

POPULATION STRUCTURE AND GROWTH DYNAMICS OF *CASTANOPSIS SIEBOLDII* IN SECONDARY-AND OLD GROWTH-SUBTROPICAL FORESTS IN SOUTHERN JAPAN

Yasuhiro KUBOTA

Abstract

Population dynamics of *C. sieboldii*, based on comparing secondary and old growth stands in the subtropical forest, was investigated. The old growth forests showed higher recruitment rate of *C. sieboldii* than that of the secondary forests. Gain of stand biomass was smaller in the old growth forests, but their biomass lost to mortality was larger than that of the secondary forests. Above ground net primary productions ranged from 1.19 kg/ha · yr to 1.57 kg/ha · yr. Relatively high species diversity in the old growth stands may be maintained by competitive effects of the *other species*.

Key words: Demography, Competition, Net primary production, Regeneration, Species diversity

Introduction

Tree communities of Yanbaru are subtropical evergreen broad-leaved forests dominated by *Castanopsis sieboldii* (SUNAKAWA & YAMAMORI, 1964, OHYAMA & YAMAMORI, 1971, SUZUKI, 1979, HATSUSHIMA & NAKAJIMA, 1979, ITOW, 1985, Oono et al., 1997). Natural forests of Yanbaru, which is located in Okinawa Island of southern Japan, support many endemic and endangered birds and mammals (see review by ITO, 1997). The area of old growth forests are rapidly diminishing due to intensive logging, consequently, most of the current forested areas are secondary stands regenerated after clear cutting (U.S. Civil Administration of the Ryukyu Islands 1953). Regeneration dynamics of the secondary forests as well as maintenance mechanisms of the intact forests have become an important issue in the management of seral stands (AIDE et al., 1995, GARCIA-MONTIEL & SCATENA, 1994, AIBA et al., 2001). Nevertheless research on the dynamics of the subtropical forests with structural attributes similar to both humid tropical montane rain forests and warm-temperate evergreen broad-leaved forests is scant in comparison to the tropical forests of Southeast Asia (but see ZHUANG & CORLETT, 1997).

Comparative analysis of permanent plots with different age or history might provide insight into structural changes (UUTTERA et al., 2000). In order to reconstruct stand development over time, it is necessary to clarify differences of structural attributes in several stands (FINEGAN, 1992, 1996, GRAU et al., 1997, DENSLow & GUZMAN, 2000), because demographic traits such as growth rate and mortality change with stand development (KOHYAMA, 1987, BORMANN & LIKERS, 1994, BAZZAZ, 1996). Differences in the spatial- and temporal-patterns of these traits are likely to drive stand dynamics (UMEKI & KIKUZAWA, 1999), may leading to a variation in species diversity in old growth stands.

This paper investigates the differences of the structures and dynamics between secondary and old growth forests in Yanbaru of Okinawa Island, southern Japan. The first object is to present an overview of the regeneration process of the most dominant species (*C. sieboldii*) from secondary

to old growth forests. The second is to examine the effects of competition among individual trees on the community dynamics. This is because intra- and inter-specific competition are important factors governing self-organization of forests (e.g., KOHYAMA, 1993, HARA et al., 1995, NAKASHIZUKA & KOHYAMA, 1995, KUBOTA & HARA, 1995). Most previous studies have presumed autogenic effects to be constant, irrespective of stand development. It is not clear whether the mode of competition among member species can be assumed to be constant throughout all the developmental stages. The first part examines the stability of competitive effects in secondary and old growth stands, and explores the community dynamics of this subtropical forest that bring the coexistence among *Castanopsis sieboldii* and a variety of subordinate species.

Study Site I

The study was conducted in Yanbaru (26° 44' N, 128° 14' E), the northern mountain part of Okinawa Island, southern Japan. This region is located between the warm-temperate and tropical zones (MIYAWAKI, 1980). Mean monthly temperature is 19 - 22 °C; mean daily temperatures in the warmest month (July) and the coldest month (January) are 27.3 °C and 14.2 °C, respectively. Precipitation ranges from 1900 to 4000 mm year⁻¹. Typhoons with strong winds and rain frequently strike the island between July and October. Winds are generally from the south or south-west in summer and from the north in winter. Stand canopies have been apparently shaped by the winds into a homogeneous, continuous surface. As a result, unlike the tropics, there is no emergent tree. The bedrock is composed mainly of tertiary sandstone, palaeozoic clay-slate, and a red-yellow forest soil that lacks humus layer develops (Forest Soil Division, GFES, 1976, KOJIMA, 1980). The study site is dominated by evergreen broad-leaved trees such as *C. sieboldii*, *Distylium racemosum*, and *Schima wallichii*. Nomenclature follows HATSUSHIMA & AMANO (1994).

Methods

Stand selection and site condition

In order to carry out intensive investigation of structural changes and growth dynamics in forests of different ages, four stands were selected from forested area based on the description by ITO (1997). In Dec. 1997 and Mar. 1998, one monitoring plot was established for each stand which are located within it on a slope at approximately 100 - 400 m elevation. Their areas range from 0.04 to 0.09 ha depending upon the topographic conditions and the stem density. Relatively small plot sizes were used in this study for minimizing topographical heterogeneity within a monitoring plot such as the presence of small ridge and valley (e.g., SHINJO et al., 1988, 1991, 1992, MIYAGI & SHINJO, 1989, 1990). Stands 1 and 2 are secondary forests of approximately 15 and 30 years, respectively. Both were subjected to clear cutting. In Stands 1, saplings of *Styrax japonicus* were planted just after logging, and no additional treatment such as mowing and thinning was conducted. The time of abandonment age of each stand was estimated from aerial photographs taken in 1977 and 1995, from the logging record of Kunigami Village, and from interviews with local inhabitants. The older Stand 3 is located in the Yona Experimental Forest of the Ryukyu University and the oldest Stand 4 is in Mt. Yonaha Cultural Properties Preservation Area (ITO, 1995). The former was once logged and naturally regenerated, and is currently more than 50-year-old, while the latter has been conserved for longer period.

In this region, most of the human operations were not recorded in detail because of the confusion during the World War II and the following occupation of the United States Military Forces. This makes the present vegetation exceedingly difficult to interpret. Therefore, in order to validate the comparative analysis among the four stands at different ages, we first examined their site conditions,

soil property and decomposition process of leaf litter fall.

Forcing a core sampler systematically in plots, we collected topsoils (0 - 15 cm) from four to nine points beneath the litter layer. The visible fine to coarse roots, stones, and plant debris in the collected samples were removed, and soil pH (in distilled water) of the sampled topsoils was measured for each plot. Remnant soil samples were oven-dried at 105 °C for 48 h, and then total nitrogen contents were determined by the micro Kjeldahl procedure (BUCHI Kjeldahl Line B-324, Switzerland).

