REGULAR PAPER

Stand stratification and woody species diversity of a subtropical forest in limestone habitat in the northern part of Okinawa Island

S. M. Feroz · K. Yoshimura · Akio Hagihara

Abstract Stand stratification and woody species diversity were studied in a subtropical forest in limestone habitat in the northern part of Okinawa Island, Japan. The forest stand consisted of four architectural layers. *Cinnamomum japonicum* Sieb. was the most dominant species as it had the highest importance value in all layers, especially in the lower three layers. Although *Rhus succedanea* L. was a major top-layer species, it might disappear because of its absence in the lower two layers. The lower two layers had similar floristic composition, while the composition of the top layer differed greatly from that of the lower two layers. The value of H' in each layer increased from the bottom to the second layer and then decreased, and the value of J' in each layer consistently increased from the bottom layer upward. The values of Shannon's index H' and Pielou's index J' were 4.27 bit and 0.74, respectively, at the stand level. The trends of H' and J' based on the cumulative height range from the top layer downward were, respectively, the same as those in each layer for the present forest in limestone habitat. However, these trends were opposite from those of a nearby subtropical forest in silicate habitat, where the values of H' and J' based on the cumulative height range decreased steadily from the bottom layer upward.

Keywords Architectural stratification ·
Limestone habitat · Mean tree weight-density relationship ·
Species diversity · Subtropical forest

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Introduction

The east- and southeast-coastal zone of the Asian continent lacks the subtropical dry belt that separates temperate forest areas from the humid tropics elsewhere in the world. The subtropical zone, which includes the chain of islands from Okinawa to Taiwan, is moist enough to allow the development of subtropical forests. Thus, forest climates with sufficient rainfall cover coastal areas of the Western Pacific from subarctic eastern Siberia to equatorial southeast Asia, giving rise to 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). Therefore, the subtropical forest of the Okinawa Islands is valuable from a phytogeographical point of view.

The subtropical area in the northern part of Okinawa Island consists mainly of silicate rock, where a well-developed evergreen broadleaf forest dominated by *Castanopsis sieboldii* (Mak.) Hatusima exists. However, a small part (approximately 2.5% of the total area of the northern part of Okinawa Island) consists of limestone (Hayashi and Kizaki 1985), where a different type of forest is developed, with an absolute lack of *C. sieboldii*.

Biological diversity is a key issue in nature conservation (Wilson 1988), and species diversity is an important component of biological diversity (Itô 1997). 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). The degree of stand stratification and 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 degree of stand stratification, i.e., architectural stratification, is an important factor in the maintenance of higher woody species diversity (Roberts and Gilliam 1995; Lindgren and Sullivan 2001; Feroz et al. 2006).

Several studies have been carried out on woody species diversity, the spatial distribution patterns of trees, woody species composition and stand stratification in silicate habitats on Okinawa Island (Itô 1997; Xu et al. 2001; Enoki 2003; Alhamd and Hagihara 2004; Enoki and Abe 2004; Kubota et al. 2004; Feroz et al. 2006). However, no such studies have been performed in limestone habitats. Therefore, the objectives of this study are (1) to describe the architectural stratification of a forest in limestone habitat, and (2) to quantify the woody species composition and diversity on the basis of architectural stratification. The results were compared with those obtained from a nearby subtropical forest in a silicate habitat (Feroz et al. 2006).

Materials and methods

Study site

The present study was conducted in a subtropical forest, located at Mt. Nekumachiji, Higashi Village, in the northern part of Okinawa Island ($26°41'5''$N and $128°8'19''$E). The bedrock consists of limestone and the soil pH is 8.1. This area is characterized by a humid-maritime subtropical climate. According to observations during 1995–2004 at Nago Meteorological Station, 27 km southwest of the study site, the mean annual temperature is 22.7 °C ± 0.1 (SE), and the mean monthly minimum temperature and the mean monthly maximum temperature are 16.4 °C ± 0.3 (SE) in January and 28.8 °C ± 0.2 (SE) in July, respectively. The warmth index is 212.8 °C ± 1.8 (SE) month, which is within the range of 180–240°C month for subtropical regions defined by Kira (1977). The mean annual rainfall is $2,176$ mm ± 171 (SE) and the mean monthly rainfall is over 100 mm throughout the year except for 94 mm ± 17 (SE) in January. Typhoons occur frequently between July and October, bringing high rainfall and strong winds.

