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Comparative Studies on Community Ecology of Two Types of Subtropical Forests Grown in Silicate and Limestone Habitats in the Northern Part of Okinawa Island, Japan

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ABSTRACT: In order to compare woody species diversity, spatial distribution of trees and stand structure on the basis of the architectural stratification between two types of subtropical forests in the northern part of Okinawa Island, Japan, tree censuses in a 750 m^2 plot in silicate habitat and a 1000 m^2 plot in limestone habitat were performed. It was found that both subtropical forests growing in silicate and limestone habitats consisted of four architectural layers. A total of 26 families, 43 genera, 60 species and 4684 individuals larger than 0.1 m high in the silicate habitat, and 31 families, 51 genera, 62 species and 4798 individuals larger than 0.0 m high in the limestone habitat, were recorded. As a result, the floristic composition in the silicate habitat was quite different from that in the limestone habitat in terms of similarity index (C_{Π} = 0.07); approximately only one-sixth of the species were in common. The floristic composition among layers was more similar in the silicate habitat than in the limestone habitat. *Castanopsis sieboldii* (Mak.) Hatusima was the most dominant species in the silicate habitat, but was completely absent in the limestone habitat where *Cinnamomum japonicum* Sieb. ex Nees was the most dominant species. The potential number of species in the silicate forest (62) was lower than that in the limestone forest (71). However, the woody species diversity was higher in the silicate forest than in the limestone forest. The values of H' and J' tended to increase from the top layer downward except for the bottom layer in the silicate forest, while this increasing trend was reversed in the limestone forest. It follows that high woody species diversity in the silicate forest depended on small-sized trees, whereas in the limestone forest it depended on big-sized trees. The spatial distribution of trees in the forests was random in each layer, except the top layer, where there existed a double-clump structure. High degree of overlapping in the spatial distribution of trees among layers suggested that light can not penetrate easily to the lower layers, so that understory trees might be shade-tolerant species. Mean tree weight decreased from the top toward the bottom layer, whereas tree density increased from the top downward. It was concluded that this trend was general in both of the forests, and this trend successfully expressed in the same form as in the mean weight-density trajectory of self-thinning plant populations.

KEY WORDS: **Architectural stratification, floristic similarity, limestone habitat, mean tree weight-density relationship, Okinawa Island, silicate habitat, spatial distribution of trees, Subtropical forest, woody species diversity.**

INTRODUCTION

The coastal areas of the Western Pacific from subarctic eastern Siberia to equatorial SE Asia have forest climates with sufficient rainfall, which develops a sequence of five forest formations: subarctic evergreen conifer forests, cool-temperate deciduous broadleaf forests, warm-temperate lucidophyll forests, subtropical forests and tropical rain forests (Kira, 1991). Within the Western Pacific sequence of thermal vegetation zones, the subtropical zone whose major part is covered by dry area, only a small part is sufficiently moist to allow the development of subtropical forests, including a chain of islands from Okinawa to Taiwan and South China. Therefore, the subtropical forest in Okinawa Islands is precious from a phytogeographical viewpoint.

In the northern part of Okinawa Island, the subtropical area mainly consists of silicate rock, where a well-developed evergreen broadleaf forest dominated by *Castanopsis sieboldii* (Mak.) Hatusima exists. However, a small part, i.e. approximately 2.5% (Hayashi and Kizaki, 1985) of the total area of

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the northern part of Okinawa Island, consists of limestone, where a different type of forest is developed without *C. sieboldii* (Miyawaki, 1989). The subtropical evergreen broadleaf forest in Okinawa Island is characterized by higher woody species diversity than forests in mainland Japan (Itô 1997). Xu et al. (2001) found out that the understory shows high woody species diversity. Furthermore, Enoki (2003), Enoki and Abe (2004) and Kubota et al. (2004) pointed out that habitat heterogeneity provided by the topography appears to be important factors for maintaining the high woody species diversity.

The diversity of tree species is fundamental to total forest biodiversity, because trees provide resources and habitats for almost all other forest species (Hall and Swaine, 1976; Huston, 1994; Whitmore, 1998; Huang et al., 2003). Measures of species diversity play a central role in ecology and conservation biology. The most commonly employed measures of species diversity are the Shannon function, species richness (number of species), and evenness (the distribution of abundance among the species, sometimes known as equitability). In addition, the spatial distribution of trees has been a major source of interest for plant ecologists because of its potential role in explaining the coexistence of tree species in species-rich forests (Bunyavejchewin et al., 2003). Analyzing the spatial distribution patterns of trees may help to determine the mechanisms important in structuring forest communities because such patterns can reflect underlying processes, such as establishment, growth, competition, reproduction, senescene and mortality, which are affected by environmental factors (Sterner et al., 1986; Dale, 1999).

The degree of canopy multi-layering and the woody species diversity increase along a latitudinal thermal gradient from higher latitudes to the tropics (Hozumi, 1975; Yamakura, 1987; Kira, 1991; Ohsawa, 1995; Kimmins, 2004). The canopy multi-layering structure, i.e. architectural stratification, is an important factor in maintaining higher woody species diversity (Roberts and Gilliam, 1995; Lindgren and Sullivan, 2001). However, there is a dearth of studies reporting the effect of the architectural stratification on the woody species diversity of two types of subtropical forests in the northern part of Okinawa Island. Therefore, the objective of this paper is to quantify woody species diversity, stand structure and spatial distributions of trees on the basis of the architectural stratification, and then compare the above parameters between the forests in the limestone and silicate habitats in the northern part of Okinawa Island.

MATERIALS AND METHODS

Study sites and sampling

Two study sites were selected in the northern part of Okinawa Island. One is located at Mt. Yonaha, Kunigami village (26º45´N and 128º10´E), and its bedrock is mainly composed of silicate, having soil pH of 4.35 (Alhamd et al., 2004; Alhamd and Hagihara, 2004; Feroz et al., 2006a). The other is located at Mt. Nekumachiji, Higashi village (26º41′N and 128º8′E), and its bedrock is mainly composed of limestone, having soil pH of 8.10 (Feroz et al., 2006b).

For the former site, a sampling plot of area 750 m^2 (25 m × 30 m) was established and divided into 120 quadrats (2.5 m × 2.5 m). The slope, altitude and direction of the plot were 24.5º, 250 m above sea level and NWW, respectively. For the latter site, a sampling plot of area 1000 m^2 (40 m x 25 m) was established and divided into 160 quadrats (2.5 m x 2.5 m). The altitude of the plot, which faced to the north with a slope of 25.4º, was 235 m above sea level. Woody plants over 0.10 m in height for the former site and all woody plants for the latter site were numbered. They were identified to species according to the nomenclature by Walker (1976). Censuses were carried out in 2001-2002 in the limestone habitat and 2003-2004 in the silicate habitat. Tree height H (m), stem diameter at breast height DBH (cm) and stem diameter at a height of $H/10$ $D_{0.1H}$ (cm) were measured.

Climate

Figure 1 is the Walter-type climatic diagram, which represents seasonal changes in mean monthly temperature and rainfall (1995~2004, Meteorological Station in Nago City, 26º36′ N and 127º58′ E) in the northern part of Okinawa Island. The mean monthly minimum temperature and the mean monthly maximum temperature are respectively 16.4 ± 0.3 (SE) ºC in January and 28.8 ± 0.2 (SE) ºC in July. The mean annual temperature is 22.8 ± 0.3 (SE) ºC. The warmth index is 213.5 ± 1.3 (SE) ºC month, which is within the range of 180 to 240 ºC month of the subtropical region defined by Kira (1977). The mean monthly rainfall is over 100 mm throughout the year except for 94 ± 17 (SE) mm in January. The mean annual rainfall is 2401 ± 136 (SE) mm yr^{-1}. Typhoons frequently occur between July and October, bringing high rainfall and strong winds.