Randomization technique with the bootstrap resampling was used to test the significant differences of pH and the total nitrogen in topsoils among the stands. Test statistic was obtained by permuting the observed data of pH or total N of the stands and then calculating the sum of the deviations over the stands. We recalculated the statistic 1000 times, generating a distribution of the sum of the deviations over the stands. By comparing these two sums of the deviations over the stands to this generated distribution, a significance level can be determined (ADAMS et al., 1997).

Decomposition rate of leaf litter of *C. sieboldii* was examined as an index of mineralization rate by the litter bag technique. *C. sieboldii* leaf litters (5 g of air-dried) were enclosed in each bag (15 cm x 15 cm with 1 mm polyethylene mesh), and the bags were placed on the forest floor. The litter bags were collected every 3 months from April 2001 to May 2002. Leaf subsamples were oven-dried at 70 °C, and the mean dry mass remaining at each interval was expressed as a percent of the initial weight and adjusted to the exponential model: $W_t/W_o = e^{-kt}$ (Olson 1963), where k (the decomposition rate) was estimated by the regression analysis. To test for significant differences among slopes, k , of the four stands, the ANCOVA was used.

Species richness and diversity

To compare species richness among the plots, the relationship between area and number of species was investigated. Resampling within a plot was repeated 500 times for each subsample size. Minimum sized subsample was set as a 2 x 2 m unit. The number of species was averaged to determine as a function of size of the subsample. To compare species richness among the stands, two jackknife estimators were used (PALMER, 1990, 1991). Species diversity was described by the Simpson diversity index, $1-D$ (LANDE, 1996), Shannon-Wiener information index, H' , and Pielou's equitability index, J' . D is the best index for comparative studies, because values of D are not affected by the sample size (tree density) and the confidence intervals become reasonably small with 50 - 100 individual samples (see review by LANDE, 1996). In order to avoid the sampling bias such as plot size, the D value was calculated at the 10 x 10 m subplot level, and then be averaged as a representative value at the plot level. Significance differences of the D value between the plots were examined by Mann-Whitney U test. Statistical analysis in terms of species richness and diversity was performed with the *PC-ORD*_{version 4} software (MCCUNE & MEFFORD, 1999).

Stand structure and dynamics

Each plot was first covered with a 2 x 2 m grid system for field survey. Thus 1325 grid cells of 2 x 2 m were established in total. Three life stages were defined for tree species: (i) canopy trees [DBH (stem diameter at breast height 1.3 m) ≥ 10 cm]; (ii) understory trees (2 m in height and < 10 cm in DBH); and (iii) saplings (10 cm ≤ height < 200 cm). All living canopy and understory trees, including all multiple stems, were tagged and identified by species. The saplings were also tagged in systematically chosen grid cells. The height, DBH, and the location of all the stems were measured. When a stem had an irregular shape at 1.3 m height, the measurement was taken at the nearest higher point where the stem was cylindrical. Either steel measuring tapes

or calipers was used to measure DBH of the tree to the nearest 1 mm or 0.1 mm, respectively. DBHs of these tagged trees were remeasured in March 2000, and the new recruits of saplings (< 2 m height) which exceeded the minimal census size (height = 2 m) were measured for DBH and identified by species. Significant difference of the sapling density, the understory density, and the canopy tree density among the stands was examined by Kruskal-Wallis test using the data at the 2 x 2 m grid level.

The relationship between DBH (x) and absolute growth rate (y) was given as logistic growth function:

$$y = a/(1 + b \cdot \exp(-c \cdot x)),$$

which is specific to the tree species in early growing stage (FORD, 1975, KIKUZAWA, 1988, HARA et al., 1991). Fitting of this model was carried out by non-linear regression analysis (Quasi-Newton method) using absolute growth rate as the dependent variable and DBH as the explanatory variable (Non-linear regression module; program from STATISTICA™ for Windows (Stat Soft Inc.)). The parameters of the model are shown in Fig.3. To test for significant differences in three parameters of the regression functions between-species or -stand, the procedure described by DOBSON (1990, pp.116-119) was used. For instance, if we test a difference of parameter 'a' in logistic growth functions between Species 1 and Species 2, we estimated parameters, a_{all} , b_{all} , and c_{all} , for the pooled species by non-linear regression analysis, calculating the sum of the independent contributions of the residual of observed values from the expected ones weighted by the residual of observed values (D_1). Next we estimated parameter, a_{sp1} , for Species 1 separately using b_{all} and c_{all} fixed as above estimated as the pooled species, calculating the sum of the independent contributions of the residual of observed values from expected ones weighted by the residual of observed values (D_2). In the probability density of the $\chi^2_{N1+N2-p}$ -distribution, the null hypothesis $a_{\text{all}} = a_{\text{sp1}}$ was tested with $D_1 - D_2$. In this way, differences of three parameters among the species and among the stands were compared.

The mortality and recruitment rates were calculated by using a logarithmic model (CONDIT et al., 1995, SHEIL & MAY, 1996). The mortality rate (% year⁻¹) is the log-transformed value of the number of initial live trees in 1997 (or 1998) divided by the number of surviving trees during 1997-2000 and by 2 (or 3) (years). The recruitment rate (% year⁻¹) is the log-transformed value of the number of live trees at the end of the study divided by the number of surviving trees during 1997-2000 and by 2 or 3 (years). Significant differences of the observed mortality and the recruitment among the stands were tested based on the sum of the deviations of the observed values from that of the resampled values generated by the bootstrap method (1000 iterations). The significant level was determined from the probability of randomized statistic equal to or larger than that of the observed statistic.

Net primary production

In order to estimate net production of the stands and seed dispersal of *C. sieboldii*, litter fall was collected in five or nine traps with a horizontal area of 0.95 m² from 1997 to 2002 in each plot. Litter fall was usually collected every three months from October 1997 to February 2002. The contents of each trap were dried at about 70 °C. After drying, the collections were sorted into five fractions: leaves, small wood, seeds, frass and unclassified materials. All the sorted collections were dried at 70 °C and weighted separately for each trap.

For *C. sieboldii*, the number of dispersed seeds was counted in the four plots from October 1997 to February 2002. Seed production in the plots was calculated by extrapolating the average density of seeds per trap area to the total plot area. Then analysis of variance (ANOVA/MANOVA module; program from STATISTICA™ for Windows (Stat Soft Inc.)) was used to test differences of seed production between-year and between-stand.

Biomass was estimated by the following equations:

$$\ln w_S = 0.92 * \ln D^2 H - 3.21 \quad (P < 0.0001, r^2=0.97),$$

$$\ln w_B = 1.02 * \ln D^2 H - 5.37 \quad (P < 0.0001, r^2=0.82),$$

$$\ln w_L = 0.82 * \ln D^2 H - 5.62 \quad (P < 0.001, r^2=0.71),$$

$$\ln L_A = 0.856 * \ln D^2 - 1.583 \quad (P < 0.001, r^2=0.83),$$

and

$$w = w_S + w_B + w_L,$$

where D and H are DBH (cm) and height (m), respectively, and w_S , w_B , and w_L are the dry weights (kg) of stem, branches, and leaves per tree, respectively, and L_A is leaf area (m²) per tree, and w is the total above-ground dry weight of the tree. These regression equations were obtained from the studies done on the Yona Experimental Forest of the Ryukyu University (KAWANABE, 1977). Above ground net primary production of stand biomass (ANPP) was calculated with the method proposed by KIRA and SHIDEI (1967) and CLARKI et al. (2001a):

$$\text{ANPP} = Y + L + G$$

where Y is the difference in standing live biomass between one measurement period and the next (including ingrowth). Above ground biomass of the minimum sized tree (2 m in height, $w = 0.01$ kg per tree) that recruited during the interval is removed from Y . L is the amount of litter/branch fall during the interval. G is the amount of losses to herbivory that is calculated from the model (FURUNO & SHIRAI, 1970, YODA, 1971):

$$G = 1.2 * E$$

where E is the amount of frass.