Field methods

A 1,000 m² (40 m × 25 m) sampling plot was established and divided into 160 quadrats (2.5 m × 2.5 m). The plot faced north with a slope of 25.4°, and the altitude was 235 m a.s.l. All woody plants, except lianas and seedlings with cotyledon, were numbered and identified to species according to the nomenclature of Hatusima (1990). Tree height H, stem diameter at breast height DBH ($H > 1.3$ m)

and stem diameter at a height of $H/10$ $D_{0.1H}$ were measured.

Data analysis

Architectural stratification

The $M-w$ diagram proposed by Hozumi (1975) was used to identify the multi-layering structure of the forest stand. Tree weight w was assumed to be proportional to $D_{0.1H}^2 H$ and 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 formula $M_n = \sum_{i-1}^{n} w_i / n$ ($n = 1,...,$ 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 segments on the $M-w$ diagram can be written by either of the following equations:

$$M = Aw + B \tag{1}$$

$$M = Cw^b \tag{2}$$

where A, B, C and b are coefficients. These functions reflect some aspects of the manner of packing trees into three-dimensional space as realized by a forest stand. Following the method proposed in a previous paper (Feroz et al. 2006), a boundary between layers was distinguished by the relationships of the first derivative S_1 and the second derivative S_2 of M with respect to w on the $M-w$ diagram.

Species dominance

Dominance of a species was defined by the importance value IV% of the species.

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

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.

Floristic similarity between layers

The following r_0-index was applied for the similarity of floristic composition among the layers:

$$r_0 = \frac{\sum_{i=1}^{s} n_{Ai} n_{Bi}}{\sqrt{\sum_{i=1}^{s} n_{Ai}^2 \sum_{i=1}^{s} n_{Bi}^2}} \tag{4}$$

which was originally obtained for the measurement of niche overlap (Kuno 1968; cf. Pianka 1973; Iwao 1977), and where S is the total number of species, n_{Ai} and n_{Bi} are the number of individuals of the ith species belonging to layer A and layer B, respectively. The value of r_0 is 1.0 when the number of individuals belonging to a species of layer A is proportional to that to the species of layer B, and is 0.0 when no common species are found between them.

Equation 4 was also applied to the similarity of floristic composition between the present forest and the subtropical forest in silicate habitat (Feroz et al. 2006). In this case, n_{Ai} and n_{Bi} were the number of individuals of the ith species belonging to the present forest and the other forest, respectively.

Overlapping of spatial distribution of trees between layers

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

$$\left.\begin{aligned} \omega_{(+)} &= \frac{\gamma - \gamma_{(ind)}}{1 - \gamma_{(ind)}} \quad \left(\gamma \geq \gamma_{(ind)}\right) \\ \omega_{(-)} &= \frac{\gamma - \gamma_{(ind)}}{\gamma_{(ind)}} \quad \left(\gamma \leq \gamma_{(ind)}\right) \end{aligned}\right) \tag{5}$$

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

$$\gamma = \frac{\sum_{j=1}^{Q_u} n_{Aj} n_{Bj}}{\sqrt{\sum_{j=1}^{Q_u} n_{Aj}^2 \sum_{j=1}^{Q_u} n_{Bj}^2}}$$

$$\gamma_{(ind)} = \frac{1}{Q_u} \frac{\sum_{j=1}^{Q_u} n_{Aj} \sum_{j=1}^{Q_u} n_{Bj}}{\sqrt{\sum_{j=1}^{Q_u} n_{Aj}^2 \sum_{j=1}^{Q_u} n_{Bj}^2}}.$$

Here, Q_u is the total number of quadrats taken as 160, 80, 40, 20 and 10 for the u-values of 1, 2, 4, 8 and 16, respectively, n_{Aj} and n_{Bj} are the number of individuals of the jth quadrats belonging to layer A and layer B, respectively. The value of ω changes from the maximum of +1.0 for complete overlap, through 0.0 for independent occurrence, to the minimum of −1.0 for complete exclusion.

In this paper, we examined spatial distribution in relation to light penetration from the top layer to lower layers. Therefore, we combined layers from the top downward to examine the overlap with lower layers. First, the overlap between the top and second layers was examined. Second, the top and second layers were combined to examine the

overlap with the third layer. Finally, the top to third layers were combined to examine overlap with the bottom layer.

