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Structure and Species Diversity of Subtropical Evergreen Broad-leaved Forest in Northern Okinawa Island, Japan

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The structure and tree species diversity of a subtropical evergreen broad-leaved forest in northern Okinawa Island, Japan, were studied. Enumeration of the six sampling plots revealed an average density of 5,580 individuals with DBH ≧ 3.0 cm/ha, having an average basal area of 55 m^2 ha^{-1}. The large-size trees of DBH ≧ 20 cm contributed 10% of the total individuals, and 49% of the total basal area. The forest showed a high diversity of tree species, which is comparable to some tropical rain forests. A total of 54 overstory species of 24 families and a total of 63 understory species of 26 families were identified in the six sampling plots. Fagaceae and Theaceae were the most important families; *Castanopsis sieboldii*, *Schima wallichii* and *Distylium racemosum* were the most important species. The diversity index and equitability index of species were 4.15 and 0.72 for the overstory plots, and 4.72 and 0.79 for the understory subplots, respectively. The diversity index for the overstory was significantly correlated to the total basal area of trees over 20 cm DBH ($p < 0.05$) and the importance value of *C. sieboldii* ($p < 0.001$), while for understory, the diversity index was not correlated to the structural parameters (all $p > 0.16$). The size distribution pattern and age structure indicated differences in regeneration strategies for canopy dominants. In population dynamics of the succession process, *C. sieboldii* and *D. racemosum* were self-maintaining types, and *S. wallichii* was a gap- or opening-dependent type.

Key words: floristic composition, forest structure, Okinawa, regeneration strategy, species diversity index, subtropical forest

Evergreen broad-leaved forest is an important forest formation peculiar to the warm-temperate and subtropical zone (Wu, 1980; Ovington, 1983), and is dominated by evergreen oaks of the genera *Quercus*, *Castanopsis* and *Lithocarpus* with associated rich evergreen tree species, such as *Persea*, *Cinnamomum*, *Ilex*, *Symplocos* and *Camellia* (Kira, 1991). Okinawa Island is located in the subtropical zone which is characterized by a maritime subtropical climate and abundant rainfall throughout the year. Thus, well-developed evergreen broad-leaved forest dominated by *Castanopsis sieboldii* Hatusima ex Yamazaki et Mashiba remains in the northern part of this island. This type of forest covers about 340 km^2, only 0.1% of total area of Japan, however, a total of 1,089 high plant species (about 28% of total in Japan) is represented in this forest (Shinjo and Miyagi, 1988). It cannot be doubted that the importance of this type of forest has been emphasized since the demands for products and particularly for ecological benefits from this forest have been increasing (Itô, 1995, 1997; Hirata *et al.*, 1998). Therefore, further studies seem to be warranted from an ecological viewpoint.

Several studies have been made on the phytosociological classification of vegetation (Suzuki, 1979; Fujiwara, 1981), forest management (Hirata *et al.*, 1980, 1991, 1995, 1998; Terazono and Chinen, 1988; Asato *et al.*, 1997), and some features of structure and floristics (Shinjo and Miyagi, 1988; Hirata, 1994; Itô, 1997; Oono *et al.*, 1997) for this subtropical evergreen broad-leaved forest. However, those reports are insufficient for understanding the community features, especially tree species diversity in this region. Our main objective in this paper is to give a detailed account of the structure and floristic composition of our site, and to discuss the tree species diversity in relation to forest structure.

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Study Area

This study was conducted at Yona Experimental Forest of the University of the Ryukyus, located in northern Okinawa Island (26°45′ N and 128°10′ E), southwest Japan. The area is characterized by a maritime subtropical climate and abundant rainfall throughout the year. The annual mean temperature is about 22°C, and the mean temperature in the coldest month, January, and the hottest month, July, are 5.4°C and 34.5°C, respectively. Even in the coldest month, the lowest temperature does not fall below 2.0°C. The mean annual rainfall is 2,680 mm with an annual maximum of 3,982 mm in 1,969 and an annual minimum of 1,905 mm in 1,977 (Yona Experiment Forest, University of the Ryukyus). Typhoons frequently occur between July and October, bringing high rainfall and strong winds to the island.

The topography of the area is hilly. The highest peak, Mt. Yonaha, is 448 m a.s.l. Deep valleys dissect the area and steep slopes predominate. The bedrock is composed mainly of sandstone and clay-slate (Yamamori, 1994), and a yellow soil develops (Forest Soil Division, GFES, 1976). The study area is covered with well-developed evergreen broad-leaved forests.

Methods

Field work was carried out in April 1996. Six plots were established randomly in evergreen broad-leaved forest which had not received any management treatment such as logging or thinning since 1,950 (Hirata, personal communication). Each plot was, 20 m × 20 m in size. All overstory trees with diameter at breast height (DBH) of 3.0 cm and over on each plot were tagged at breast height, numbered, and identified to species. Tree height (H) and DBH, as well as crown position, were measured. The number of understory tree species with DBH less than 3 cm or height over 10 cm was counted in one regularly selected 5 m × 5 m subplot in the center of the main plot, and their heights were also recorded.