Measurement of competitive effect

In order to assess competitive effects, we analyzed the crowding index of individual trees, which is the cumulative foliage area of neighbor trees higher than the focal tree (KUBOTA & HARA, 1996, HARA et al., 1995). It expresses the asymmetric competitive effect on the focal tree, in other words, the shading effect. The crowding index of individual trees was calculated at three neighborhood radii, 2 m, 3 m, and 5 m to find the best value for analyzing between-tree interaction (see below). Periodic (wrapped-around) boundary conditions, i.e. opposite edges of the plot were joined to form a torus were employed (YOKOZAWA et al., 1998), because trees close to the plot edges had neighbors outside the plot that were not measured.

Trees were grouped into *C. sieboldii* and the other species to better describe the community dynamics, because *C. sieboldii* was very dominant and practically determined the structure of the stand (SHINZATO et al., 1986). We calculated crowding indices of *C. sieboldii* and other species (pooled) trees, respectively. To examine inter- and intra-specific competitive effects between *C. sieboldii* and the other species, multiple linear regression analysis was conducted using DBH increment of each tree as the dependent variable and the log-transformed DBH and the crowding index as the explanatory variables for pooled data of each species (Multiple-linear regression module; program from STATISTICA™ for Windows (Stat Soft Inc.)). The DBH increment was Freedman-Turkey-transformed to have a constant variance of residuals. Then inter- and intra-specific competitive effects of *C. sieboldii* and other species were investigated. Significance of the estimated values was tested by using a forward stepwise method at $P < 0.05$, and comparison of the estimated coefficients with possible values they take if individuals were randomly distributed in each stand. In this case, the null hypothesis is that bivariate spatial interactions between two groups of *C. sieboldii* and other species is independent. Based on the highest and the lowest values of competitive effects obtained from the randomized points, ninety-five percent confidence envelopes were drawn (DUNCAN,

1991, NANAMI et al., 1999).

Results

Stand structure

Topsoils (15 cm) at all the sites were weakly acidic ranging from 4.07 to 5.21. Total N was quite low, although total N of Stand 4 was slightly higher than that of the other stands. No significant difference in soil acidity (pH) and total N among the four stands were shown (Table 1, $P > 0.1$ by randomization test based on the resampling data using the bootstrap method with 1000 iterations), although stand biomass and tree density do vary with stand history. Decomposition rate also did not differ significantly between the four stands (ANCOVA, $P > 0.9$). Significant correlations among log-transformed tree density, above-ground biomass, and mean above ground tree weight (Table 2, $P < 0.05$) can be ascribed to a difference of the stand ages among the plots, rather than the differences of the site conditions.

C. sieboldii commonly dominated throughout secondary and old growth forests (Table 2). Species richness with jackknife estimators was higher in younger secondary forests than in old growth forests (Fig.1, Table 3). Stand 1 had the greatest number of species in spite of its smaller plot area. High species richness in secondary forests was due to the occurrence of light demanding pioneer tree species such as *Euscaphis japonica*, *Mallotus japonicus*, *Ligustrum liukiense* and *Pittosporum tobira*. But species diversity was slightly higher in old growth forests (Mann-Whitney *U* test, $P < 0.05$, Table 3), which is consistent with the findings that species diversity increases with forest age in old forests (age = 50 yr) of Yanbaru reported by ITO (1997).

Table 1. Description and site data for secondary forests and old growth forest.

	Plot			
	Stand-1	Stand-2	Stand-3	Stand-4
Age (yr)	15	30	50-100	100<
History	Clear cut /Secondary	Clear cut /Secondary	Old Growth	Old growth
Altitude (m)	340	200	300	410
Bedrock ¹	Tertiary sandstone, palaeozoic clay-slate, yellow soil	Tertiary sandstone, palaeozoic clay-slate, yellow soil	Tertiary sandstone, palaeozoic clay-slate, yellow soil	Tertiary sandstone, palaeozoic clay-slate, yellow soil
pH (H ₂ O) ²	4.91	5.21	4.07	4.65
Total N (%) ³	0.23	0.12	0.18	0.41
Decomposition rate (<i>k</i>) of leaf litter ⁴	1.94	1.63	1.58	2.09
T _{1/2} (years) ⁵	0.36	0.43	0.44	0.33

1 Based on KOJIMA (1980)

2 pH. Values were not different among the stands (randomization test with the bootstrap resampling (1000 times), $P < 0.526$)

3 Total N. Values were not different among the stands (randomization test with the bootstrap resampling (1000 times), $P < 0.126$)

4 Decomposition rate of leaf litter is calculated from a negative exponential model: $Wt/Wo = e^{-kt}$ (OLSON, 1963).

5 Half-life time (T_{1/2}) for litter was calculated from the Olson equation.

Table 2. Relationship between structural attributes, sapling density and tree density in secondary forests and old growth forest.

History	Plot (age)			
	Stand-1 (15)	Stand-2 (30)	Stand-3 (50-100)	Stand-4 (100<)
	Clear cut /Secondary	Clear cut /Secondary	Old Growth	Old growth
Tree density (m ²)	2.99	1.52	0.92	0.84
Stand biomass (kg/m ²)	9.44	15.93	22.27	23.92
Stand leaf mass (kg/m ²)	0.39	0.56	0.64	0.64
Mean tree weight (kg)	3.1 ± 6.5	9.7 ± 20.5	23.9 ± 83.9	27.9 ± 133.7
Maximum tree height (m)	10	14.2	12.6	13.63
Sapling density of <i>C. sieboldii</i> (/m ²)	0.05 (0.06)	0.23 (0.36)	0.82 (0.18)	0.78 (0.07)
Sapling density of other species (/m ²)	3.75 (0.73)	0.73 (0.42)	2.51 (0.26)	5.82 (0.89)
Understory tree density of <i>C. sieboldii</i> (/m ²)	0.29 (0.29)	0.16 (0.06)	0.01 (0.01)	0.02 (0.03)
Understory tree density of other species (/m ²)	1.35 (1.00)	0.71 (0.40)	0.68 (0.08)	0.55 (0.12)
Understory tree density of <i>C. sieboldii</i> (/m ²)	0.02 (0.01)	0.04 (0.07)	0.03 (0.02)	0.01 (0.03)
Understory tree density of other species (/m ²)	0.02 (0.01)	0.03 (0.03)	0.08 (0.01)	0.05 (0.03)

Three life stages were defined for tree species: (i) canopy trees [DBH (stem diameter at breast height 1.3 m) > 10 cm]; (ii) understory trees (> 2 m in height and < 10 cm in DBH); and (iii) saplings (10 cm < height < 200 cm). Figures in parenthesis are the density of sprouting stems. Sapling, understory tree and canopy tree densities among stands were tested by Kruskal-Wallis test using grid based densities within each stand. Sapling and understory tree densities were significantly different among stands (P<0.001).