Species–area relationship

The expected number of species S_q, appearing 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):

$$S_q = \sum_{i=1}^{s} \left[1 - \left(\frac{Q - q_i}{q} \right) \bigg/ \left(\frac{Q}{q} \right) \right] \tag{6}$$

where q_i is the number of quadrats in which the ith species occurred, and S is the total number of species. In this study, S_q-values were obtained for q-values of 1, 2, 4, 8, 16, 32, 64, 128 and 160.

Diversity indices

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 and equitability (evenness), respectively:

$$H' = \sum_{i=1}^{s} \frac{n_i}{N} \log_2 \frac{N}{n_i} \tag{7}$$

$$J' = \frac{H'}{H'_{max}} \quad \left(H'_{max} \log_2 S \right) \tag{8}$$

where N is the total number of individuals.

Regression analysis

The coefficients for nonlinear equations were determined with statistical analysis software (KaleidaGraph V. 4.0, Synergy Software, Reading, PA). However, the coefficients for linear and curvilinear equations were determined using the ordinary least-squares method.

Results

Architectural stratification

The $M−w$ diagram is illustrated in Fig. 1a. As is clear from Fig. 1b, the $M−w$ diagram shows four phases, the first, second and fourth of which have the properties of Eq. 1, i.e., Type I of the C–D curve tribe that contains eight types (Shinozaki and Kira 1961), whereas the third phase has the properties of Eq. 2, i.e., a power function. As a result, it was confirmed that the forest consists of four layers. Figure 1c shows the extrema, represented by arrows, that apparently emerged in the $S_2−\ln w$ relationship. Tree weights at

Fig. 1 Relationships of (**a**) mean tree weight M, (**b**) the first derivative S_1 and (**c**) the second derivative S_2 to tree weight w on logarithmic coordinates. In the $M–w$ diagram (**a**), 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; and $A = 332$ 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 $b = 0.284$ ($R^2 = 0.92$)
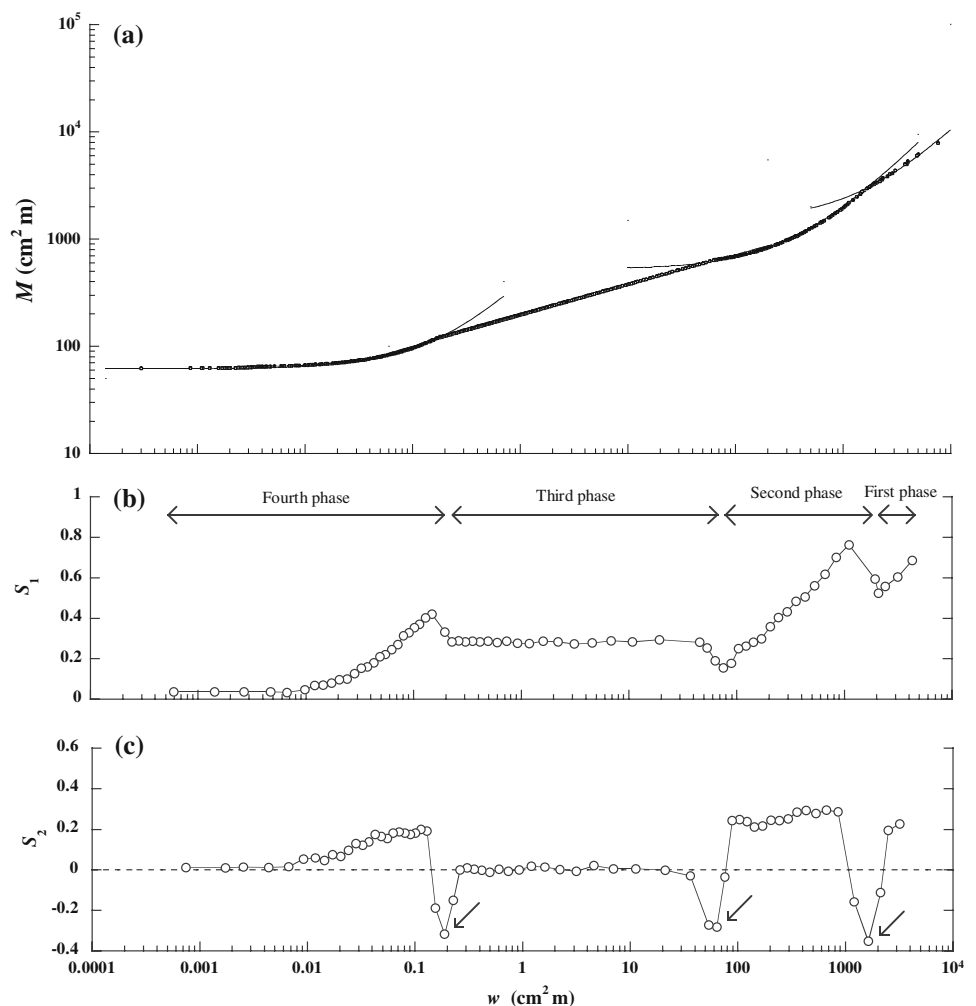
boundaries between layers were estimated to be 1,640, 63.9 and 0.188 cm^2 m as w at the extrema in Fig. 1c.