Dominant species in each plot were defined by an analysis of the importance values of species (Gonzalez and Zak, 1996). The importance value of a species was calculated as described by Basnet (1992):

$$IV\,(\%) = (RBA + RD)\,/\,2$$

where *RD* (%) was relative density calculated by summing the number of stems for a given species in a plot, dividing by the total number of stems of all species in the plot, and multiplying by 100; *RBA* (%) was relative basal area calculated in the same way using the basal area instead of the number of stems.

The family importance value (*FIV*; Mori *et al.*, 1983) was used to assess the contribution of each family to the stand. *FIV* combines relative family richness, relative density and relative basal area into one value; its maximum value is 100. Species diversity was shown by using the Shannon-Wiener index (H') and equitability index (J'). H' and J' for overstory species were calculated according to the following formulae (Pielou, 1975):

$$H' = -\Sigma\,(Pi \cdot \log_2 Pi)$$

$$J' = H'\,/\,\log_2 S$$

where Pi was the importance value of the ith species; S was the number of species occurring in each sampling plot. In addition, H' and J' for understory species were calculated in the same way using the relative density instead of the importance value.

The nomenclature of species in the present paper follows 'Flora of the Ryukyus, South of Amami Island' edited by Hatusima and Amano (1994).

Results

1 Characteristics of forest structure

The General description for the sampling plots is summarized in Table 1. Within the sampling plots, there was no much difference for mean heights in the overstory (DBH ≧ 3.0 cm), and the tallest trees were only 14 m tall, which were exclusively *C. sieboldii* and *Schima wallichii* Kort. ssp. *liukiuensis* Bloemb. For the mean DBH, P-4 had the greatest value (11.4 cm), the other five plots had, however, almost the same value (range from 8.2 to 9.5 cm). Density for the overstory ranged from 3,875 to 6,625 stems ha^{-1}; size-class density decreased with each 10 cm rise. The relative density averaged 70.5% ranging from 61.3 to 77.6% for 3.0 ≦ DBH < 10 cm and only 9.9% for DBH ≧ 20 cm. Only one tree had a DBH over 50 cm (*C. sieboldii*, 56 cm DBH). Total basal area ranged from 45.4 to 61.7 m^2 ha^{-1}, of which the large-size trees (DBH ≧ 20 cm) contributed 42.1 to 67.4% except

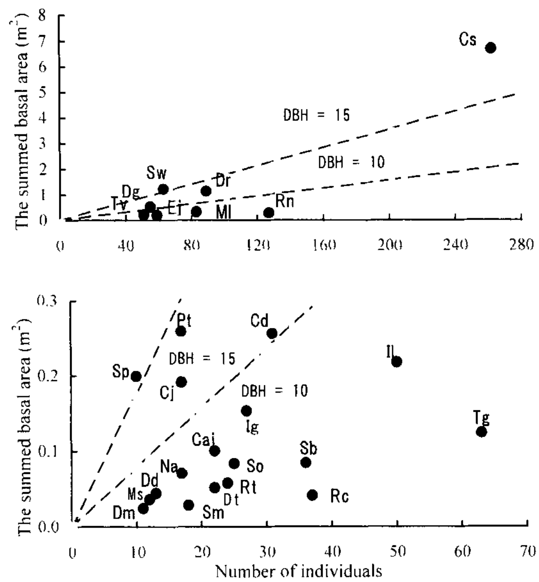

Fig. 1 Relationship between summed basal area and number of individuals for main overstory species which had ten individuals or more in the combined sampling plots. Some abbreviations are given in Table 2; the others are: Caj, *Camellia japonica*; Cd, *Cinnamomum doederleinii*; Cj, *Cleyera japonica*; Dd, *Diplospora dubia*; Dm, *Diospyros morrisiana*; Dt, *Dendrodendren trifidus*; Ig, *Ilex goshiensis*; Il, *I. Liukiuensis*; Ms, *Meliosma simplicifolia* ssp. *rigida*; Na, *Neolitsea aciculate*; Pt, *Persea thunbergii*; Rc, *Randia canthioides*; Rt, *Rhododendren tashiroi*; Sb, *Syzgium buxifolium*; Sm, *Symplocos microcalyx*; So, *Schefflera octophylla*; Sp, *S. prunifolia*; Tg, *Terstroemia gymnanthera*.

Table 1 Mean DBH (cm), mean tree height (m), density (stems ha^{-1}) and basal area (m^2 ha^{-1}) in the sampling plots.