In the secondary forests (Stands 1 and 2) the size (DBH) structure of *C. sieboldii* showed almost bell-shaped distributions with positive skewness and bimodality (Fig. 2). The percentages of sprouting stems in the secondary forests were almost 40 %. In contrast, the old growth forests (Stands 3 and 4) showed inverse J-shaped DBH distributions. These DBH distributions significantly differed from one another (Kolmogorov-Smirnov two-sample test, *P* < 0.025). Sapling density of *C. sieboldii* was different among the stands. Most saplings of the secondary forests were sprouted ones, while those of the old growth forests were originated from seeds. Sapling density of the old growth forests were greater than those of the secondary forests (Table 2, Kruskal-Wallis test, *P* < 0.01).

However note that tree density in understory weakened in old growth stands. These differences imply the differences of regeneration and forest stratification in developmental stages.

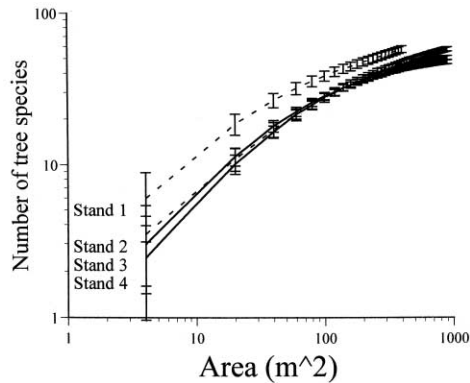


Fig.1. Relationship between the number of species and area in a subtropical forest, Okinawa Island, southern Japan. Subsampling was repeated 500 times for each subsample size. The number of species was averaged to determine as a function of size of the subsample. To compare species richness among the stands, two jackknife estimators were used (PALMER, 1990, 1991). Species richness estimated by jackknife estimators is shown in Table 3. Secondary forests (Stands 1 and 2) and old growth forests (Stands 3 and 4) are shown as broken lines and solid lines, respectively.

Table 3. Number of observed species (S), number of species estimated by the first order jackknife estimate ($Jack1$), number of species estimated by the second order jackknife estimate ($Jack2$), and species diversity indices of trees in 900 m² plots of Yanbaru. Trees of which height was > 2.0 m. In order to avoid the sampling bias such as plot size, the D value was calculated at the 10 x 10 m subplot level, and then be averaged as a representative value at the plot level.

Plot	S	$Jack1^{(1)}$	$Jack2^{(2)}$	$1-D^{(3)}$	$H^{(4)}$	$J^{(5)}$
Stand 1	56	73	83	0.924	4.501	0.772
Stand 2	53	70	75	0.891	4.027	0.721
Stand 3	49	57	56	0.935	4.612	0.821
Stand 4	48	51	51	0.952	4.831	0.870

$$(1) \text{ Jack}^1 = S + r_1 \cdot (n-1)/n,$$

where S is the observed number of species, r_1 is the number of species occurring in one sample unit, and n is the number of sample units.

$$(2) \text{ Jack}^2 = S + r_1 \cdot (2n-3)/n - r_2 \cdot (n-2)/(n \cdot (n-1)),$$

where r_2 is the number of species occurring in exact two sample units (Palmer 1990, 1991).

$$(3) D = \sum_{i=1}^s \left\{ n_i (n_i - 1) / N(N - 1) \right\}$$

$$(4) H' = - \sum_{i=1}^s P_i \cdot \log_2 P_i$$

where n_i is the number of trees and P_i the relative frequency of trees of the i -th species in each plot.

$$(5) J = H / H \text{ max where } H \text{ max} = \log_2 S,$$

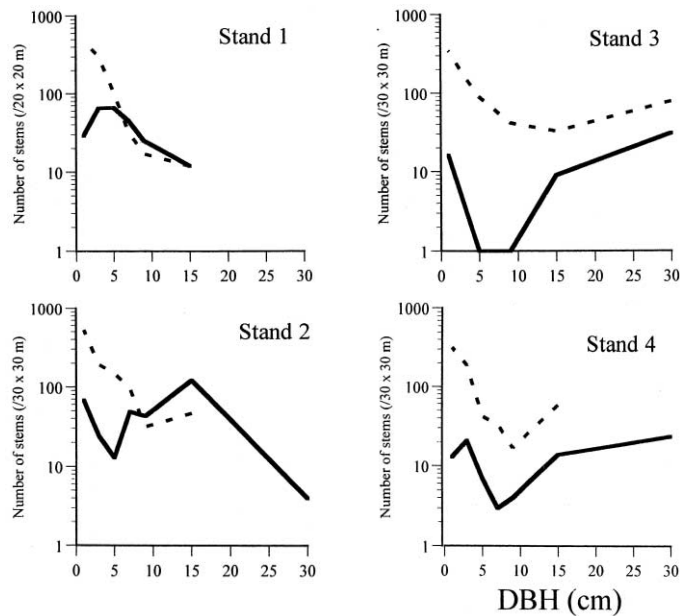


Fig.2. Size (DBH: stem diameter at breast height 1.3 m) distribution of the most abundant species, *Castanopsis sieboldii* (solid lines), and *other species* (broken lines) in each plot. Stands 1 and 2 are forests of approximately 15 and 30 years, respectively. Stands 4 and 5 are old growth forest. See text and Table 1 for details.

Stand dynamics

A total of 895 seeds (38 seeds/m² · yr) of *C. sieboldii* during 1998-2001 was counted in the four plots. Stand 1 had no seed-rain for these four years. The total estimated seed productions over all the four sites were 2, 17, 95, and 0 seeds/m² in 1998, 1999, 2000, and 2001, respectively. In the old growth forests (Stands 3 and 4), seed production of *C. sieboldii* was significantly different between years ($P < 0.05$, Repeated-Measures ANOVA). The largest seed production in 2000 was regarded as a masting, and in this mast year, the density of seeds tended to be greater in the old growth forests than in the secondary forests (Table 4), although the significant difference among Stands 2, 3, and 4 was not detected ($P > 0.05$, ANOVA). The old growth forests showed higher recruitment rate of *C. sieboldii* than that of the secondary forests ($P < 0.001$ by randomization test)(Table 4). Mortality of *C. sieboldii* and the other species at the stand level was not different among the stands ($P > 0.09$ by randomization test).