DATA ANALYSIS

Architectural stratification

The Mean tree weight-Weight of individual trees

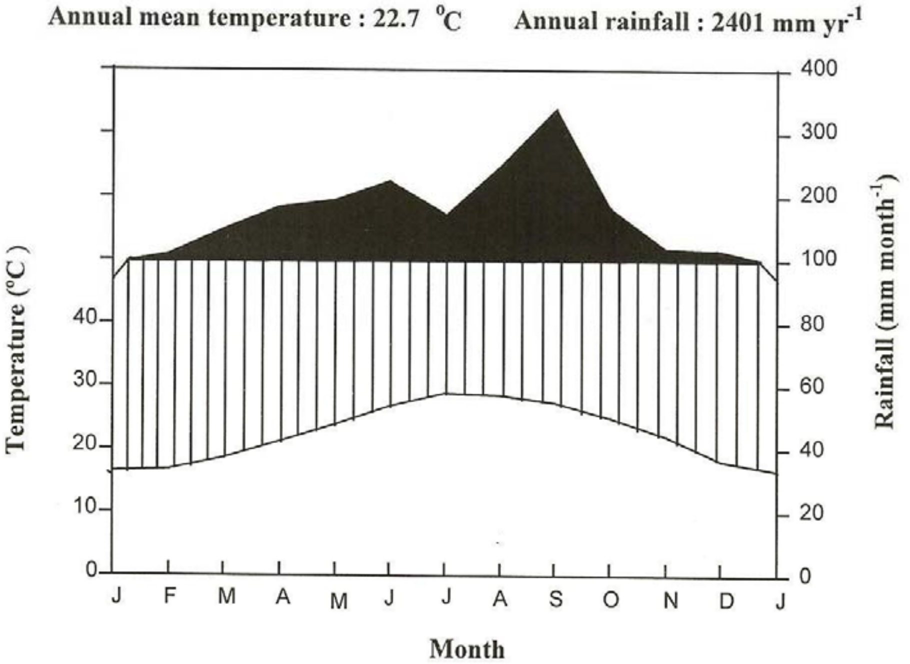

Fig. 1. Walter-type climatic diagram (average during 10 years: 1995-2004) based on the data obtained from the meteorological station, Nago City, Okinawa.

(M–w) diagram proposed by Hozumi (1975) was used to identify the multi-layering structure of the forest stands. Tree weight w (cm^2 m) was assumed to be proportional to $D_{0.1H}{}^2\, H$ and it was arranged in descending order. Average tree weight M_n from the maximum tree weight w_1 to the nth tree weight was calculated using the form of $M_n = \sum_{i=1}^{n} w_i \big/ n$ (n = 1,…., total number of trees N). If the M–w diagram is constructed by plotting the values of M against the corresponding values of w on logarithmic coordinates, then some segments on the M–w diagram are formed. Each segment is related to the layer with the specific characteristics of the beta–type distribution designated by Hozumi (1971, 1975). Hozumi (1975) pointed out that the segments on the M–w diagram can be written by either of the following equations:

$$M = A\,w + B \tag{1}$$

$$M = C\,w^b \tag{2}$$

where A, B, C and b are coefficients. These functions reflect some aspect of the manners of packing trees into the three-dimensional space as realized by a forest stand.

Species dominance

Dominance of a species was defined by the importance value IV (%) of the species:

$$IV = \left(\frac{n_i}{\sum_{i=1}^{Q} n_i} \times 100 + \frac{a_i}{\sum_{i=1}^{Q} a_i} \times 100 + \frac{f_i}{\sum_{i=1}^{Q} f_i} \times 100 \right) \Bigg/ 3 \tag{3}$$

where n_i is the number of individuals of the ith species, a_i is the basal area at a height of H/10 of the ith species, f_i is the number of quadrats in which the ith species appeared and Q is the total number of quadrats.

Species-area relationship

The expected number of species S_q appeared within the number of quadrats q selected at random from the total number of quadrats Q was calculated from the equation proposed by Shinozaki (1963) (cf. Hurlbert, 1971):

$$S_q = \sum_{i=1}^{s} \left[1 - \binom{Q - q_i}{q} \Big/ \binom{Q}{q} \right] \tag{4}$$

where q_i is the number of quadrats in which the ith species occurred and S is the total number of species. The S_q -values were obtained for q-values of 1, 2, 4, 8, 16, 32, 64 and 120 for the forest in silicate habitat, and 1, 2, 4, 8, 16, 32, 64, 128 and 160 for the forest in limestone habitat.

Floristic similarity

The similarity of floristic composition between layers was calculated using the following index C_Π (Horn, 1966; Kimoto, 1967; cf. Morishita, 1959):

$$C_\Pi = \frac{2\sum_{i=1}^{s} n_{\mathrm{A}i} n_{\mathrm{B}i}}{(\Pi_\mathrm{A} + \Pi_\mathrm{B}) N_\mathrm{A} N_\mathrm{B}} \tag{5}$$

$$(\Pi_\mathrm{A} = \sum_{i=1}^{s} n_{\mathrm{A}i}{}^2 \Big/ N_\mathrm{A}{}^2,\ \Pi_\mathrm{B} = \sum_{i=1}^{s} n_{\mathrm{B}i}{}^2 \Big/ N_\mathrm{B}{}^2)$$

where S is the total number of species, $n_{\mathrm{A}i}$ and $n_{\mathrm{B}i}$ are the number of individuals of the ith species respectively belonging to Layer A and Layer B. The value of C_Π is 1.0 when the number of individuals belonging to a species is the same between the two layers for all species, i.e. floristic composition is completely the same between the layers, and is 0.0 when no common species is found between them.

Equation (5) was also applied for measuring the degree of similarity in floristic composition between the silicate and limestone forests. In this case, S is the total number of species in the two forests, $n_{\mathrm{A}i}$ and $n_{\mathrm{B}i}$ are the number of individuals of the ith species respectively belonging to the silicate and limestone forests.

Species diversity

The following two indices of Shannon's index (MacArthur and MacArthur, 1961) H' and Pielou's (1969) index J' were used to measure woody species diversity or equitability (evenness):

$$H' = \sum_{i=1}^{s} \frac{n_i}{N} \log_2 \frac{N}{n_i} \tag{6}$$

$$J' = \frac{H'}{H'_{\max}} \quad (H'_{\max} = \log_2 S) \tag{7}$$

where N is the total number of individuals.

Spatial distributions of trees

The unit-size $\overset{*}{m}_u - m_u$ method and the ρ–index with successive changes of quadrat sizes (Iwao, 1972) were used to analyze the spatial distribution of trees. Mean density m_u is defined as:

$$m_u = \frac{\sum_{j=1}^{q_u} n_j}{q_u} \tag{8}$$

where n_j is the number of individuals in the jth quadrat and q_u is the total number of quadrats when the quadrat size is u. The q_u-values were 120, 60, 30, 15, 7, 4 and 2 respectively for the u-values of 1 (2.5 m × 2.5 m), 2, 4, 8, 16, 30 and 60 for the silicate forest, and 160, 80, 40, 20, 10, 5 and 2 respectively for the u-values of 1, 2, 4, 8, 16, 32 and 64 for the limestone forests. Mean crowding $\overset{*}{m}_u$ is defined by Lloyd (1967) as:

$$\overset{*}{m}_u = \frac{\sum_{j=1}^{q_u} n_j (n_j - 1)}{\sum_{j=1}^{q_u} n_j} \tag{9}$$

If the basic component of the spatial distribution is a single individual tree, individual trees are considered to be randomly distributed when $\overset{*}{m}_u = m_u$, aggregated when $\overset{*}{m}_u > m_u$ and uniformly distributed when $\overset{*}{m}_u < m_u$ for any quadrat size. In order to provide knowledge on the distribution pattern of clumps, Iwao (1972) proposed the ρ–index.

$$\rho_u = \frac{\overset{*}{m}_u - \overset{*}{m}_{u-1}}{m_u - m_{u-1}} \tag{10}$$

where for the smallest quadrat size (u = 1), $\rho_1 = \overset{*}{m}_1 / m_1$. When the values of ρ_u are plotted against the quadrat sizes, a peak of the curve may suggests the clump area.