Plot number	P-1	P-2	P-3	P-4	P-5	P-6
Altitude (m)	310	310	290	290	295	230
Aspect	S40E	N50E	N30E	N60W	N40W	N75W
Inclination (degree)	26	28	25	32	30	24
Mean DBH	8.8	8.4	8.8	11.4	9.5	8.2
Mean tree height	6.4	6.0	6.6	7.1	6.4	7.5
Density						
3.0 cm ≦ DBH < 10 cm	3950	4675	4400	2375	3850	4500
10 cm ≦ DBH < 20 cm	750	875	1375	750	925	2000
20 cm ≦ DBH	475	475	475	750	750	125
Total	5175	6025	6250	3875	5525	6625
Basal area						
3.0 cm ≦ DBH < 10 cm	9.11	12.21	11.64	6.44	9.58	12.39
10 cm ≦ DBH < 20 cm	12.81	12.63	20.36	12.63	15.62	28.22
20 cm ≦ DBH	32.60	29.91	23.22	39.51	36.48	4.76
Total	54.52	54.75	55.22	58.58	61.68	45.37

for P-6 where the figure was only 10.5%.

The tree size variation for mainly overstory species is given in Fig. 1. Species whose mean DBH was 15 cm or more were exclusively *C. sieboldii*, *S. wallichii* and *Symplocos prunifolia* S. et Z.; and only five species (9%) had mean DBH between 10 and 15 cm: they were *Persea thunbergii* Kosterm., *Distylium racemosum* S. et Z., *Cleyera japonica* Thunb., *Daphniphyllum glaucescens* Bl. ssp. *teijsmannii* Huang and *Cinnamomum doederleinii* Engl. The aforementioned 8 species contributed the vast majority (79.3%) of the total basal area in the sampling plots, even though they comprised only 40.7% of the total individuals. However, the following three species, *Ternstroemia gymnanthera* Beddome, *Randia canthioides* Champ. ex Benth. and *Rapanea neriifolia* Mez., comprised 3.3% and 17.0% of the total basal area and the total individuals, respectively. This indicated that those species had a large number of individuals with very small diameter at breast height.

DBH distributions of the sampling plots and of the dominant tree species are given in Figs. 2 and 3, respectively. All of the six sampling plots showed the same size-class distribution patterns, a typical reverse-J type (Fig. 2), which was formed by species having the highest frequency in the small DBH classes with a gradual decrease in the number of indi-

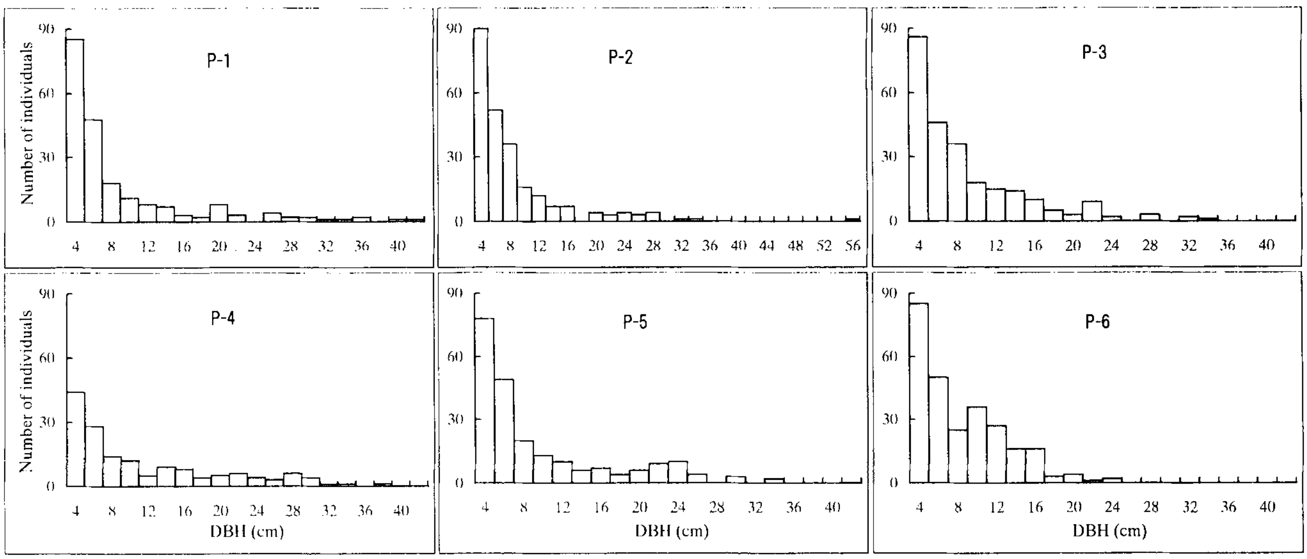

Fig. 2 DBH class frequency distribution for the entire plot in northern Okinawa. All plots are based on the number of individuals with DBH $\geqq$ 3.0 cm.