Gain of stand biomass was smaller in the old growth forests, but their biomass lost to mortality was larger than that of the secondary forests (Table 5). Most dead trees in the secondary forests were standing dead and belong to small size classes. But in the old growth forests (Stands 3 and 4), high mortality was observed in the large size class, which was due to a typhoon in September 1999. As a result, above ground net primary productions (ANPP) as the sum of the amount of litter fall, gain of stand biomass, and lost to predation, ranged from 1.19 kg/ha · yr (Stand 3) to 1.57 kg/ha · yr (Stand 1).

Table 4. Regeneration dynamics of subtropical forests based on seed dispersal, calculated recruitment and mortality of secondary forests and old growth forests.

History	Plot (age)			
	Stand-1 (15)	Stand-2 (30)	Stand-3 (50-100)	Stand-4 (100<)
	Clear cut /Secondary	Clear cut /Secondary	Old Growth	Old growth
Seed dispersal density of <i>C. sieboldii</i> (yr, m ²)*	0	1.5 ± 2.2	31.0 ± 41.8	5.5 ± 5.8
Recruitment rate of <i>C. sieboldii</i> (%/yr) [#]	0.85	1.44	3.34	6.31
Recruitment rate of other species (%/yr) [#]	2.01	1.21	1.30	1.64
Mortality rate of <i>C. sieboldii</i> (%/yr) [#]	2.51	5.24	3.34	7.16
Mortality rate of other species (%/yr) [#]	2.22	3.05	2.08	1.08

* Seed production in stand was investigated during 1997 - 2001, and values are the mean (+ S.D.) of four years. Differences between years and stands were tested by ANOVA.

Mortality and recruitment rates were estimated by using a logarithmic model of CONDIT et al. (1995), SHEIL & MAY (1996), and CONDIT et al. (1999). Then significant difference was tested by randomization test with the bootstrap resampling (1000 times).

Table 5. Patterns of dynamical traits and net primary production in the subtropical forests, Okinawa Island, southern Japan.

History	Plot (age)			
	Stand-1 (15)	Stand-2 (30)	Stand-3 (50-100)	Stand-4 (100<)
	Clear cut /Secondary	Clear cut /Secondary	Old Growth	Old growth
Gain of stand biomass (kg/m ² , yr)	0.7954	0.6806	0.3825	0.4614
Loss of stand biomass (kg/m ² , yr)	0.0453	0.1274	0.1232	0.5090
Growth of stand biomass (kg/m ² , yr)	0.7501	0.5532	0.2593	-0.0476
Litter fall (kg/m ² , yr)	0.76 ± 0.08	0.72 ± 0.05	0.78 ± 0.25	0.89 ± 0.12
Loss of stand biomass by predation (kg/m ² , yr)	0.0153 ± 0.0006	0.0281 ± 0.0095	0.0253 ± 0.0074	0.0243 ± 0.0016
Net primary production* (kg/m ² , yr)	1.5707	1.4287	1.1878	1.3757

* Above ground net primary production of stand biomass (ANPP) was calculated based on the method of CLARKI et al. (2001), the sum of the amount of fine litterfall, increment of stand biomass, and lost to consumers.

Tree growth and competition

The results of non-linear regression analysis with Quasi-Newton method are shown in Fig.3. All the three parameters in the logistic growth function were different between *C. sieboldii* and

the other species regardless of the stand ages. Population of *C. sieboldii* had larger a (0.33 - 0.74) in the logistic growth function, which means the upper limits of absolute growth rate, than that (0.13 - 0.46) of any other species (Fig. 3) ($P < 0.0001$ by Log likelihood ratio test between *C. sieboldii* and the other species in each stand), implies that individual trees of *C. sieboldii* grew faster, especially in the canopy. Also the three parameters differed among the stands ($P < 0.0001$ by Log likelihood ratio test based on pair-wise among the three parameters in the stands). The non-linear regression by the logistic function gave higher r^2 -values in the secondary forests than those in the old growth forests. For *C. sieboldii* in the secondary forests (Stands 1 and 2), the growth rates of DBH indicate strong size-dependent growth patterns. On the other hand, the old growth forests (Stands 3 and 4) showed size-dependent asymptotic growth patterns with large variances ($1 - r^2 > 0.73$).

Competitive effects on individuals were detected at 5 m neighborhood radius, rather than at 2

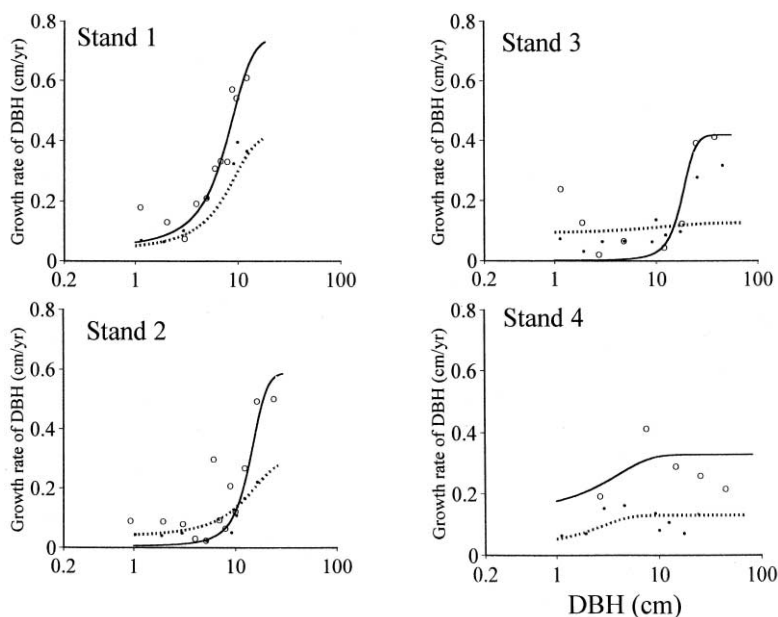


Fig.3. Relationships between DBH and absolute growth rate of *DBH* for individual trees of *Castanopsis sieboldii* (solid lines and open circles) and *other species* (broken lines and solid circles). Individual stems of Stand 1 and 2 are divided into DBH size class at 1- and 5cm intervals, whereas those of Stand 3 and 4 at 1-, 5- and 10-cm intervals so that each DBH class contains at least about 10 stems. The function form of the relationship between DBH (x) and absolute growth rate (y) is given as logistic growth model:

Stand 1, *C. sieboldii*, $y = 0.74/(1 + 15.95*exp(-0.38*x))$ ($r^2= 0.43$),
other species, $y = 0.42/(1 + 10.05*exp(-0.32*x))$ ($r^2= 0.22$);
 Stand 2, *C. sieboldii*, $y = 0.76/(1 + 24.39*exp(-0.19*x))$ ($r^2= 0.47$),
other species, $y = 0.46/(1 + 10.73*exp(-0.15*x))$ ($r^2= 0.05$);
 Stand 3, *C. sieboldii*, $y = 0.50/(1 + 888.55*exp(-0.32*x))$ ($r^2= 0.27$),
other species, $y = 0.38/(1 + 7.67*exp(-0.09*x))$ ($r^2= 0.05$);
 Stand 4, *C. sieboldii*, $y = 0.33/(1 + 1.34*exp(-0.42*x))$ ($r^2= 0.03$),
other species, $y = 0.13/(1 + 3.17*exp(-0.77*x))$ ($r^2= 0.08$).