Overlapping in spatial distributions of trees between layers

The ω-index, which is proposed by Iwao (1977) for analyzing spatial association between species, was applied to measure the degree of overlapping in spatial distributions of trees among layers with successive changes of quadrat size u.

$$\left.\begin{aligned} \omega_{(+)} &= \frac{\gamma - \gamma_{(\mathrm{ind})}}{1 - \gamma_{(\mathrm{ind})}} \quad (\gamma \ge \gamma_{(\mathrm{ind})}) \\ \omega_{(-)} &= \frac{\gamma - \gamma_{(\mathrm{ind})}}{\gamma_{(\mathrm{ind})}} \quad (\gamma \le \gamma_{(\mathrm{ind})}) \end{aligned}\right\} \tag{11}$$

where γ and $\gamma_{(\mathrm{ind})}$ are respectively given in the forms:

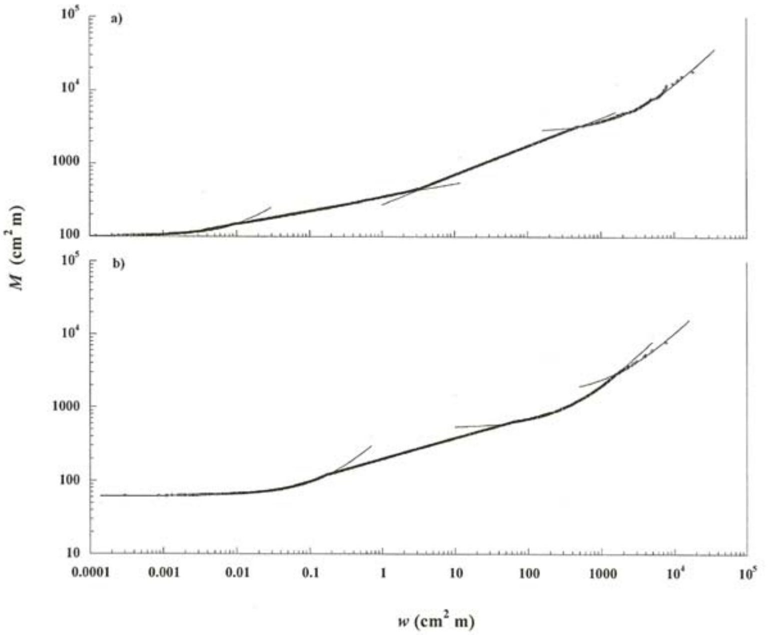

Fig. 2. Relationships of mean tree weight M to tree weight w on logarithmic coordinates. In the silicate forest (a), the regression curves for the top and bottom layers are given by Eq. (1), where $A = 0.940$ and $B = 2743$ cm^2 m ($R^2 = 0.99$) for the top layer and $A = 4931$ and $B = 101$ cm^2 m ($R^2 = 0.97$) for the bottom layer. The regression curves for the second and third layers are given by Eq. (2), where $C = 272$ cm^{2-b} m^{1-b} and $b = 0.397$ ($R^2 = 0.91$) for the second layer and $C = 349$ cm^{2-b} m^{1-b} and $b = 0.184$ ($R^2 = 0.94$) for the third layer. In the limestone forest (b), the regression curves for the top, second and bottom layers are given by Eq. (1), where $A = 0.903$ and $B = 1492$ cm^2 m ($R^2 = 0.99$) for the top layer; $A = 1.49$ and $B = 524$ cm^2 m ($R^2 = 0.98$) for the second layer; $A = 332$ and $B = 61.5$ cm^2 m ($R^2 = 0.97$) for the bottom layer. The regression curve for the third layer is given by Eq. (2), where $C = 192$ cm^{2-b} m^{1-b} and $b = 0.284$ ($R^2 = 0.92$).

$$\gamma = \frac{\sum_{j=1}^{Q_u} n_{\mathrm{A}j} n_{\mathrm{B}j}}{\sqrt{\sum_{j=1}^{Q_u} {n_{\mathrm{A}j}}^2 \sum_{j=1}^{Q_u} {n_{\mathrm{B}j}}^2}}$$

$$\gamma_{(\mathrm{ind})} = \frac{1}{Q_u} \frac{\sum_{j=1}^{Q_u} n_{\mathrm{A}j} \sum_{j=1}^{Q_u} n_{\mathrm{B}j}}{\sqrt{\sum_{j=1}^{Q_u} {n_{\mathrm{A}j}}^2 \sum_{j=1}^{Q_u} {n_{\mathrm{B}j}}^2}}$$

Here, Q_u is the total number of quadrats taken as 120, 60, 30, 15 and 7 respectively for the u-values of 1 (2.5 m × 2.5 m), 2, 4, 8 and 16 for the silicate forest, and 160, 80, 40, 20 and 10 respectively for the u-values of 1, 2, 4, 8 and 16 for the limestone forest, $n_{\mathrm{A}j}$ and $n_{\mathrm{B}j}$ are the number of individuals of the jth quadrat respectively belonging to Layer A and Layer B.

The γ means the square root of coefficient of determination between $n_{\mathrm{A}j}$ and $n_{\mathrm{B}j}$ for measuring their closeness to a straight line passing through origin. The $\gamma_{(\mathrm{ind})}$ is the γ-value in the case of independent distributions of $n_{\mathrm{A}j}$ and $n_{\mathrm{B}j}$. The value of ω changes from the maximum of +1.0 for complete overlapping, through 0.0 for independent occurrence, to the minimum of –1.0 for complete exclusion.

Dendrogram

The dendrograms for analyzing the degrees of floristic similarity among layers were constructed following Mountford's (1962) method, or unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1973).

Regression analysis

The coefficients for nonlinear equations were determined with statistical analysis software (KaleidaGraph V. 4.0, Synergy Software, USA). On the other hand, the coefficients for linear and curvilinear equations were determined by the ordinary least-squares method.

RESULTS

Architectural stratification

The M–w diagrams are illustrated in Fig. 2. The forests in silicate and limestone habitats both consisted of four architectural layers, which were confirmed using the first and the second derivatives on the M–w diagram (Feroz et al., 2006a, b). Tree

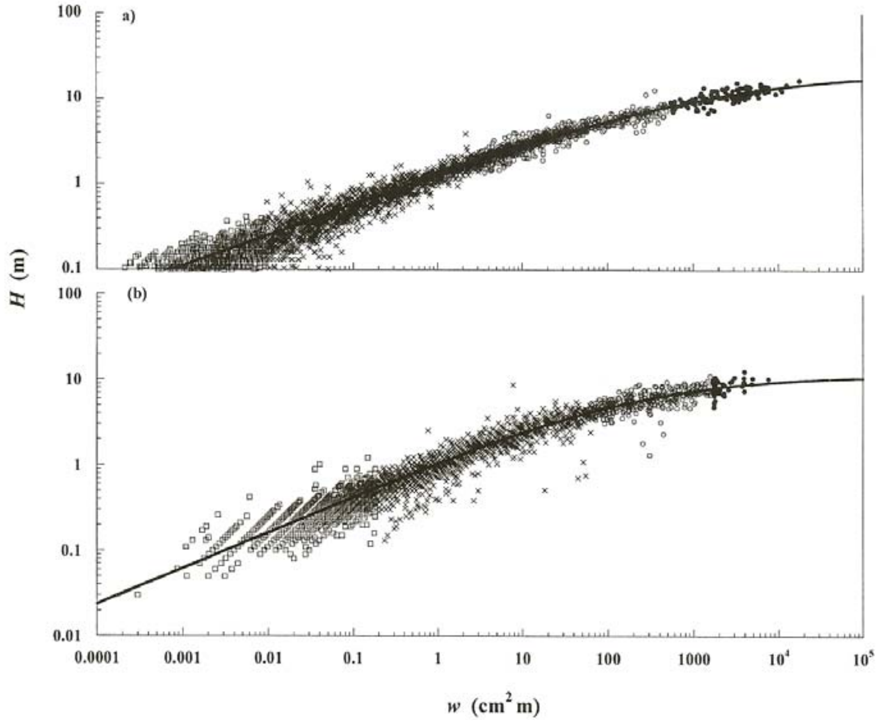

Fig. 3. Relationships between tree height H and weight w. In the silicate forest (a), the regression curve is given by Eq. (12) ($R^2 = 0.97$). ●, top layer (8.0 m $< H \leq$ 16.5 m); ○, second layer (1.9 m $< H \leq$ 8.0 m); ×, third layer (0.25 m $< H \leq$ 1.9 m); □, bottom layer (0.10 m $\leq H \leq$ 0.25 m). In the limestone forest (b), the regression curve is given by Eq. (13) ($R^2 = 0.95$). Symbols are the same as in (a). Top layer (7.8 m $< H \leq$ 12.3 m); second layer (4.1 m $< H \leq$ 7.8 m); third layer (0.53 m $< H \leq$ 4.1 m); bottom layer (0.0 m $< H \leq$ 0.53 m).

weights at boundaries between layers were estimated as 508, 3.18 and 0.00953 cm^2 m in the silicate forest and 1640, 63.9 and 0.188 cm^2 m in the limestone forest.

Figure 3 shows the relationships between tree height H and weight w respectively for the silicate and limestone forests, which were respectively formulated (cf. Kira and Ogawa, 1971) as follows:

$$\frac{1}{H} = \frac{1}{1.37w^{0.361}} + \frac{1}{21.0} \tag{12}$$

$$\frac{1}{H} = \frac{1}{1.13w^{0.415}} + \frac{1}{11.5} \tag{13}$$

The heights of the boundaries were determined as 8.0, 1.9 and 0.25 m in the silicate forest and 7.8, 4.1 and 0.53 m in the limestone forest by substituting the tree weights at boundaries obtained above for w respectively in Eqs. (12) and (13). Therefore, in the silicate forest, the height range was 8.0 m $< H \leq$ 16.5 m for the top layer, 1.9 m $< H \leq$ 8.0 m for the second layer, 0.25 m $< H \leq$ 1.9 m for the third layer and 0.10 m $\leq H \leq$ 0.25 m for the bottom layer, and in the limestone forest, 7.8 m $< H \leq$ 12.3 m for the top layer, 4.1 m $< H \leq$ 7.8 m for the second layer, 0.53 m $< H \leq$ 4.1 m for the third layer and 0.0 m $< H \leq$ 0.53 m for the bottom layer.