The relationship between tree height H and weight w (cf. Kira and Ogawa 1971) (Fig. 2) was formulated as:

$$\frac{1}{H} = \frac{1}{1.13w^{0.415}} + \frac{1}{11.52}. \tag{9}$$

The rank of tree height correlated well with that of tree weight (Spearman's rank correlation coefficient $r_s = 0.96$, $t = 242$, $P \cong 0$). The boundary heights were determined as 7.83, 4.10 and 0.53 m by substituting the tree weights at the boundaries between layers obtained above for w in Eq. 9. Therefore, the height range of a layer was $7.83 < H \leq 12.3$ m for the top layer, $4.10 < H \leq 7.83$ m for the second layer, $0.53 < H \leq 4.10$ m for the third layer and $0.0 < H \leq 0.53$ m for the bottom layer.

Species dominance

Table 1 lists the importance value IV of ten woody species in order of species rank in the 0.1 ha sampling plot, together with the four layers. The plot contained 4,798 woody individuals, which belong to 62 species, 51 genera and 31

families. The most species-rich families were Moraceae and Lauraceae, which contained seven and six species, respectively. Moraceae consisted of the genera of *Ficus* and *Morus*, of which *Ficus* is the most species-rich genus with six species. Out of the 62 species, only 7 species (11%) consisted of a single individual. *Cinnamomum japonicum* Sieb. 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 (Table 1). Although *Rhus succedanea* L. was the second dominant species in regards to the IV (7.63%), it disappeared in the lower two layers. On the other hand, some of the top ranking species, such as *Turpinia ternata* Nakai, *Citrus depressa* Hay., *Psychotria manillensis* Bartl. ex DC., *Helwingia liukiuensis* Hatusima, *Machilus thunbergii* S. et Z., *Tarenna gyokushinkwa* Ohwi and *Litsea japonica* (Thunb.) Juss., were absent in the top layer.

Floristic similarity among layers

Among six combinations of layers, the highest floristic similarity was found between the third and bottom layers ($r_0 = 0.88$, Table 2). The lowest similarities were found

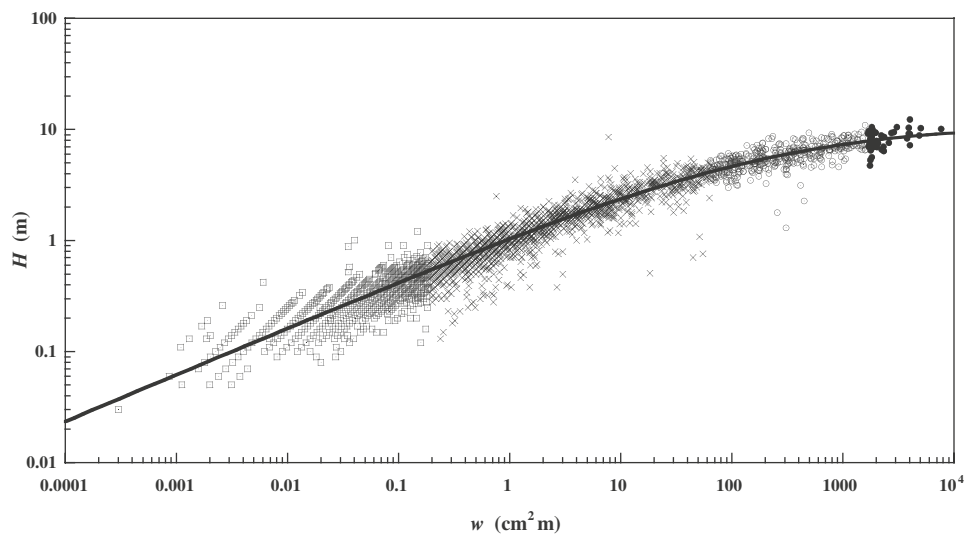**Table 1** Ten dominant species in order of species rank determined by the importance value IV in the total stand