Fitting of this model was conducted for absolute growth rate of each stem as the dependent variable and DBH as the explanatory variable for each of *C. sieboldii* and *other species*.

m or 3 m radii, which is almost consistent with the distance (max. 5.8 m) of the crown spread for canopy trees of *C. sieboldii*. In the following, therefore, only the results of 5 m radius were discussed below. The mode and the intensity of intra-and inter-specific competition are shown in Table 6. These effects are assessed by the *P* level and 95 % confidence limits based on the randomized simulations. At first, multiple linear regression analysis was conducted using the forward stepwise method at *P* < 0.05. Competitive effects were expressed as the coefficients of the model between Freedman-Turkey-transformed DBH growth rate of each individual tree as the dependent variable, and log-transformed DBH and crowding indices of *C. sieboldii* and the *other species* as the Table 6.

Table 6. Intra- and Inter-specific competitive effects among species on the growth rate of DBH of individual trees of secondary forests and old growth forests.

	Inter-specific competition		Intra-specific competition	
	From <i>C.sieboldii</i> to other species	From other species to <i>C.sieboldii</i>	Between trees of <i>C.sieboldii</i>	Between trees of other species
Stand 1 (secondary)	ns (-0.016 ~ -0.169)	-0.202* (-0.001 ~ -0.503)	-0.313*+ (-0.130 ~ -0.309)	-0.240* (0.086 ~ -0.240)
Stand 2 (secondary)	ns (-0.016 ~ -0.182)	-0.320* (-0.063 ~ -0.401)	-0.570*+ (-0.414 ~ -0.543)	-0.216* (-0.065 ~ -0.229)
Stand 3 (old growth)	-0.122* (0.07 ~ -0.133)	-0.602*+ (0.208 ~ -0.529)	ns (0.195 ~ -0.290)	ns (-0.018 ~ -0.123)
Stand 4 (old growth)	ns (0.089 ~ -0.108)	-0.400*+ (0.232 ~ -0.200)	ns (0.201 ~ -0.186)	ns (.0.141 ~ -0.097)

Multiple linear regression analysis was conducted. The DBH increment as the dependent variable was Freedman-Tukey transformed to have a constant variance of residuals.

* Denote significant values at *P* < 0.05 based on the multiple linear regression analysis.

+ Denote values out of random at 95 percent based on the randomized simulation.

Figures in parenthesis are 95 percent confidence intervals for competitive coefficients calculated from the nineteen simulations using the random point process.

explanatory variables. Then these coefficients were compared with 95 % confidence limits of that coefficient generated by multiple linear regression analysis using randomized dispersion of individual trees. Like this procedure is more accurate/conservative to ascertain the mode/intensity of competition.

As a result, the mode of competition was quite different among the four stands. In the secondary forests (Stands 1 and 2), *C. sieboldii* showed the evidence of intraspecific competition, although competition in Stand 1 was weak (because the competitive effect among *C. sieboldii* trees was almost equal to the highest value of that generated by randomized dispersion of individual trees). Interspecific competitive effects of the *other species* on *C. sieboldii* and intraspecific competitive effects within the *other species* trees were smaller than 95 % confidence limits calculated by the randomized simulations. In the old growth forests (Stands 3 and 4), interspecific competition of *C. sieboldii* was detected. Intraspecific competitive effects of *C. sieboldii* or *other species* were not entered into the regression, indicating the growth of *C. sieboldii* was regulated by *other species*.

Discussion

OLIVER (1980) and OLIVER and LARSON (1996) proposed a conceptual model describing the reconstruction process from establishment, thinning, and transition to the steady state following disturbances, based on the dendrochronology of individual trees in a cool-temperate forest. DENSLOW and GUZMAN (2000) investigated the variation of stand structure in a tropical moist forest according to the 4-phase model of the secondary succession: stand initiation, stem exclusion, understory reinitiation, and old growth. In short, the debate on the development process of forests is often based on the chronosequence of plots of various stand ages (FOSTER, 1990, BROWN & LUGO, 1990, KITAYAMA et al., 1995, GRAU, et al., 1997, STEININGER, 2000), which is feasible rather than monitoring stand development over several decades.

In this study, although trees of *C. sieboldii* in the secondary forests have just reached the reproductive stage, the understory of the stands was not fully reinitiated (e.g., lower recruitment rate of *C. sieboldii*) (Table 4), thus the secondary forests developing following clear cutting seem to be in a relatively early developmental phase. We could find a symptom of reinitiation in Stand 2, which had a little amount of seed production and saplings originated from seeds. On the other hand, the old growth forests had the inverse J-shaped DBH distributions and the high sapling density, can be realized at a late developmental phase with understory reinitiation (e.g., higher recruitment rate of *C. sieboldii*). If we use assumptions of a chronosequence analysis to demonstrate structural and dynamical differences between the secondary and old growth forests, it might be possible to illustrate regeneration dynamics over stand development, like those described in previous studies. Note that this does not necessarily indicate that these stands developed as a "successional continuum" in terms of species composition.

High density forests with small mean above-ground biomass (Stands 1 and 2) are at an early developmental stage, while low-density forests with high biomass (Stands 3 and 4) are mature. Moreover *C. sieboldii* is a dominant species throughout developmental phases, determining the canopy structure of the subtropical forests (c.f., SHIMIZU et al. 1988). These results imply that stand biomass composed of *C. sieboldii* and a variety of subordinate species develops with competition such as self-thinning among trees (YODA et al., 1963). In order to reveal the community dynamics, it is reasonable to examine the mode of competition between *C. sieboldii* and the *other species*. For example, YAMAMOTO (1994) suggested that population structure of *Castanopsis* spp. shifts to the regeneration niche of a pioneer species, due to interspecific competition of *Distylium racemosum* co-occurring in the late developmental stage.

Our present study showed that competitive effects and growth patterns are different among developmental phases of forests (KOHYAMA, 1987). In particular, canopy trees of *C. sieboldii* in the secondary forests grew faster than those of any other species (Fig. 3). This enables the cohort of *C. sieboldii* to regenerate in open sites and to reach the canopy quickly, undergoing intraspecific competition (that may be attributable to the high density of sprouting stems) (Table 2). Thus, relatively high ANPP (Table 5), which is comparable to that of montane tropical forests reviewed by CLARK et al. (2001b), seems to reflect on growth and sprouting abilities of *C. sieboldii*.