Species dominance

Table 1 lists importance values IV of five woody species for each layer in each of the forests in order of species rank, which was determined from IV in the total stand. In the silicate forest, a total of 26 families, 43 genera, 60 species and 4684 woody individuals were recorded. The most species-rich family was Rubiaceae, which contained 12 species. *Symplocos*, *Lasianthus* and *Ilex* were the species-rich genera, each of which contained five species. Out of the 60 species, only three species (5%) consisted of a single individual. *Castanopsis sieboldii* (Mak.) Hatusima appeared in all layers with the highest importance value, especially with a tremendously high value of 44% in the top layer. The population size of this species was the largest with a large number of trees, saplings and seedlings (17% of the total number of individuals). These phenomena indicate that *C. sieboldii* is the most dominant and climax species in the forest. *Schima wallichii* (DC.) Korth. was the second dominant species in terms of IV of 9.30% in the total stand. A quite high IV of 22.8% of *S. wallichi* in the top layer compared with the very low IV (ranging from 0.62 to 1.69%) in the lower three layers indicates the heliophilic nature of the species.

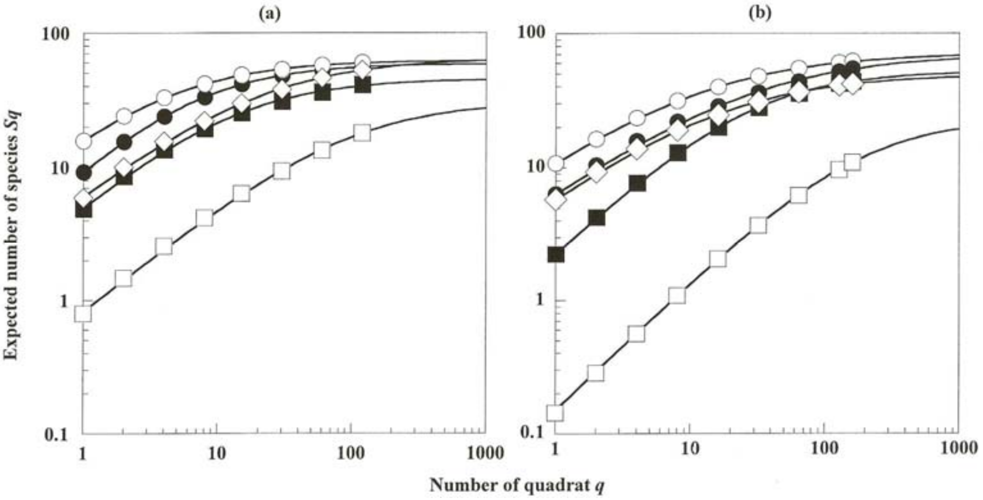

Fig. 4. Species–area curves (area of one quadrat: 2.5 m x 2.5 m). ○, total stand; □, top layer; ■, second layer; ●, third layer; ◇, bottom layer. In the silicate forest (a), the curves are given by Eq. (14), where $c = 21.0$, $d = 0.856$ and $S_{max} = 62.4$ ($R^2 \cong 1.0$) for the total stand; $c = 0.822$, $d = 0.828$ and $S_{max} = 32.8$ ($R^2 \cong 1.0$) for the top layer; $c = 5.57$, $d = 0.850$ and $S_{max} = 47.0$ ($R^2 \cong 1.0$) for the second layer; $c = 10.9$, $d = 0.928$ and $S_{max} = 60.30$ ($R^2 \cong 1.0$) for the third layer; $c = 6.58$, $d = 0.805$ and $S_{max} = 61.1$ ($R^2 \cong 1.0$) for the bottom layer. In the limestone forest (b), the curves are given by the same equation, where $c = 12.6$, $d = 0.709$ and $S_{max} = 71.2$ ($R^2 \cong 1.0$) for the total stand; $c = 0.14$, $d = 0.998$ and $S_{max} = 26.3$ ($R^2 \cong 1.0$) for the top layer; $c = 2.35$, $d = 0.939$ and $S_{max} = 52.9$ ($R^2 \cong 1.0$) for the second layer; $c = 6.96$, $d = 0.696$ and $S_{max} = 66.4$ ($R^2 \cong 1.0$) for the third layer; $c = 6.52$, $d = 0.734$ and $S_{max} = 50.3$ ($R^2 \cong 1.0$) for the bottom layer.

However, in the limestone forest, a total of 31 families, 51 genera, 62 species and 4798 woody individuals were recorded. The most species-rich families were Moraceae and Lauraceae, which contained seven and six species, respectively. *Ficus* is the most species-rich genus, which contained six species. Out of the 62 species, only seven species (11%) consisted of a single individual. *Cinnamomum japonicum* Sieb. ex Nees was the most dominant species in terms of the highest *IV* in the total stand and in all layers, especially in the lower three layers. Although *Rhus succedanea* L. was the second dominant species with the *IV* of 7.63%, it was not found in the lower two layers.

Species–area relationship

As shown in Fig. 4, the expected number of species increased, and then tended to be saturated with increasing number of quadrats for the silicate forest, whereas it slightly increased with increasing number of quadrats for the limestone forest. The relationships of the expected number of species S_q to the number of quadrats q in each layer and the total stand were well approximated by the following equation (Ogawa, 1980; cf. Hagihara, 1995):

$$\frac{1}{S_q} = \frac{1}{cq^d} + \frac{1}{S_{\max}} \tag{14}$$

where c and d are coefficients, and $S_{\max}$ is the expected maximum number of species.

In the silicate forest, the expected maximum number of species was estimated to be 62 in the total stand. The $S_{\max}$ increased from 26 in the top layer, through 46 in the second layer and 61 in the third layer, to 65 in the bottom layer. Therefore, the bottom layer showed the highest potential number of species. This result was different from the limestone forest, where the expected maximum number of species was estimated to be 71 in the total stand. The third layer showed the highest potential number of species as the $S_{\max}$ increased from 26 in the top layer, through 53 in the second layer, to 66 in the third layer, but decreased to 50 in the bottom layer.

Floristic similarity

The floristic similarities among layers of each forest were classified using dendrograms of similarity index C_Π, as shown in Fig. 5. In the silicate forest, the strongest similarity in floristic composition was marked between the second and the third layers with a C_Π-value of 0.80. The next was between the second, third and the bottom layers with a C_Π-value of 0.64. The lowest C_Π-value of 0.48 was between the top and the lower three layers. On the other hand, in the limestone forest, the third and the bottom layers showed the highest similarity in floristic composition with a C_Π-value of 0.82. The next highest similarity was between the third, bottom and the second layers

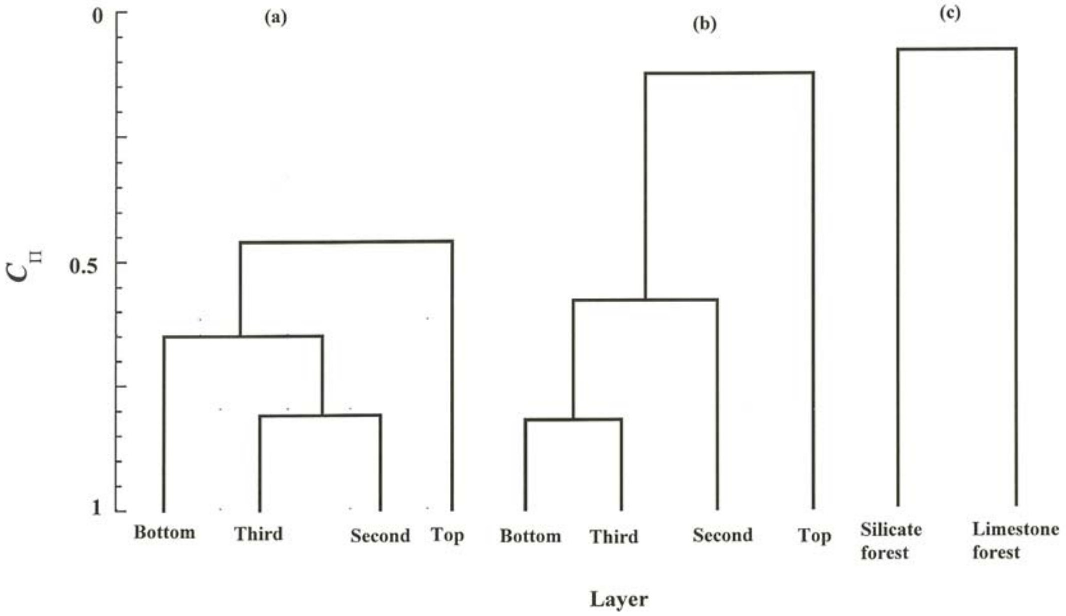

Fig. 5. Dendrograms of the degree of similarity C_Π in floristic composition among layers in the silicate forest (a), in the limestone forest (b) and between the silicate and limestone forests (c).

with a C_Π-value of 0.59. The lowest C_Π-value of 0.14 was between the top and the lower three layers. Between the silicate and limestone forests, the value of similarity index in floristic composition was very low with a C_Π-value of 0.07. This result indicates that these two forests are quite different from each other in floristic composition.