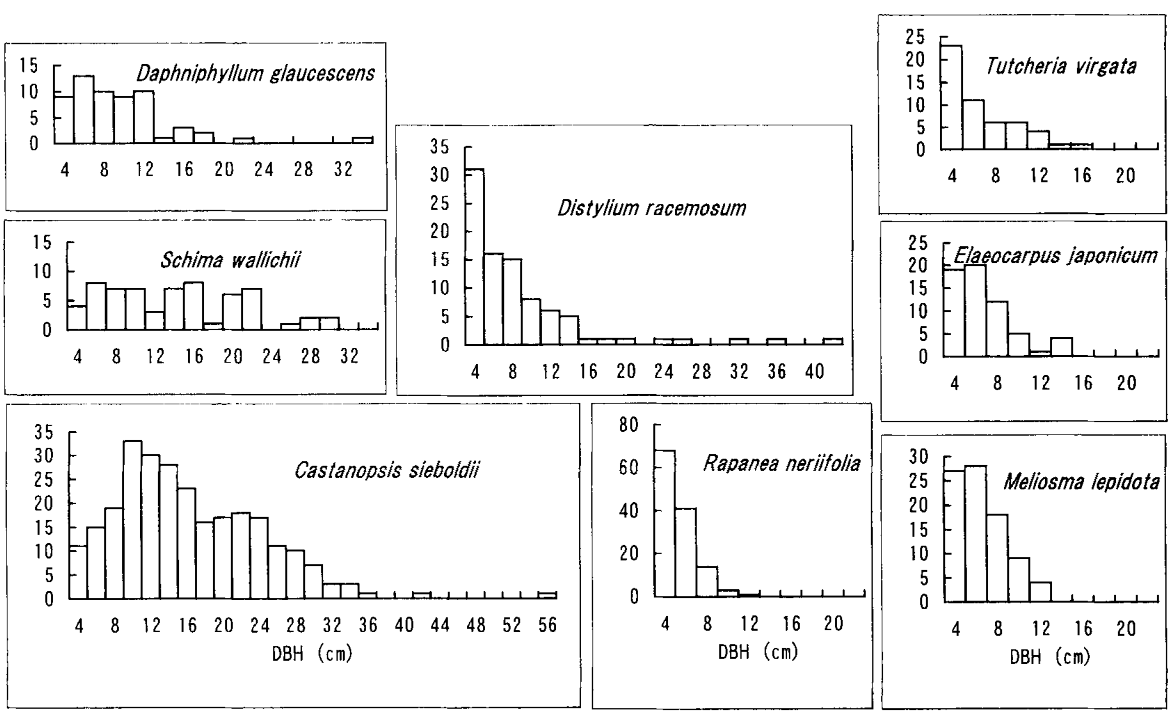

Fig. 3 DBH class frequency distribution for the dominant tree species (DBH $\geqq$ 3.0 cm) in the sampling plots. Data are based on the total of six sampling plots.

viduals towards the larger classes. The results from Kolmogorov-Smirnov test demonstrated that the size-class distribution patterns did not differ significantly ($p > 0.05$) among the sampling plots except for P-6 (Table 2). For the dominant species, generally, the following three distribution patterns of tree size-class were found (Fig. 3). The above-mentioned reverse-J type was for subcanopy dominants such as *D. racemosum*, *R. neriifolia*, *Meliosma lepidota* Bl. ssp. *squamulosa* Beus., *Elaeocarpus japonicum* S. et Z. and *Tutcheria virgata* Nakai. The sporadic type indicates that the adjacent classes are badly represented; frequency rises again more or less sharply in intermediate classes, such as *C. sieboldii*, *S. wallichii*, *D. racemosum* and *D. glaucescens*. The unimodal type is formed by species having the highest frequency in the intermediate classes with lower frequency in the smaller and larger classes, such as *C. sieboldii*. The size-class distribution patterns did not differ significantly ($p > 0.05$) among the subcanopy dominants. However, they differed significantly among the canopy dominants excluding those between *D. racemosum* and *D. glaucescens* (Table 3).

2 Floristic composition and species diversity

The overstory plots contained a total of 54 tree species, of which only 13 species were encountered in all six plots and 15 species were encountered only in one plot; the understory subplots contained a total of 63 shrub and tree species. The understory subplots had 19 species not found in the overstory. There appeared 24 and 26 families in the overstory and understory, respectively. The diversity index and equitability index for species were 4.15 and 0.72 for overstory plots, and 4.72 and 0.79 for the understory subplots, respectively. Of the six sampling plots, P-1 ranked first in diversity indices for the overstory, P-2 ranked first for understory, while P-6 ranked last for both of the overstory and understory (Tables 4 and 5).