In the late developmental stage, however, *C. sieboldii* gave no indication of intraspecific competition, and interspecific competition prevailed, which suggests that *C. sieboldii* is regulated by suppression from other species. In the old growth forests, weak domination of *C. sieboldii* in the understory [despite plenty of seed dispersal, sapling density and recruitment (Table 2, 4)] may be a result of the severe interspecific competitive effects from canopy trees of *other species* to understory trees of *C. sieboldii*. Comparison between the secondary forests and the old growth forests reveals a

trend toward the steady state with gap disturbance which plays a role in regeneration dynamics of understory trees. For example, the growth rate of biomass decreased with increasing stand age (Table 5). This may be explained by the reason that the gain of stand biomass is canceled by the loss of biomass due to gap disturbances, especially in the old growth stand. This is also reflected by weak size-dependent growth with a large variance of *C. sieboldii* in the old growth forests, which may be caused by heterogeneity in terms of light environment (Fig. 3). The present results suggest that relatively high species diversity in the old growth stands can be maintained by competitive effects of the *other species*, which reduces the monopolization of *C. sieboldii*, and by gap disturbances which gives opportunities of regeneration for the *other species*.

In conclusion, structural attributes and growth dynamics showed different patterns between the secondary and the old growth forests, although the observed patterns qualitatively differ only among the four stands. Variation in the mode and the intensity of competition may reflect on the degree of the heterogeneity of the stand structures through the forest development, and the shifting from intra- to inter-specific competition, which probably associates with the spatial structure of trees. Because spatial dispersion such as clustering/regularity of individual trees has a large influence on detectability of competitive effects among individual trees [reported in detail in a following paper (SHIMATANI & KUBOTA, manuscript in review)]. Compositional convergence representing the domination of *C. sieboldii* with a variety of subordinate species can be understood as the combined effect of stand structure and the mode of competition.

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References

- ADAMS, D.C., GUREVITCH, J. & ROSENBERG, M.S. 1997. Resampling tests for meta-analysis of ecological data. *Ecology* 78: 1277-1283.
- AIBA, S., HILL, D.A. & AGETSUMA, N. 2001. Comparison between old-growth stands and secondary stands regeneration after clear-felling in warm-temperate forests of Yakushima, southern Japan. *For. Ecol. Manage.* 140: 163-175.
- AIDE, T.M., ZIMMERMAN, J.K., HERRERA, L. & ROSARIO, M. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *For. Ecol. Manage.* 77: 77-86.
- BAZZAZ, F.A. 1996. *Plants in changing environments*. Linking physiological, population, and community ecology. 320pp. Cambridge University Press.
- BORMANN, F.H. & LIKENS, G.E. 1994. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, Berlin.
- BROWN, S. & LUGO, A.E. 1990 Tropical secondary forests. *Journal of Tropical Ecology* 6: 1-32.
- CLARK, D.A., BROWN, S., KICKLIGHTER, D.W., CHAMBERS, J.Q., THOMLINSON, J.R. & NI, J. 2001a.

- Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11: 356-370.
- CLARK, D.A., BROWN, S., KICKLIGHTER, D.W., CHAMBERS, J.Q., THOMLINSON, J.R., NI, J. & HOLLAND, E.A. 2001b. Net primary production in tropical forests: an evaluation and synthesis of existing data. *Ecological Applications* 11: 371-384.
- CONDIT, R., HUBBELL, S.P. & FOSTER, R.B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65: 419-439.
- DENSLow, J.S. & GUZMAN, G.S. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *J. Veg. Sci.* 11: 201-212.
- DOBSON, A.J. 1990. *An Introduction to Generalized Linear Models*. Chapman and Hall.
- DUNCAN, R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. *J. Ecology* 79: 1073-1084.
- FINEGAN, B. 1992. The management potential of neotropical secondary lowland rainforest. *For. Ecol. Manage.* 47: 295-321.
- FINEGAN, B. 1996. Pattern and process in neotropical secondary rain forests: The first 100 years of succession. *Trends in Ecology and Evolution* 11: 119-123.
- FORD, E.D. 1975. Competition and stand structure in some even-aged plant monocultures. *J. Ecology* 63: 311-333.
- FOREST SOIL DIVISION, GFES. 1976. Forest soil classification in Japan. Bull. Govt. For. Exp. Sta. 280: 1-28 (in Japanese).
- FOSTER, R.B. 1990. Long-term change in the successional forest community of the Rio Manu floodplain, pp.565-572. In A.H. Gentry, ed., *Four Neotropical Rainforests*. Yale University Press, New Haven, CT.
- FURUNO, T. & SHIRAI, K. 1970. On the feeding especially of the black-marked prominent (*Phalera flavescens* Bremer et Grey) and the black-back prominent (*Clostera anastomosis tristis* Staudinger). *Bulletin of the Kyoto University Forests* 41: 26-40.
- GARCIA-MONTIEL, D. & SCATENA, F.N. 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. *For. Ecol. Manage.* 63: 57-78.
- GRAU, H.R., ARTURI, M.F., BROWN, A.D. & ACENOLAZA, P.G. 1997. Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests. *For. Ecol. Manage.* 95: 161-171.
- HARA, T., KIMURA, M. & KIKUZAWA, K. 1991. Growth patterns of tree height and stem diameter in populations of *Abies veitchii*, *A. mariesii* and *Betula ermanii*. *J. Ecology* 79: 1085-1098.
- HARA, T., NISHIMURA, N. & YAMAMOTO, S. 1995. Tree competition and species coexistence in a cool-temperate old-growth forest in southwestern Japan. *J. Veg. Sci.* 6: 565-574.
- HATUSHIMA, S. & AMANO, T. 1994. *Flora of the Ryukyus, South of Amami Island* (Second edition). The biological society of Okinawa. 393pp.
- HATUSHIMA, S. & NAKAJIMA, K. 1979. *Flowers of the Ryukyu Islands*. 368pp. Kohdansha, Tokyo (in Japanese).
- ITO, Y. 1995. *Forests of Yanbaru, Okinawa: Why could we not conserve its nature of outstanding universal value?* Iwanami Shoten, Tokyo (in Japanese).
- ITO, Y. 1997. Diversity of forest tree species in Yanbaru, the northern part of Okinawa Island. *Plant Ecology* 133: 125-133.
- ITOW, S. 1985. Species diversity-climate-isolation relationships in warm-temperate and subtropical evergreen broadleaved forests on Kyushu, the Ryukyus and the Bonins. *Origin and evolution of diversity in plants and plant communities*: 32-42. Edited by Hiroshi Hara, Academia Scientific