Woody species diversity in the stratified forest stands

In the silicate forest, the values of H' and J' tended to increase from the top layer downward, except for the bottom layer, whereas in the limestone forest, they tended to increase from the bottom layer upward, except for the H'-value of the top layer (Table 2). When species diversity compared among layers, the highest value of H' (4.73 bit) was in the third layer for the silicate forest. This is because the highest species richness (56 species) and the second highest evenness (0.80) in the third layer resulted in the highest H'-value. However, for the limestone forest, the highest value of H' (4.41 bit) was in the second layer, though species richness (44 species) and evenness (0.81) were the second highest. On the other hand, the lowest value of H' was in the top layer for both of the forests. This is ascribed to quite low species richness (18 species for the silicate forest; 11 species for the limestone forest) as compared with those in other layers. In addition, for the silicate forest, the values of H' in the second layer and in the bottom layer were nearly the same, while the value of J' was higher in the second layer than in the bottom layer. This is because an increase of species richness from the second layer (41 species) to the bottom layer (53 species) could compensate for a decrease of evenness J' from the second layer to the bottom layer. For the limestone forest, an increase of H'-value from the bottom layer to the third layer corresponds to increases of species richness and evenness in the same direction.

Spatial distributions of trees

The spatial distribution patterns of trees for each layer are shown in Fig. 6 based on the unit-size $\overset{*}{m}_u - m_u$ relation and the ρ-index against quadrat size u. For both of the forests, the spatial distribution of the basic component for all layers except the top layer was a single individual and its distribution was random, because the $\overset{*}{m}_u - m_u$ relation lines did not differ from the Poisson line at a significant level of 0.01. In the top layer, however, the spatial distribution of trees showed a special trend. The ρ-index showed three peaks in the silicate and limestone forests respectively at quadrat size 1, 4 and 30, and 1, 8 and 32. The first peak at quadrat size 1 may be occasional appearance due to the underdispersion of individual trees, and the second

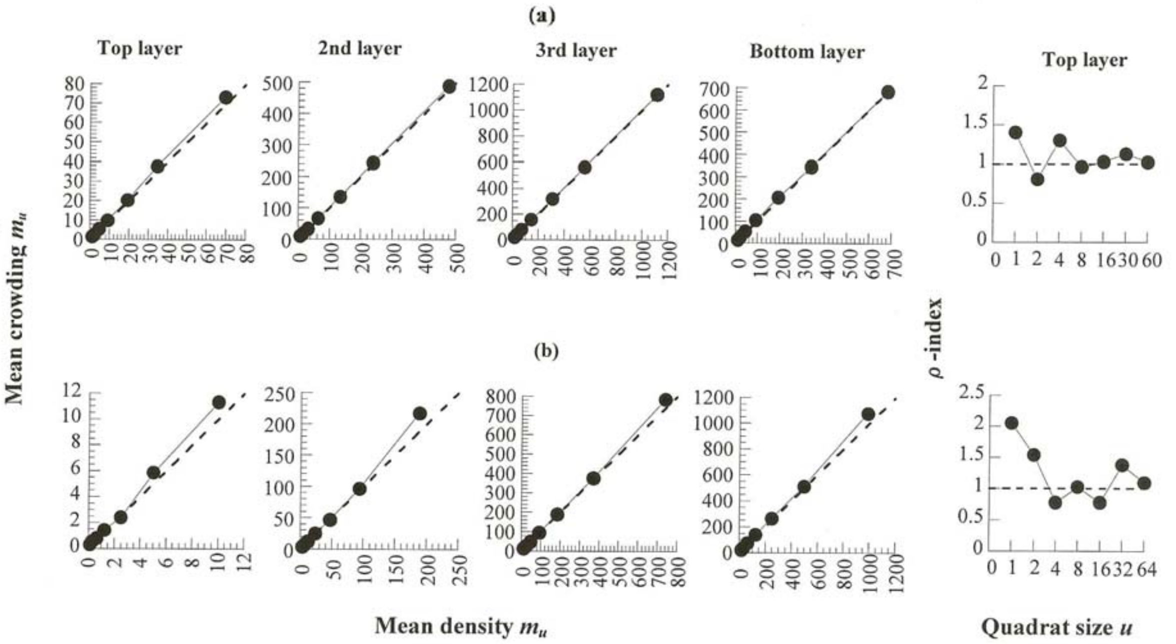

Fig. 6. A schematic representation showing the relationships between mean crowding $\overset{*}{m}_u$ and mean density m_u , and ρ -index with successive changes of quadrat size u in the silicate forest (a) and in the limestone forest (b).

and third peaks may perhaps be related to topography or large scale disturbance, especially large stones, may create large gaps in the limestone forest. As a result, the top layer probably consists of a double clump, the small and large clumps of which were respectively 25 m^2 and 187.5 m^2 in the silicate forest and 50 m^2 and 200 m^2 in the limestone forest. Mean area occupied by individuals of the top layer trees was 9.1 ± 0.60 (SE) m^2 in the silicate forest and 15 ± 0.02 (SE) m^2 in the limestone forest. As a result, the small clump may include three individuals and the large clump may include around eight small clumps in the silicate forest, whereas in the limestone forest, the small clump may include three individuals and the large clump may include around four small clumps.

Overlapping in spatial distributions of trees among layers

The degree of overlapping ω with successive changes of quadrat sizes in spatial distributions of trees among layers combined from the top layer downward is shown in Fig. 7. In the silicate forest, the spatial distributions of trees were overlapped between the top and the second layers, between the top and second layers and the third layer, and also between the top, second and third layers and the bottom layer. Similarly, in the limestone forest, the spatial distributions of trees were overlapped between the top and second layers and the third layer, and between the top, second and third layers and the bottom layer. Only a different degree of overlapping occurred between the top and the second layers, where the spatial distributions of trees tended to be exclusive. These results may indicate that trees appeared in the upper two layers in the limestone forest can catch sufficient light, while light can not penetrate easily to the lower three layers in the silicate forest and lower two layers in the limestone forest.

Mean tree weight and density among layers

As shown in Fig. 8, mean tree weight $\overline{w_i}$ of the ith layer decreased from the top (i = 1) toward the bottom layer (i = 4), whereas the opposite trend was observed for the tree density ρ_i of the ith layer. This trend was well expressed for both of the forest in silicate and limestone habitats in the form:

$$\overline{w_i} = K\rho_i^{-\alpha}\left(1-\frac{\rho_i}{\rho_o}\right) \tag{15}$$

where the values of coefficients K , α , and ρ_o were estimated as 2.23 x 10^8 cm^2 m ha$^{-\alpha}$, 1.49 and 24575 ha^{-1}, respectively for the silicate forest, and 92734 cm^2 m ha$^{-\alpha}$, 0.613 and 21827 ha^{-1}, respectively for the limestone forest.

