for trees in a temperate old-growth evergreen broad-leaved forest in Japan. Plant Ecology 151: 181–197.

Nakashizuka T., Iida S., Tanaka H., Shibata M., Abe S., Masaki T. et al. 1992. Community dynamics of Ogawa Forest Reserve, a species rich deciduous forest, central Japan. Vegetatio 103: 105–112.

Ohwi J. and Kitagawa M. 1992. New Flora of Japan. Shibundo, Tokyo.

Rebertus A.J. and Veblen T.T. 1993. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. J. Veg. Sci. 4: 641–654.

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

Shinozaki K., Yoda K., Hozumi K. and Kira T. 1964b. A quantitative analysis of plant form – the pipe model theory II. Further evidence of the theory and its application in forest ecology. Jpn. J. Ecol. 14: 133–139.

Takada T. and Iwasa Y. 1986. Size distribution dynamics of plants with interaction by shading. Ecol. Modelling 33: 173–184.

Thomas S.C. and Weiner J. 1989. Including competitive asymmetry in measures of local interference in plant populations. Oecologia (Berl.) 80: 349–355.

Weiner J. 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. 5: 360–364.

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

Wyszomirski T. 1992. Detecting and displaying size bimodality: kurtosis, skewness and bimodalizable distributions. J. Theor. Biol. 158: 109–128.

Yamamoto S. 1992. Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. Bot. Mag. Tokyo 105: 29–45.

Yamamoto S., Nishimura N. and Matsui K. 1995. Natural disturbance and tree species coexistence in an old-growth beech-dwarf bamboo forest, southwestern Japan. J. Veg. Sci. 6: 875–886.

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.

Yokozawa M. and Hara T. 1995. Foliage profile, size structure and stem diameter-plant height relationship in crowded plant populations. Ann. Bot. 76: 271–285.