In the sampling plots, 22 percent of the overstory species (12 of 54 species) had only one or two individuals; 9 species (16%) had over 50 individuals. 33 percent of the understory species (21 of 63 species) had only one or two individuals; 4 species (6%) had over 50 individuals. *C. sieboldii* had the highest importance value ranging from 26.9 to 49.2 for the overstory in the six plots, about 3 to 4 times that of *D. racemosum* which had the second highest importance value (range from 7.0 to 11.6). This demonstrated that *C. sieboldii* ranked as the dominant species in this subtropical evergreen broad-leaved forest in Okinawa (Table 4). The sub-dominant species was, however, somewhat different among the sampling plots. According to family importance value (FIV), the dominant families for this forest were Fagaceae (25.0), Theaceae (15.5), Lauraceae (6.2), Hamamelidaceae (5.7), Aquifoliaceae (5.7) and Symplocaceae (5.6). In the understory, the main dominants were *C. sieboldii* (15.8 for IV), *Ardisia quinquegona* Bl. (11.6), *R. neriifolia* (9.5), and *R. canthioides* (5.1); and dominant families were Myrsinaceae (21.2), Fagaceae (15.8), Rubiaceae (15.6), Lauraceae (9.0), Theaceae (7.3) and Euphorbiaceae (5.2) (Table 5).

3 Understory (DBH < 3.0 cm and H ≧ 10 cm)

Density for understory (DBH < 3.0 cm, or H ≧ 10 cm) averaged 181 individuals ranging from 147 to 208 individuals per subplot (5 m × 5 m in size; Table 5). The majority of understory individuals were contributed by juvenile canopy and subcanopy dominant species, particularly for *C. sieboldii* (15.8%), *R. neriifolia* (9.5%) and *D. glaucescens* ssp. *teijsmannii* (4.0%). The species only found in the understory comprised 25.3% of the total individuals, of which 11.6% for *A. quinquegona*, 3.2% for *Antidesma japonicum* S. et Z. and 3.1% for *Lasianthus fordii* Hance. However *Cleyera japonica*, *M. lepidota*, *Rhododendron tashiroi* Maxim., *S. wallichii*, *Symplocos microcalyx* Hayata and *T. gymnanthera* had rather fewer individuals and comprised only 2.1% of the total understory individuals, even though they comprised 19.9% of the

Table 2 Comparison of the size-class distribution patterns among the sampling plots.

	P-1	P-2	P-3	P-4	P-5
P-2	ns				
P-3	ns	ns			
P-4	ns	*	ns		
P-5	ns	ns	ns	ns	
P-6	**	*	ns	**	**

Between-plot differences were examined by Kolmogorov-Smirnov test: **, significant difference at $p < 0.01$; *, significant difference at $p < 0.05$; ns, non-significant difference.

Table 3 Comparison of the size-class distribution patterns among canopy and subcanopy dominants in the conbined sampling plots.

	Subcanopy dominant				Canopy dominant		
	Cs	Dr	Sw	Dg	Rn	Ml	Ej
Dr	***						
Sw	***	***					
Dg	***	ns	***				
Rn	***	***	***	***			
Ml	***	***	***	***	ns		
Ej	***	***	***	***	ns	ns	
Tv	***	***	***	***	ns	ns	ns

Between species differences were examined by Kolmogorov-Smirnov test: ***, significant difference at $p < 0.001$; ns, non-significant difference ($p > 0.10$). Cs, *Castanopsis sieboldii*; Dr, *Distylium racemosum*; Sw, *Schima wallichii*; Dg, *Daphniphyllum glaucescens*; Rn, *Rapanea neriifolia*; Ml, *Meliosma lepidota*; Ej, *Elaeocarpus japonicum*; Tv, *Tutcheria virgata*.

Table 4 Diversity indices and importance value of each family (FIV) and dominant species (IV) for trees whose DBH ≧ 3.0 cm in the sampling plots.