Species rank	Species	Family	IV (%)				
			Top layer	Second layer	Third layer	Bottom layer	Total stand
1	*Cinnamomum japonicum* Sieb.	Lauraceae	4.32	10.61	12.75	20.19	13.08
2	*Rhus succedanea* L.	Anacardiaceae	28.33	10.29	0.0	0.0	7.63
3	*Turpinia ternata* Nakai	Staphyleaceae	0.0	9.86	10.18	11.74	7.03
4	*Citrus depressa* Hay.	Rutaceae	0.0	3.03	5.07	10.63	6.93
5	*Psychotria manillensis* Bartl. ex DC.	Rubiaceae	0.0	0.0	5.12	4.18	4.40
6	*Helwingia liukiuensis* Hatusima	Cornaceae	0.0	0.58	4.36	2.87	3.80
7	*Machilus thunbergii* S. et Z.	Lauraceae	0.0	4.93	4.81	5.67	3.57
8	*Tarenna gyokushinkwa* Ohwi	Rubiaceae	0.0	1.97	4.39	3.03	3.47
9	*Ardisia sieboldii* Miq.	Myrsinaceae	5.27	3.21	3.23	2.24	3.37
10	*Litsea japonica* (Thunb.) Juss.	Lauraceae	0.0	1.03	1.75	2.40	2.83

Table 2 Degree of similarity r_0 in floristic composition between layers

Layer	Second	Third	Bottom
Top	0.57	0.12	0.10
Second		0.63	0.59
Third			0.88

between the top and third layers ($r_0 = 0.12$) and between the top and bottom layers ($r_0 = 0.10$). The second layer showed an intermediate composition ($r_0 = 0.57$, 0.63 and 0.59 with the top, third and bottom layers, respectively).

Overlap in spatial distributions of trees among layers

Trees in the second layer tended to show an exclusive distribution compared to those in the top layer (Fig. 3). However, trees in the third and bottom layers showed overlapping distributions with those in the upper layers

combined. These results may indicate that trees in the upper two layers can catch a sufficient amount of light, while light cannot penetrate easily into the lower two layers.

Species–area relationship

The expected number of species S_q increased, but tended to become saturated with increasing number of quadrats q (Fig. 4). The relationships of S_q to q in each layer and in the total stand were well approximated by Eq. 10 (Ogawa 1980; cf. Hagihara 1995):

$$\frac{1}{S_q} = \frac{1}{cq^d} + \frac{1}{S_{\max}} \tag{10}$$

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

The expected maximum number of species $S_{\max}$ was estimated to be 71 in the total stand. $S_{\max}$ increased from 26
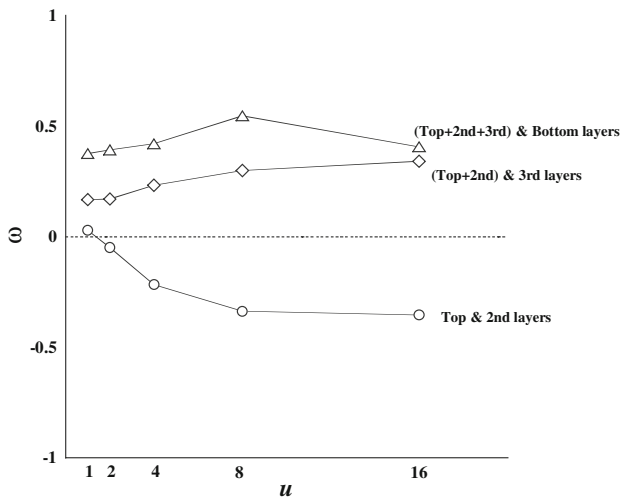
Fig. 3 Degree of overlap ω with successive changes of quadrat size u in the spatial distributions of trees. The smallest quadrat size ($u = 1$) is 2.5 m $\times$ 2.5 m
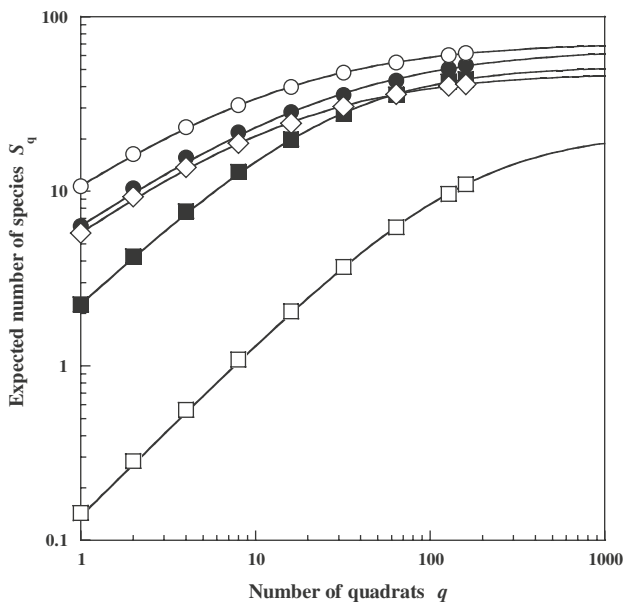