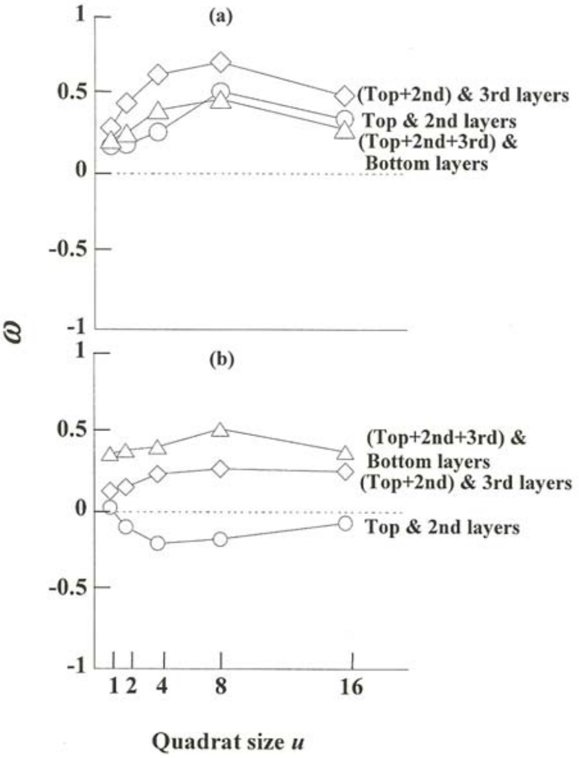

Fig. 7. Degree of overlapping ω with successive changes of quadrat size u in spatial distributions of trees in the silicate forest (a) and in the limestone forest (b). The smallest quadrat size (u = 1) is 2.5 m × 2.5 m.

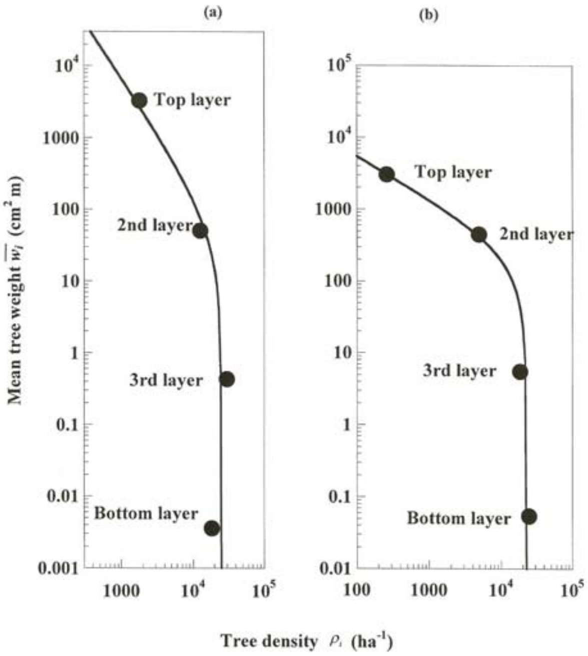

Fig. 8. Relationships between mean tree weight $\overline{w_i}$ and tree density ρ_i among the layers. The curves are given by Eq. (15) in the silicate forest ($R^2 = 0.98$) (a) and in the limestone forest ($R^2 \cong 1.0$) (b).

DISCUSSION

All species in the silicate forest are evergreen broadleaf, whereas 84% of the total species in the limestone forest are evergreen broadleaf and the rest (16% of the total species) are deciduous. The number of species between these two forests is almost the same, but the potential number of species in the silicate forest (62) was lower than that in the limestone forest (72). The facultative shade species (light-tolerant under high light conditions and shade-tolerant under low light conditions) can grow from the bottom to the top layer. In the silicate forest, *Castanopsis sieboldii* (Mak.) Hatusima was typically a facultative shade species as well as a climax species as it appeared in all layers with the highest importance value (Table 1). *Schima wallichii* (DC.) Korth. was typically a pioneer species as it appeared in the top layer with a tremendously high importance value, while it had a very low importance value in the lower three layers. The silicate forest is probably stable in species composition, because the expected number of species almost saturated with increasing area for total stand and each layer (Fig. 4a).

In the limestone forest, *Cinnamomum japonicum* Sieb. ex Nees was also typically a facultative shade species as it appeared in all layers with the highest or the third highest importance value. *Rhus succedanea* L. was typically a pioneer species as it appeared only in the upper two layers with the highest or second highest importance value (Table 1). In addition, some species with only few individuals in one specific layer (e.g. one species with one individual in the top layer, three species with one or two individuals in the second layer, five species with one individual in the third layer) may have possibilities to disappear. On the contrary, some species may newly invade the gaps created by stones. Such type of species composition, i.e. disappearance and appearance of species, can be persistent owing to continuous natural disturbance. Hence, the limestone forest seems to be most likely stable with the continuously changeable species composition.

The similarity in floristic composition between the top layer and the lower three layers in the silicate forest was weak, i.e. approximately one-third of the species from the lower three layers may be able to grow into the top layer. In the limestone forest, however, the floristic composition between the top layer and the lower three layers was almost exclusive, i.e. approximately one-sixth of the species from the lower three layers may be able to grow into the top layer. This is because the top layer consists of pioneer and facultative shade species, whereas the lower layers consist of shade and facultative shade species.

Table 1. Five dominant species in the silicate (750 m^2) (a) and the limestone (1000 m^2) forests (b) in order of species rank determined by importance value *IV* in the total stand.

(a)

Species rank	Name of species	*IV* (%)				
		Top layer	Second layer	Third layer	Bottom layer	Total stand
1	*Castanopsis sieboldii* (Mak.) Hatusima	43.60	12.63	26.12	21.74	21.30
2	*Schima wallichii* (DC.) Korth.	22.34	1.78	0.62	1.69	9.30
3	*Elaeocarpus japonicus* Sieb. et Zucc.	10.16	7.56	1.73	2.78	4.61
4	*Myrsine seguinii* Lév'l.	–	4.14	5.46	7.01	3.92
5	*Ardisia quinquegona* Bl.	–	4.97	6.88	3.72	3.74

(b)

Species rank	Name of species	Top layer	Second layer	Third layer	Bottom layer	Total stand
1	*Cinnamomum japonicum* Sieb.ex Nees	4.09	10.61	12.75	20.19	13.08
2	*Rhus succedanea* L.	30.60	10.29	–	–	7.63
3	*Turpinia ternata* Nakai	–	11.74	9.38	10.74	7.03
4	*Citrus depressa* Hayata	–	3.03	5.07	10.63	6.93
5	*Psychotria manillensis* Bartl.	–	–	5.12	4.18	4.40

Table 2. Diversity indices among layers in the silicate (a) and the limestone forests (b).

(a)

Layer	Height range (m)	No. of trees	No. of species	H' (bit)	J'
Top	$8.0 < H \leq 16.5$	139	18	2.75	0.66
Second	$1.9 < H \leq 8.0$	953	42	4.37	0.81
Third	$0.25 < H \leq 1.9$	2226	56	4.73	0.80
Bottom	$0.10 \leq H \leq 0.25$	1366	51	4.33	0.73

(b)

Layer	Height range (m)	No. of trees	No. of species	H' (bit)	J'
Top	$7.8 < H \leq 12.3$	25	11	3.05	0.88
Second	$4.1 < H \leq 7.8$	469	44	4.41	0.81
Third	$0.53 < H \leq 4.1$	1843	55	4.33	0.75
Bottom	$0.0 < H \leq 0.53$	2461	42	3.52	0.65

The floristic composition was more similar among layers in the silicate forest than in the limestone forest (Figs. 5a and b).

It has been reported that the flora in silicate soil differs from that in limestone (Schulze et al., 2005). Within Okinawa Island, a very low similarity in floristic composition was observed between the silicate forest and the limestone forest, which is concluded from the low value of similarity index (C_{Π} = 0.07) between these two habitats (Fig. 5c), though approximately one-sixth species were common. This is mainly due to the different characteristics of species habited in the different substrates with a variation of soil chemistry. For example, *Castanopsis sieboldii* was the most dominant species in silicate soil, but it was completely absent in limestone. The question as to which factors cause this absence of *C. sieboldii* in limestone habitat may be answered at the level of soil chemistry, i.e. alkalinity. Generally, differences in flora are related to differences in geology (Schulze et al., 2005). According to Gigon (1987), most silicate soil plants do not grow on limestone because of the soil chemistry.

It is known that the diversity of a community depends on two things: species richness and the evenness with which the individuals are apportioned among them (Pielou, 1975). As the lower layers contained many species relative to their smaller height ranges (Table 2), obviously these layers support high species richness of the forests. For example, 88% of the total species with 29% of the total individuals in the silicate forest and 66% of the total species with 51% of the total individuals in the limestone forest packed within such thin bottom layers of 15 cm and 53 cm deep, respectively.

In the silicate forest, the value of H' for small-sized trees having $H \geq 0.10$ m was quite high as compared to that of H' for large-sized trees having DBH ≥ 4.5 cm (Table 3). This is mainly caused by a large number of species for small-sized trees, though higher J' -value has a small influence on the high value of H'. This result and the trend of increasing diversity with successively decreasing height of layers from the top downward (Fig. 9) represent that small-sized trees in the lower layers have an important role in maintaining high woody species diversity in the silicate forest. Since small-sized trees provide a natural habitat for animals living on the forest floor, conservation of small-sized trees in the lower layers is indispensable to sound maintenance of Okinawan evergreen broadleaf forests in silicate habitat.