Plot number	P-1	P-2	P-3	P-4	P-5	P-6	Total
Species richness	32	34	36	33	34	23	54
Diversity index	4.09	3.92	3.88	3.62	3.77	2.81	3.97
Equitability index	0.82	0.77	0.75	0.72	0.74	0.62	0.69
Importance value							
Fagaceae; 2 species	**22.20**	**21.20**	**22.06**	**24.78**	**25.45**	**34.23**	**25.04**
Castanopsis sieboldii Hatusima (Cs)	**26.92**	**30.33**	**31.70**	**35.65**	**36.70**	**49.17**	**35.18**
Theaceae; 8 species	**15.48**	**14.03**	**14.70**	**21.16**	**18.64**	**13.61**	**15.50**
Schima wallichii ssp. *liukiuensis* Bloemb. (Sw)	**5.17**	2.18	**7.09**	**11.25**	**5.03**	**12.12**	**6.97**
Tutcheria virgata Nakai (Tv)	**6.20**	4.70		3.64	2.59		2.69
Lauraceae; 5 species	**6.68**	**7.50**	4.27	4.47	**7.10**	**6.25**	**6.23**
Hamamelidaceae; 1 species	**6.49**	**6.49**	**6.23**	**8.75**	**7.16**		**5.68**
Distylium rasemosum S. et Z. (Dr)	**8.17**	**8.27**	**7.95**	**11.61**	**9.27**		**7.60**
Aquifoliaceae; 4 species	4.91	**5.70**	4.27	**6.62**	**6.93**	**7.81**	**5.66**
Symplocaceae; 6 species	4.81	**6.09**	**7.46**	2.76	**5.01**	3.64	**5.61**
Rubiaceae; 5 species	**6.68**	**5.13**	4.27	4.02	4.10	3.84	4.81
Myrsinaceae; 1 species	**6.04**	**5.11**	3.43	4.93	**5.69**	**5.30**	4.65
Rapanea neriifolia Mez. (Rn)	3.47	**7.50**	**6.20**	3.75	**5.88**	**7.07**	**5.78**
Sabiaceae; 2 species	**8.58**	**7.10**	**6.33**	2.56	3.69	1.59	4.47
Meliosma lepidota ssp. *squamulosa* Beus. (Ml)	**7.24**	**7.14**	**6.48**	2.32	2.31	0.21	4.28
Elaeocarpaceae; 2 species	**6.08**	3.43	1.89	2.61	2.19	4.12	3.35
Elaeocarpus japonicus S. et Z. (Ej)	**5.72**	3.68	1.45	2.40	1.82	4.00	3.13
Daphniphyllaceae; 1 species	1.84	4.67	**5.74**	2.58	2.07	**5.37**	3.30
Daphniphyllum glaucescens Huang (Dg)	1.20	**5.54**	**7.22**	2.36	1.64	**5.88**	4.03
Araliaceae; 2 species	4.70	4.16	1.07	4.43	3.67	1.88	2.74
Ericaceae; 2 species	1.98	1.66	3.02	3.47	2.45	2.08	2.26
Myrtaceae; 1 species	2.35	1.55	2.27	1.75	1.49	3.48	1.72
Rosaceae; 2 species		1.54	1.39	1.24	1.20	2.51	1.67
Podocarpaceae; 2 species		1.13	2.73	1.48			1.47
Ebenaceae; 1 species	1.77	1.44	1.07		1.63		0.95
Myricaceae; 1 species		1.19	1.50		1.17	1.84	0.85
Styracaceae; 1 species	2.08						0.78
Magnoliaceae; 1 species			1.41	1.32			0.74
Celastraceae; 1 species			1.08	1.24	1.15	1.60	0.73
Oleaceae; 1 species			1.09				0.65
Anacardiaceae; 1 species			1.09				0.65
Euphorbiaceae; 1 species				1.24			0.64

The dominant families and species of each plot are given in bold figures.

Table 5 Density, mean height, diversity indices, and dominant species of shrub and tree with number of individuals/relative density (%) in the understorey (DBH ≦ 3.0 cm, or H ≧ 10 cm) for the six subplots of 5 m × 5 m in size.

Plot number	P-1	P-2	P-3	P-4	P-5	P-6	Total
Density (number per subplot)	147	194	208	201	178	160	1088
Mean height (cm)	116.0	67.6	57.7	86.3	62.2	106.7	80.6
Species richness	27	37	31	38	34	25	63
Diversity index	3.75	4.54	4.01	4.53	4.40	3.48	4.72
Equitability index	0.79	0.87	0.81	0.86	0.86	0.72	0.79
Dominant species							
Castanopsis sieboldii Hatusima	7 /4.8	25 /12.9	33 /15.9	10 /5.0	25 /14.0	72 /45.0	172 /15.8
Ardisia quinquegona Bl.*	49 /33.3	17 /8.8	2 /1.0	31 /15.4	25 /14.0	2 /1.3	126 /11.6
Rapanea neriifolia Mez.	7 /4.8	20 /10.3	45 /21.6	2 /1.0	11 /6.2	18 /11.2	103 /9.5
Randia canthioides Champion	8 /5.4	9 /4.6	12 /5.8	15 /7.5	8 /4.5	4 /2.5	56 /5.1
Distylium rasemosum S. et Z.	3 /2.0	3 /1.5	21 /10.1	15 /7.5	1 /0.6		43 /4.0
Elaeocarpus japonicus S. et Z.	4 /2.7	9 /4.6	3 /1.4	6 /3.0	7 /3.9	9 /5.6	38 /3.5
Cinnamomum doederleinii Engl.	1 /0.7	5 /2.6	11 /5.3	12 /6.0	2 /1.1	4 /2.5	35 /3.2
Tutcheria virgata Nakai	12 /8.2	16 /8.2	3 /1.4	2 /1.0	1 /0.6		34 /3.1
Lasianthus fordii Hance*	4 /2.7	1 /0.5	3 /1.4	18 /9.0	8 /4.5		34 /3.1
Daphniphyllum glaucescens Huang	2 /1.4	3 /1.5	6 /2.9	14 /7.0	2 /1.1	5 /3.1	32 /2.9
Tarenna gracilipes Ohwi*	1 /0.7	10 /5.1	6 /2.9	5 /2.5	9 /5.1		31 /2.8
Psychotria rubra Poir.*	12 /8.2	5 /2.6		4 /2.0	6 /3.4		27 /2.5
Syzgium buxifolium Hook. et Arn.	2 /1.4	2 /1.0	7 /3.4	2 /1.0	5 /2.8	9 /5.6	27 /2.5
Neolitsea sericea Koidz.			12 /5.8			4 /2.5	16 /1.5
Glochidion zeylanicum A. Juss.*	1 /0.6			2 /0.7	17 /5.7		20 /1.2

Dominant species dominated at least one plot. *Species found only in the understorey.