- Book Inc., Tokyo.
- KAWANABE, S. 1977. A subtropical broad-leaved forest at Yona, Okinawa. Primary productivity of Japanese forests: productivity of terrestrial communities. In: T. Shidei and T. Kira.(eds), *JIBP synthesis* vol. 16: 268-279. University of Tokyo Press, Tokyo.
- KIKUZAWA, K. 1988. Intraspecific competition in a natural stand of *Betula ermanii*. *Annals of Botany* 61: 727-734.
- KIRA, T. & SHIDEI, T. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology* 17: 70-87.
- KITAYAMA, K., MUELLER-DOMBOIS, D. & VITOUSEK, P.M. 1995. Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. *J. Veg. Sci.* 6: 211-222.
- KOHYAMA, T. 1987. Stand dynamics in a primary warm-temperate rain forest analyzed by the diffusion equation. *Bot. Mag. Tokyo* 100: 305-317.
- 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.
- KOJIMA, T. 1980. Forest soil in Okinawa - soil classification, property, distribution and vegetation. *Res. Bull. FFPRI* 309: 117-157.
- KUBOTA, Y. & HARA, T. 1995. Tree competition and species coexistence in a sub-boreal forest, northern Japan. *Annals of Botany* 76: 503-512.
- KUBOTA, Y. & HARA, T. 1996. Sapling allometry and competition of *Picea jezoensis* and *Abies sachalinensis* in a subboreal coniferous forest, northern Japan. *Annals of Botany* 77: 529-538.
- LANDE, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *OIKOS* 76: 5-13.
- MCCUNE, B. & MEFFORD, M.J. 1999. PC-ORD. *Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design, Gleneden Beach, Oregon, USA.
- MIYAWAKI, A. 1980. Vegetation of Japan, Yakushima. *Vegetation of Japan* vol. 1. (ed. Miyawaki A.) 376pp. Shibundo Co., Ltd. Publishers, Tokyo (in Japanese).
- MIYAGI, K. & SHINJO, K. 1989. A comparative study on vegetations of different aged-forests around Mt. Nishime, north of Okinawa Island. Pp. 1-95. Researches on the habitat conditions of endemic bird species: Interime report II. Nature Conservation Section, Okinawa Prefectural Government, Naha (in Japanese).
- MIYAGI, K. & SHINJO, K. 1990. A comparative study on vegetations of different aged-forests near Mt. Terukubi, north of Okinawa Island. Pp. 1-109. *Researches on the habitat conditions of endemic bird species: Interime report II*. Nature Conservation Section, Okinawa Prefectural Government, Naha (in Japanese).
- NAKASHIZUKA, T. & KOHYAMA, T. 1995. The significance of the asymmetric effect of crowding for coexistence in a mixed temperate forest. *J. Veg. Sci.* 6: 509-516.
- NANAMI, S., KAWAGUCHI, H. & YAMAKURA, T. 1999. Dioecy-induced spatial patterns of two codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. *Journal of Ecology* 87: 678-687.
- OLIVER, C.D. 1980. Forest development in north America following major disturbances. *For. Ecol. Manage.* 3: 153-168.
- OLIVER, C.D. & LARSON, B.C. 1996. *Forest stand dynamics*, Wiley, New York, NY.
- OLSON, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322-331.
- OHYAMA, H. & YAMAMORI, N. 1971. Studies on the management of the natural broad-leaves forest I -Stand composition of the natural broad-leaves forest on the northern part of Okinawa-. *Research Reports of Faculty of Agriculture, Ryukyu University* 18:248-266 (in Japanese with English summary).

- OONO, K., HARA, M., FUJIWARA, M. & HIRATA, K. 1997. Comparative Studies on Floristic Composition of the *Lucidophyll* Forests in Southern Kyushu, Ryukyu and Taiwan. *Natural History Research, Special Issue* No. 4: 17-79.
- PALMER, M.W. 1990. The estimation of species richness by extrapolation. *Ecology* 71: 1195-1198.
- PALMER, M.W. 1991. Estimation species richness: the second-order jackknife reconsidered. *Ecology* 72: 1512-1513.
- SHEIL, D. & MAY, R.M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84: 91-100.
- SHIMIZU, Y., YAHARA, T. & SUGIMURA, K. 1988. Regeneration process after logging of the subtropical broad-leaved evergreen forest on Amami Ohshima Island. *Komazawa Chiri* 24: 31-56 (in Japanese with English summary).
- SHINJO, K. & MIYAGI, Y. 1988. Flora of Kunigami Area of Okinawa Island. Pp. 117-193. *Research series of national monuments of Okinawa Prefecture. No. 30 Urgent research on national monuments in Kunigami Area*. Education Committee, Okinawa Prefectural Government (in Japanese).
- SHINJO, K., MIYAGI, Y. & NIJIMA, Y. 1991. A comparative study on vegetations of different aged-forests near Mt. Tamatsuji, north of Okinawa Island. Pp. 1-67. *Researches on the habitat conditions of endemic bird species: Interim report IV*. Nature Conservation Section, Okinawa Prefectural Government, Naha (in Japanese).
- SHINJO, K., NIJIMA, Y., MIYAGI, Y., SHIMABUKURO, H., ONAGA, T. & KANEMOTO, T. 1992. A comparative study on vegetations of different aged-forests at eastern part of the northern montane area of Okinawa Island. Pp. 1-122. *Researches on the habitat conditions of endemic bird species: Interim report V*. Nature Conservation Section, Okinawa Prefectural Government, Naha (in Japanese).
- SHINZATO, T., TABA, K., HIRATA, E. & YAMAMORI, N. 1986. Regeneration of *Castanopsis sieboldii* forest. 1 Studies on stratification and age structure of a natural stand. *Research Reports of Faculty of Agriculture, Ryukyu University* 33: 245-256 (in Japanese with English summary).
- STEININGER, M.K. (2000) Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *Journal of Tropical Ecology* 16: 689-708.
- SUNAKAWA, S. & YAMAMORI, N. 1964. Stand composition of mature broad-leaved trees. *Research Reports of Faculty of Agriculture, Ryukyu University* 11: 83-101 (in Japanese with English summary).
- SUZUKI, K. 1979. Vegetation of the Ryukyu Islands, Japan. *Bulletin of the Institute of Environmental Science and Technology, Yokohama National University* 5: 87-160 (in Japanese with English summary).
- U.S. CIVIL ADMINISTRATION OF THE RYUKYU ISLANDS 1953. *Ryukyu Islands Forest Situation*. Special Bulletin No.2
- UMEKI, K. & KIKUZAWA, K. 1999. Long-term growth dynamics of natural forests in Hokkaido, northern Japan. *J. Veg. Sci.* 10: 815-824.
- UUTTERA, J., TOKOLA, T. & MALTAMO, M. 2000. Differences in the structure of primary and managed forests in East Kalimantan, Indonesia. *For. Ecol. Manage.* 129: 63-74.
- YAMAMOTO, S. 1994. Gap regeneration in primary evergreen broad-leaved forests with or without a major canopy tree, *Distylium racemosum*, southwestern Japan: A comparative analysis. *Ecol. Res.* 9: 295-302.
- YODA, K., KIRA, T., OGAWA, H. & HOZUMI, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* 14: 107-129.
- YODA, K. 1971. *Forest Ecology*. Tsukiji Shokan, Tokyo (in Japanese).
- YOKOZAWA, M., KUBOTA, Y. & HARA, T. 1998. Effects of competition mode on spatial pattern dynamics in plant communities. *Ecological Modeling* 106: 1-16.

ZHUANG, X.Y. & CORLETT, R.T. 1997. Forest and forest succession in Hong Kong, China. *Journal of Tropical Ecology* 14: 857-866.