Fig. 4 Species–area curves (area of one quadrat: 2.5 m $\times$ 2.5 m). *Open circles* Total stand, *open squares* top layer, *filled squares* second layer, *filled circles* third layer, *open diamonds* bottom layer. The curves are given by Eq. 10, where $c = 12.6$, $d = 0.709$ and $S_{max} = 71.2$ ($R^2 \cong 1.0$) 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

in the top layer, through 53 in the second layer, to 66 in the third layer, but decreased to 50 in the bottom layer. Therefore, the third layer had the highest potential number of species. This result was different in the nearby subtropical forest in silicate habitat, where the expected maximum number of species was in the bottom layer (Feroz et al. 2006).

Woody species diversity and evenness in the stratified forest stand

The value of J' increased consistently from the bottom layer upward, whereas the value of H' increased from the bottom to the second layer, but showed the lowest value in the top layer (Table 3). This is ascribed to the second highest species richness (44 species) in the second layer and quite low species richness (11 species) in the top layer compared to other layers. An increase in H'-value from the bottom layer to the third layer corresponds to increases in species richness (42 species in the bottom layer and 55 species in the third layer) and increases in J' in the same direction.

Mean tree weight and density among the layers

The 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 tree density ρ_i of the ith layer (Fig. 5). This trend was well expressed in the form (Feroz et al. 2006):

$$\overline{w_i} = K\rho_i^{-\alpha}\left(1 - \frac{\rho_i}{\rho_o}\right) \tag{11}$$

where the values of coefficients K, α and ρ_o were 92,734 cm^2 m ha$^{-\alpha}$, 0.613 and 21,827 ha^{-1}, respectively. For small values of ρ_i as compared with the ρ_o-value, i.e., for the upper layers, the following equation may hold:

$$\overline{w_i} = K\rho_i^{-\alpha}. \tag{12}$$

Mean tree weight $\overline{w_i}$ decreased from the top toward the bottom layer as the cube of mean tree height $\overline{H_i}$ decreased in the same direction (Fig. 6). The relationship was formulated as follows:

$$\overline{w_i} = 2.37\left(\overline{H_i}^3\right)^{1.05}. \tag{13}$$

Since the exponent value of 1.05 was not significantly different from 1.0 ($t = 1.08$, $P = 0.39$), the value may be assumed to be 1.0. Therefore, $\overline{w_i}$, having three dimensions, is most likely proportional to the cube of $\overline{H_i}$, having one dimension.

Considering Eqs. 12 and 13, the following equation can be deduced:

$$\overline{H_i} = k\rho_i^{-h} \tag{14}$$

where $h \cong 0.204$ ($=\alpha/3$) and k is a coefficient.

Discussion

Hozumi (1975) found that the number of layers distinguished by the $M-w$ diagram increases along a latitudinal

Table 3 Diversity indices for the stratified forest stand in a 1,000 m^2 plot in the northern part of Okinawa Island