Table 3. Comparison in species diversity, tree density and basal area between the silicate and limestone forests.

Study site (Stand age)	Sample area (ha)	Tree size	Basal area ($m^2 ha^{-1}$)	No. of trees (stem ha^{-1})	S	H' (bit)	J'	Source
Silicate	0.075	$H \geq 0.10$ m	50.3	62452	60	4.83	0.82	Feroz et al. 2006a
		DBH ≥ 4.5 cm	43.2	3080	32	3.80	0.77	
	0.04	DBH ≥ 3.0 cm			26	3.68	0.74	Xu et al. 2001
(≥50 yr)	0.04	DBH ≥ 4.5 cm			29.4	4.26	0.83	Itô 1997
(40-49 yr)	0.04	DBH ≥ 4.5 cm			24.8	3.73	0.81	
(30-39 yr)	0.04	DBH ≥ 4.5 cm			25.6	3.35	0.72	
(20-29 yr)	0.04	DBH ≥ 4.5 cm			23.7	3.32	0.73	
Limestone	0.1	$H > 0.0$ m	38.0	47980	62	4.21	0.73	Feroz et al. 2006b
		DBH ≥ 4.5 cm	28.1	3350	40	4.35	0.82	

S, the number of species per sample area.

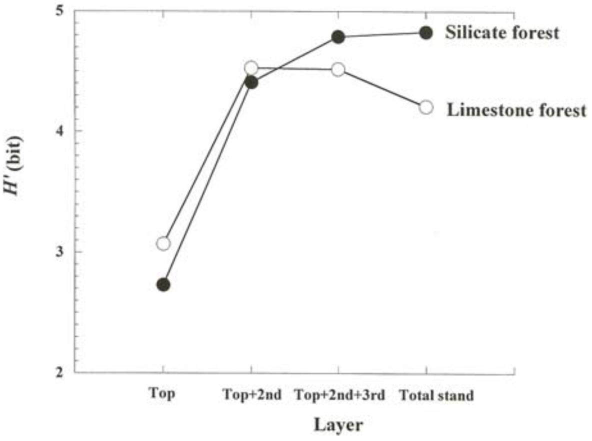

Fig. 9. Trends of H' along the layers combined from the top downward in the silicate forest (a) and in the limestone forest (b).

On the other hand, in the limestone forest, the value of H' for large-sized trees having DBH ≥ 4.5 cm was quite high as compared to that of H' for the total stand (Table 3). This is mainly caused by a high evenness for large-sized trees, though smaller number of species has an influence on the low value of H'. This result and the trend of increasing diversity up to the second layer and then decreasing downward (Fig. 9) may represent that the large-sized trees are important in maintaining high woody species diversity. Thus, it may be thought within the limits of this study that the decreasing trend of H' from the second layer downward is a characteristic of the subtropical forest in limestone habitat in the northern part of Okinawa Island.

Furthermore, the values of the diversity indices (H' and J') for the total stand in the silicate forest were higher than those in the limestone forest (Table 3). Therefore, it is most likely obvious in the northern part of Okinawa Island that the subtropical evergreen broadleaf forest in silicate habitat has higher woody species diversity than the forest in limestone habitat. However, woody species diversity for large-sized trees is lower in the silicate forest than in the limestone forest, because the values of H' and J' for trees having DBH ≥ 4.5 cm were lower in the silicate forest (Itô, 1997; Xu et al., 2001) than in the limestone forest.

In Table 3, tree density and basal area for $D_{0.1H}$ of the subtropical evergreen broadleaf forest in silicate habitat were, respectively, 62452 stem ha^{-1} and 50.3 m^2 ha^{-1} for trees having $H \geq 0.10$ m. These results were considerably higher than the values of 47980 stem ha^{-1} and 38.0 m^2 ha^{-1} for total trees of the subtropical forest in limestone habitat. However, for trees having DBH ≥ 4.5 cm, tree density of 3080 stem ha^{-1} of the silicate forest was a little bit lower than that of 3350 stem ha^{-1} of the limestone forest, whereas basal area of 43.2 m^2 ha^{-1} of the silicate forest was quite high compared to that of 28.1 m^2 ha^{-1} of the limestone forest. These results suggest that as a whole the forest in silicate habitat is largely populated with a large basal area as compared with the forest in limestone habitat. As far as the large-sized trees (DBH ≥ 4.5 cm) are concerned, the silicate forest is somewhat lowly populated with a quite large basal area in comparison with the limestone forest. Therefore, the biomass of the stand is higher in the silicate forest than in the limestone forest. In fact, the silicate forest had a high canopy height (less than 16.5 m) compared to the limestone forest (less than 12.3 m).

The spatial distribution of trees of the two forests was random for the lower three layers, but the top layer trees were distributed with small and large clumps (Fig. 6). This type of distribution pattern is probably general for the subtropical forest. Further studies are required for the distribution pattern, especially for the top layer's trees to ascertain the generality of the result. High degree of overlapping in spatial distributions of trees among the layers in the silicate and limestone forests suggested that light can not penetrate easily to the lower layers. As a result, most species in the lower layers might be shade-tolerant in both of the forests.

A general trend described by Eq. (15) was found for the relationship of mean tree weight to tree density in each layer for both of the forests, i.e. mean tree weight decreased from the top toward the bottom layer, whereas tree density increased from the top downward (Fig. 8). This trend resembled the mean plant weight–density trajectory of self-thinning even-aged plant populations (Hagihara, 2000), which start growing from initial plant densities lower than the initial plant density of the population obeying the -3/2 power law of self-thinning (Yoda et al., 1963). The relationship of mean tree height to tree density for the upper two layers in the silicate forest supported Yamakura's quasi -1/2 power law of tree height, because the α-value in Eq. (15) was close to 3/2 (Feroz et al., 2006a). Our formulated equation is more general than Yamakura's quasi -1/2 power law of tree height, because the equation describes lower layers as well.

The subtropical forests in Okinawa Island consisted of four architectural layers. The floristic composition in the silicate habitat was quite different from that in the limestone habitat in terms of the similarity index; approximately only one-sixth of the species were in common. On the other hand, the floristic composition among layers was more similar in the silicate habitat than in the limestone habitat. *Castanopsis sieboldii* was the most dominant species in the silicate habitat, whereas it was completely absent in the limestone habitat, where *Cinnamomum japonicum* was the most dominant species. The trend of increasing diversity with successively decreasing height of layers from the top downward represents that high woody species diversity depended on small-sized trees in the silicate forest. However, this trend was different from the limestone forest, where diversity tended to increase up to the second layer and then decreased downward. It may represent that the large-sized trees are important in maintaining high woody species diversity in the limestone forest. In addition, the woody species diversity was higher in the silicate forest than in the limestone forest. The spatial distribution of trees in the forests was random in each layer, except the top layer. The understory trees in both of the forests might be shade-tolerant, because light can not penetrate easily to the lower layers. This result was concluded from high degree of overlapping among layers in the spatial distribution of trees. Mean tree weight decreased from the top toward the bottom layer, whereas tree density increased from the top downward. This trend was general in both of the forests and successfully expressed in the same form as in the mean weight–density trajectory of self-thinning plant populations.

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LITERATURE CITED

Alhamd, L. and A. Hagihara. 2004. Litterfall of a subtropical evergreen broad-leaved forest in Okinawa Island, Japan. Tropics. **13**: 255-268.

Alhamd, L., S. Arakaki and A. Hagihara. 2004. Decomposition of leaf litter of four tree species in a subtropical evergreen broad-leaved forest, Okinawa Island, Japan. For. Ecol. Manage. **202**: 1-11.

Bunyavejchewin, S., J. V. LaFrankie, P. J. Baker, M. Kanzaki, P. S. Ashton and T. Yamakura. 2003. Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. For. Ecol. Manage. **175**: 87-101.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge, UK. 626pp

Enoki, T. 2003. Microtopography and distribution of canopy trees in a subtropical evergreen broad-leaved forest in the northern part of Okinawa Island, Japan. Ecol. Res. **18**: 103-113.

Enoki, T. and A. Abe. 2004. Saplings distribution in relation to topography and canopy openness in an evergreen broad-leaved forest. Plant Ecol. **173**: 283-291.

Feroz, S. M., A. Hagihara and M. Yokota. 2006a. Stand structure and woody species diversity in relation to the stand stratification in a subtropical evergreen broadleaf forest, Okinawa Island. J. Plant Res. **119**: 293-301.