Table 6 Comparison of species diversity for some evergreen broad-leaved forests in Japan.

Location	MT (°C)	Number of species	Diversity index	Equitability index	Source and plot size
Nara[1]	12.0	16	3.08	0.77	Nakane 1975; 0.12 ha (P-A, C and E; DBH ≧ 4 cm)
Miyazaki	16.9	50	—	—	Tanouchi and Yamamoto 1995; 4.0 ha (DBH ≧ 4.5 cm)
Kumamoto	—	14	3.04	0.81	Omura *et al.* 1969; 0.04 ha (mean values; DBH ≧ 4.5 cm)
Amami Ohshima	21.1	49	—	—	Terashi 1983; 0.24 ha (six 20 × 20 m plots; DBH ≧ 3.0 cm)
Okinawa	22.0	52	—	—	Enoki *et al.* 1999; 4.0 ha (DBH ≧ 10 cm)
Okinawa	22.0	54	4.15	0.72	This study; 0.24 ha (six 20 × 20m plots; DBH ≧ 3.0 cm)
Okinawa	22.0	32	3.68	0.74	This study; 0.04 ha (mean values; DBH ≧ 3.0 cm)

MT is mean temperature. [1]The diversity indices are calculated from the original data by author.

total overstory individuals.

Discussion

1 Forest structure comparison with other sites

The average stem density for evergreen broad-leaved forest (DBH ≧ 3.0 cm) in Okinawa was estimated to be 5,580 stems ha^{-1}, having an average basal area of 55 m^2 ha^{-1}. Recent comparable data include, 1,400 stems ha^{-1} and 48 m^2 ha^{-1} for evergreen oak forest (DBH ≧ 4.5 cm) at Nara (Nakane, 1975); 3,900 stems ha^{-1} and 48 m^2 ha^{-1} for evergreen broad-leaved forest (DBH ≧ 5.0 cm) at Miyazaki (Tanouchi and Yamamoto, 1995); and 2,590 stems ha^{-1} and 53 m^2 ha^{-1} for evergreen broad-leaved forest (old growth, DBH ≧ 3.0 cm) at Amami Ohshima (Terashi, 1983). This indicates that the Okinawan forest is largely populated with a high value for basal area. Similar results were reported by Hara *et al.* (1996a) and Hirata (1994). The aforementioned stem density and basal area for Okinawan forest were also higher than some subtropical and tropical rainforests around the world. Examples are 3,480 stems ha^{-1} and 25.6 m^2 ha^{-1} (H > 5 m) for a Chinese subtropical primary forest (Young and Herwitz, 1995); 1,310 stems ha^{-1} (H > 1 m) for an Australian subtropical rainforest (Lowman, 1988); 2,140 stems ha^{-1} and 33 m^2 ha^{-1} for a subtropical rainforest (H > 5 m) in Hawaii (Hatfield *et al.*, 1996); and 3,710 stems ha^{-1} and 43 m^2 ha^{-1} for a tropical rainforest (DBH ≧ 2.5 cm) in Papua New Guinea (Wright *et al.*, 1997). Furthermore, the Okinawan evergreen broad-leaved forest had a relatively low canopy (usually less than 15 m tall) compared to the above-mentioned subtropical and tropical rainforests (usually over 25 m tall). Thus, the productivity of this forest was also low (Kawanabe, 1977) although its total basal area was high. The possible reasons for this low productivity may be ascribed to the low canopy, and the poor edaphic condition (strong acidity and shortage of P and K; Xu, unpublished data) as well.