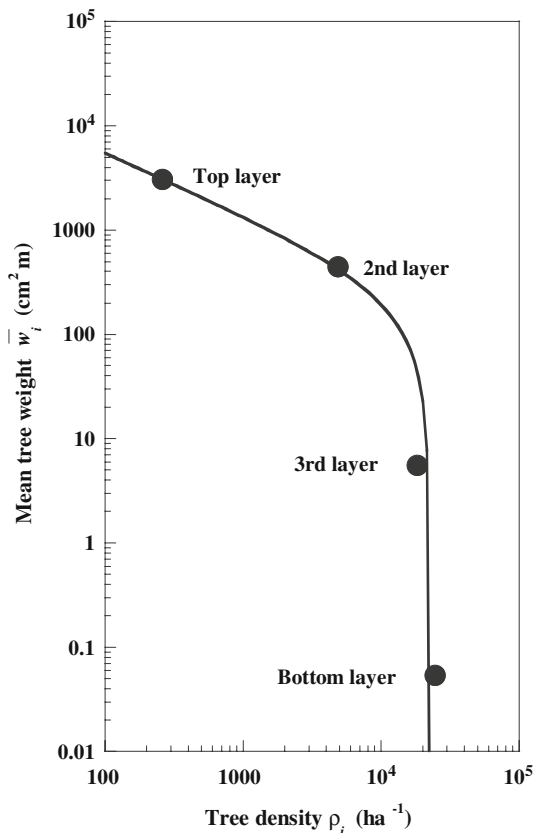| Layer	Height range (m)	Cumulative height range (m)	No. of trees	No. of trees[a]	No. of species	No. of species[a]	H' (bit)	H' (bit)[a]	J'	J'[a]
Top	$7.83 < H \leq 12.3$	$7.83 < H \leq 12.3$	25	25	11	11	3.05	3.05	0.88	0.88
Second	$4.10 < H \leq 7.83$	$4.10 < H \leq 12.3$	469	513	44	45	4.41	4.49	0.81	0.82
Third	$0.53 < H \leq 4.10$	$0.53 < H \leq 12.3$	1,843	2,347	54	60	4.33	4.46	0.75	0.78
Bottom	$0.0 < H \leq 0.53$	$0.0 < H \leq 12.3$	2,461	4,798	42	62	3.52	4.27	0.65	0.74

[a] Based on the cumulative height range from the top

Fig. 5 Relationship between mean tree weight $\overline{w_i}$ and tree density ρ_i. The curve is given by Eq. 11, where $R^2 \cong 1.0$

Fig. 6 Curvilinear relationship between mean tree weight $\overline{w_i}$ and the cube of mean tree height $\overline{H_i}^3$. The regression line is given by Eq. 13, where R^2 is 0.98

thermal gradient from the northern conifer forests to the tropical rain forests. The present forest consisted of four layers. Feroz et al. (2006) revealed that a subtropical forest in a silicate habitat near the present forest also consists of four layers. Therefore, the subtropical forests in any habitat on Okinawa Island may consist of four architectural layers.

The floristic composition was similar between the third and bottom layers, while the composition of the top layer differed greatly from these layers (Table 2). This would be because the lower two layers consist of many individuals of shade species (understory species) and a relatively small number of juveniles of facultative shade species that are light-tolerant as adult and shade-tolerant as juvenile
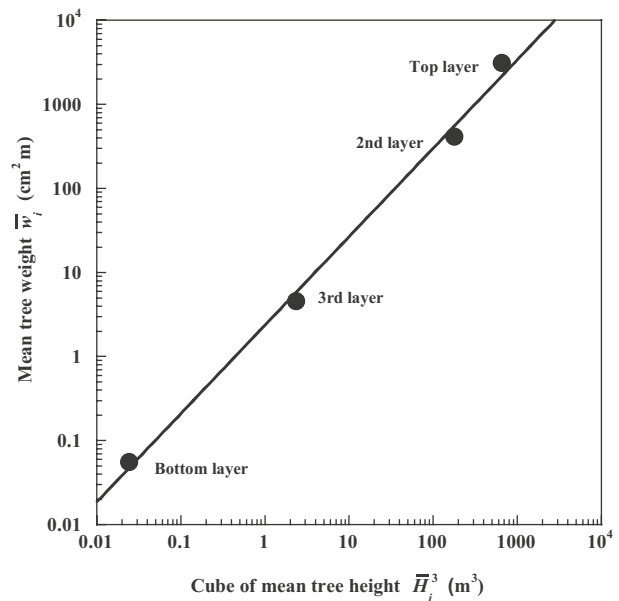
(Yasugi et al. 1996), whereas the top layer consists of many individuals of sun species (shade-intolerant species) and relatively small number of adults of facultative shade species. The second layer showed a composition intermediate between that of the top layer and the lower two layers.