Feroz, S. M., K. Yoshimura and A. Hagihara. 2006b. Architectural stratification and woody species diversity of a subtropical forest grown in a limestone habitat in Okinawa Island, Japan. Enformatika. **17**: 237-242.

Gigon, A. 1987. A hierarchic approach in causal ecosystem analysis. In: The calcifuge-calcicole problem in alpine grasslands. Ecological studies vol. 61. Springer, Heidelberg, Germany. pp. 228-244.

Hagihara, A. 1995 The Size-Dependence curve as a generalized Competition-Density curve. Jpn. J. For. Plann. **24**: 15-23.

Hagihara, A. 2000. Time-trajectory of mean phytomass and density in self-thinning plant populations. Bull. Fac. Sci., Univ. Ryukyus. **70**: 99-112.

Hall, J. B. and M. D. Swaine. 1976. Classification and ecology of closed-canopy forest in Ghana. J. Ecol. **64**: 913-951.

Hayashi, D. and K. Kizaki. 1985. Geology of the middle and northern parts of Okinawa Island. In: Kizaki, K. (ed.), Geology of the Ryukyu Archipelago (in Japanese). Okinawa Times, Naha, Japan. pp. 93-106.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. **100**: 419-424.

Hozumi, K. 1971. Studies on the frequency distribution of the weight of individual trees in a forest stand. III. A beta-type distribution. Jpn. J. Ecol. **21**: 152-167.

Hozumi, K. 1975. Studies on the frequency distribution of the weight of individual trees in a forest stand. V. The *M-w* diagram for various types of forest stands. Jpn. J. Ecol. **25**: 123-131.

Huang, W., V. Pohjonen, S. Johansson, M. Nashanda, M. I. L. Katigula and O. Luukkanen. 2003. Species diversity, forest structure and species composition in Tanzanian tropical forests. For. Ecol. Manage. **173**: 11-24.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology. **133**: 125-133.

Huston, M. A. 1994. Biological diversity. Cambridge University Press, Cambridge, UK. 681pp.

Itô, Y. 1997. Diversity of forest tree species in Yanbaru, the northern part of Okinawa Island. Plant Ecol. **133**: 125-133.

Iwao, S. 1972. Application of the $\overset{*}{m}_u - m_u$ method to the analysis of spatial patterns by changing the quadrat size. Res. Popul. Ecol. **14**: 97-128.

Iwao, S. 1977. Analysis of spatial association mean crowding. Res. Popul. Ecol. **18**: 243-260.

Kimmins, J. P. 2004. Forest ecology. Pearson Education, Inc., New Jersey, USA. 611pp.

Kimoto, S. 1967. Some quantitative analysis on the Chrysomelid fauna of the Ryukyu Archipelago. Esakia. **6**: 27-54.

Kira, T. 1977. Introduction. Forest vegetation of Japan. In: Shidei, T. and T. Kira (eds.), Primary productivity of Japanese forests. Productivity of terrestrial communities. University of Tokyo Press, Tokyo, Japan. pp. 1-9 and p. 14.

Kira, T. 1991. Forest ecosystems of east and southest Aisa in a global perspective. Ecol. Res. **6**: 185-200.

Kira, T. and H. Ogawa. 1971. Assessment of primary production in tropical and equatorial forests. In: Productivity of forest ecosystems. Unesco, Paris, France. pp. 309-321.

Kubota, Y., H. Murata and K. Kikuzawa. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. J. Ecol. **92**: 230-240.

Lindgren, P. M. F. and T. P. Sullivan. 2001. Influence of alternative vegetation management treatments on conifer plantation attributes: abundance, species diversity, and structural diversity. For. Ecol. Manage. **142**: 163-182.

Lloyd, M. 1967. Mean crowding. J. Anim. Ecol. **36**: 1-30.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology. **42**: 594-598.

Miyawaki, A. (ed.). 1989. Vegetation of Japan Vol. 10. Okinawa and Ogasawara (in Japanese). Shibundo Co. Ltd., Tokyo, Japan. 676pp.

Morishita, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci., Kyushu Univ. Ser. E. (Biology) **3**: 65-80.

Mountford, M. D. 1962. An index of similarity and its application to classificatory problems. In: Murphy, P. W. (ed.), Progress in soil zoology. Butterworths, London, UK. pp. 43-50.

Ogawa, H. 1980. Structure and function of populations (in Japanese). Asakura-shoten, Tokyo, Japan. 221pp.

Ohsawa, M. 1995. Latitudinal comparison of altitudinal changes in forest structure, leaf-type, and species richness in humid monsoon Asia. Vegetatio. **121**: 3-10.

Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley & Sons, Inc., New York, USA. 286pp.

Pielou, E. C. 1975. Ecological diversity. John Wiley & Sons, Inc., New York, USA. 165pp.

Roberts, M. R. and F. S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol. Appl. **5**: 969-977.

Schulze, E.-D., E. Beck and K. Müller-Hohenstein. 2005. Plant ecology. Springer, Heidelberg, Germany. 702pp.

Shinozaki, K. 1963. Note on the species-area curve (in Japanese). Proc. Ann. Mtg. Ecol. Soc. Japan, Tokyo, Japan. p. 5.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco, USA. 572pp.

Sterner, R. W, A. R. Christine and G. E.Schatz.1986.Testing for life historical changes in spatial patterns of four tropical tree species. J. Ecol. **74**: 621-633.

Walker, E. H. 1976. Flora of Okinawa and the Southern Ryukyu Islands. Smithsonian Institution Press, Washington, D.C., USA. 1159pp.

Whitmore, T. C. 1998. An introduction to tropical rain forests. Oxford University Press, London, UK. 282pp.

Xu, X., E. Hirata, Y. Tokashiki and T. Shinohara. 2001. Structure and species diversity of subtropical evergreen broad-leaved forest in northern Okinawa Island, Japan. J. For. Res. **6**: 203-210.

Yamakura, T. 1987. An empirical approach to the analysis of forest stratification. I. Proposed graphical method derived by using an empirical distribution function. Bot. Mag. Tokyo. **101**: 153-162.

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

日本沖繩島上兩亞熱帶森林生育地（矽酸岩及石灰岩）的群落特性之比較

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摘　　要

本研究探討兩亞熱帶森林的森林結構，以及在不同垂直分層中木本植物歧異度和空間分佈之特性。調查區域位於日本沖繩島北方，為生長在矽酸岩及石灰岩生育地上之森林，調查樣區大小分別為750及1000平方公尺。結果顯示，兩森林中之垂直結構皆可分成四層。於矽酸岩生育地樣區中，總計有4684株高度高於0.1公尺之個體，分屬26科，43屬及60種。於石灰岩生育地樣區中，則總計有4798株高度高於0.0公尺之個體，分屬31科，51屬及62種。兩樣區之植物組成相似度很低($C_{\Pi} = 0.07$)，只有約六分之一的物種為兩樣區所共有。比較各垂直分層間的組成時，矽酸岩樣區層次間的物種相似性較高，而石灰岩樣區則較低。在矽酸岩樣區中最優勢的物種為 *Castanopsis sieboldii* (Mak.) Hatusima，但此物種於石灰岩樣區中完全闕如。於石灰岩樣區中的最優勢物種為 *Cinnamomum japonicum* Sieb. ex Nees。比較兩樣區中的潛在物種數目時，矽酸岩樣區的值（62）較低於石灰岩樣區中的潛在數目（71）。然而，木本植物歧異度則於矽酸岩樣區中較高。當比較層次間的歧異度指數（H' 及 J' 值）時，其值於矽酸岩樣區為從樹冠層往底層漸次增加（除了最低的地被層稍有降低），而在石灰岩樣區中，歧異度指數值的增加方向恰為相反。此結果表示，矽酸岩樣區中的高物種歧異度，主要取決於小徑級的個體，而石灰岩樣區中的物種歧異度，主要取決於大徑級的個體。植株數於各樹冠層次間的空間分布上，多屬於隨機分布，除了樹冠層的植株數於兩個空間尺度上有聚集的現象。在此兩樣區中，各層次的個體在空間上具有高度重疊性，顯示了光度無法輕易到達森林下層，所以下層組成可能多為耐陰物種。兩樣區中平均植株的重量 (直徑和高度的函數) 為由森林上層往下層減輕，但是植株密度則由上層往下層增加。本研究顯示了此結構為兩樣區森林所共有之特性，而此特性符合在平均植株重量與密度分析中的自我疏伐模式。

關鍵詞：森林層次結構、植物組成相似性、石灰岩生育地、植物平均重量與密度關係、沖繩島、矽酸岩生育地、植株空間分佈、亞熱帶森林、木本植物歧異度。

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