2 Species diversity

In recent years a number of authors have drawn together and ruled the principal result for species diversity of Okinawan evergreen broad-leaved forest (Itow *et al.*, 1984; Sinjo and Miyagi, 1988; Itô, 1997; Oono *et al.*, 1997; Enoki *et al.*, 1999). Oono *et al.* (1997) reported that the species diversity was somewhat lower in the Ryukyu Islands (including Okinawa Island) than in the mainland of Japan. It is difficult to compare our data to Oono's because of different methodologies. However, it is apparent that in Okinawa, the montane is very low (the highest peak only 448 m a.s.l.), and the slopes are short and steep. Thus, only small foot-slope appears. These topographical traits may be very different from those in Kyushu. Consequently, small sampling size should be responsible for the lower species diversity in Okinawa. Itô (1997) drew the conclusion that the species diversity increased with forest age, and shown higher species diversity of the forests on Okinawa than of those on the mainland Japan. In the present study, we analyzed the relationships between tree species diversity and structural characteristics. The statistical analysis demonstrated that the diversity index for the understory was not significantly correlated (all $p > 0.16$) to the structural parameters (such as stem density, basal area, and importance value of *C. sieboldii*). However, the diversity index for the overstory was significantly correlated to total basal area of trees over 20 cm DBH ($p < 0.05$), and importance value of *C. sieboldii* ($p < 0.001$). A total of 54 overstory tree species was encountered at six 0.04 ha plots in our site; the average number of overstory species per plot was 32, and the diversity index and equitability index averaged 3.68 and 0.74, respectively. More recent studies recorded 52 canopy tree species (DBH > 10 cm) in a 4-ha plot (Enoki *et al.*, 1999), and 69 tree species (DBH ≧ 3.0 cm) within a 1-ha square plot (Yasuda *et al.*, 1999). These values are rather higher than for other evergreen broad-leaved forests in Japan (Table 6), which are in agreement with the results from the above-mentioned inventories. Higher species diversity for Okinawan evergreen broad-leaved forest may be partly attributed to the biogeographical history and warm, moist climate (Kira, 1989, 1991). Hiura (1995) showed that the cumulative temperature of the growth season is strongly and primarily correlated with the species diversity of Japanese beech forests. Itow (1988) reported a strong relationship between species diversity index and warmth index along the eastern humid zone of Asia from tropical (Malay Peninsula) to warm-temperate zone (Kyushu). The more energy available, the more species are able to exist, hence species richness and species equitability increases. Our site, located in the warmest southernmost Japan, has high species diversity (Itow *et al.*, 1984; Itô, 1997), which is even comparable to that of some tropical rainforests. For example in Puerto Rico, America, a 0.72 ha plot has 51 tree species (DBH > 4.0 cm) and a diversity index of 4.0 (Crow, 1980). In another example in the Caribbean island of St. Lucia, West Indies, a 0.62 ha sampling area has 50 tree and shrub species (from sixty-two 10 m × 10 m plots, DBH ≧ 1.0 cm; Gonzales and Zak, 1996).

3 Regeneration strategies of canopy dominants

C. sieboldii is a long-lived climax species and occupies the canopy layer in Okinawan evergreen broad-leaved forests (Hirata, 1994). *S. wallichii* is known to be a pioneer species, fast-growing and able to invade a disturbed site in a subtropical area (Ohsawa and Ohtsuka, 1989). This species is also the major canopy dominant. *D. racemosum* is, however, somewhat different from the above-mentioned two species, in that it is a rather shade-tolerant species, mainly occupying the subcanopy layer although it is able to continuously grow up into the canopy layer, and also becomes canopy dominant in some stands.

The size variation of individuals is an important aspect for describing community structure; it also indicates the establishment process and shade-tolerance of a population (Okitsu *et al.*, 1995), and from it the interspecies relationship can be derived. The size distribution for these three species indicates differences in their regeneration strategies. The distribution pattern of *C. sieboldii* was unimodal (Fig. 3), which had the largest population size in the sampling plots. Moreover, *C. sieboldii* had a large seedling and sapling population, and can regenerate from stump sprouts. Multiple stems from a stump resulting from past harvesting or thinning are often observed. Those characteristics of *C. sieboldii* may have enabled it to maintain its dominance in this forest through the process of gap regeneration. *S. wallichii* had a small population size with few saplings and seedlings in the stands (Fig. 3 and Table 3). The distribution pattern of *S. wallichii* was a sporadic type, which was rather different from that of *C. sieboldii* (Kolmogorov-Smirnov test, $p < 0.005$). Hara *et al.* (1996a and 1996b) also observed that the size distribution for *S. wallichii* lacked small individuals and its juveniles appeared only in the canopy gaps. This distribution pattern indicates that *S. wallichii* is a light-demanding species (Ohsawa and Ohtsuka, 1989), and cannot maintain itself under a closed canopy. However, the distribution of *D. racemosum* presented a clear reverse-J type, and it had many saplings and seedlings in the stands. Under closed canopy, *D. racemosum* can grow well (Hirata *et al.*, 1995). This species, regarded as shade-tolerant, can regenerate under a densely closed canopy (Sato *et al.*, 1994; Takyu and Ohsawa, 1997). The age structures indicated that the recruitments of *C. sieboldii* and *D. racemosum* were almost continual and had a large proportion of young individuals less than 10 years old; while that of *S. wallichii* was intermittent with few young individuals (Hirata, 1994). These results suggest that in the population dynamics of the succession process, *C. sieboldii* and *D. racemosum* are a self-maintaining type, and *S. wallichii* is a gap- or opening-dependent type.

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