Cinnamomum japonicum Sieb. was typically a facultative shade species as it appeared in all layers with the highest or the third highest importance value. On the other hand, *R. succedanea* L. was typically a sun species as it appeared only in the upper two layers with the highest or second highest importance value (Table 1), which may indicate its disappearance in the future. In addition, some species with only a 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 also possibly disappear. On the contrary, some species may newly invade the gaps created by stones. This type of changing species composition, i.e., disappearance and appearance of species, can be persistent owing to

Table 4 Comparison in basal area and tree density between forests in limestone and silicate habitats in the northern part of Okinawa Island. *DBH* Diameter at breast height

Study site	Sample area (ha)	Tree size	Basal area (m² ha⁻¹)	No. of trees (ha⁻¹)	Source
Limestone	0.1	$H > 0.0$ m	38	47,980	Present study
	0.1	DBH $\geq$ 4.5 cm	28.1	3,350	
Silicate	0.075	$H \geq 0.10$ m	50.3	62,452	Feroz et al. (2006)
	0.075	DBH $\geq$ 4.5 cm	43.2	3,080	

continuous natural disturbance. Hence, the present forest seems to be most likely stable, albeit with a continuously changing species composition.

It has long been observed that species in limestone habitat differ from those in silicate rock (Schulze et al. 2005). Within Okinawa Island, the species composition of the present forest in a limestone habitat with a soil pH of 8.1 was quite different from that of the subtropical forest in a silicate habitat with a soil pH of 4.35 (Alhamd et al. 2004; Alhamd and Hagihara 2004; Feroz et al. 2006). This result is inferred from the low value of the similarity index ($r_0 = 0.07$) between these two habitats. However, the comparison was made between small plot sizes in both the present limestone forest (0.1 ha) and the silicate forest (0.075 ha).

Diversity indices H' and J' based on the cumulative height range from the top layer downward showed, respectively, the same trends as those in each layer, i.e., H' increased from the bottom to the second layer and then decreased, and J' consistently increased from the bottom layer upward (Table 3). However, these trends differed from those in the nearby subtropical forest in silicate habitat, where H' and J' (based on the cumulative height range) decreased progressively from the bottom layer upward (Feroz et al. 2006). This means that large-sized trees play an important role in maintaining high woody species diversity in limestone habitats, whereas small-sized trees play an important role in maintaining high woody species diversity in silicate habitats.

Tree density and basal area for $D_{0.1H}$ in the present forest were 47,980 ha⁻¹ and 38 m² ha⁻¹, respectively, at the stand level (Table 4). These results were considerably lower than the values of 62,452 ha⁻¹ and 50.3 m² ha⁻¹ ($H \geq 0.10$ m) in the subtropical forest in silicate habitat (Feroz et al. 2006). However, for trees having DBH $\geq$ 4.5 cm, the tree density in the limestone forest (3,350 ha⁻¹) was slightly higher than that in the silicate forest (3,080 ha⁻¹), whereas the basal area of 28.1 m² ha⁻¹ in the limestone forest was quite low compared to that of 43.2 m² ha⁻¹ in the silicate forest. These results suggest that, as a whole, the forest in the limestone habitat is sparsely populated with a low basal area as compared to the forest in the silicate habitat. As far as large-sized trees (DBH $\geq$ 4.5 cm) are concerned, the forest in the limestone

habitat is more densely populated and has a lower basal area than the forest in the silicate habitat. In addition, the present limestone habitat forest had a low canopy height (less than 12.3 m) as compared to the silicate habitat forest (less than 16.5 m) (Feroz et al. 2006).

The relationship of mean tree weight to tree density in each layer was well described by Eq. 11, which is analogous to the process of self-thinning plant populations (Hagihara 2000). In the present forest, this relationship showed the same trend as that in the subtropical forest in silicate habitat (Feroz et al. 2006). This may be a general phenomenon for subtropical forests. Moreover, Yamakura (1988) examined the relationships between mean tree height $\overline{H_i}$, whose minimum was 3.7 m, and tree density ρ_i for 38 forest stands with two or three layers of different forest formations. As a result, he found that the power relationship described by Eq. 14 exists between $\overline{H_i}$ and ρ_i, and most of the estimates of h range from 0.2 to 0.8. The present value of h was within the range of h-values reported by Yamakura (1988). Thus, the power relationship between mean tree height and tree density for the upper layers in the present forest supports Yamakura's (1988) statements.

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