

Architectural Stratification and Woody Species Diversity of a Subtropical Forest Grown in a Limestone Habitat in Okinawa Island, Japan

S. M. Feroz, K. Yoshimura, and A. Hagihara

Abstract—The forest stand consisted of four layers. The species composition between the third and the bottom layers was almost similar, whereas it was almost exclusive between the top and the lower three layers. The values of Shannon's index H' and Pielou's index J' tended to increase from the bottom layer upward, except for H' -value of the top layer. The values of H' and J' were 4.21 bit and 0.73, respectively, for the total stand. High woody species diversity of the forest depended on large trees in the upper layers, which trend was different from a subtropical evergreen broadleaf forest grown in silicate habitat in the northern part of Okinawa Island. The spatial distribution of trees was overlapped between the third and the bottom layers, whereas it was independent or slightly exclusive between the top and the lower three layers. Mean tree weight of each layer decreased from the top toward the bottom layer, whereas the corresponding tree density increased from the top downward. This relationship was analogous to the process of self-thinning plant populations.

Keywords—Canopy multi-layering, limestone habitat, mean tree weight-density relationship, species diversity, subtropical forest.

I. INTRODUCTION

BIOLOGICAL diversity is a key issue to nature conservation ([1]) and species diversity is one of the important components of the biological diversity ([2]). The diversity of tree species is fundamental to total forest biodiversity, because trees provide resources and habitats for almost all other forest species ([3]-[7]). Generally tree species diversity in a forest varies greatly from place to place mainly due to variation in biogeography, habitat and disturbance ([6]).

It is known that woody species diversity increases sharply along a latitudinal thermal gradient from higher latitudes to the tropics ([8], [9]) in accordance with a greater degree of stand multi-layering toward warmer regions ([10]-[12]). The

architectural stratification is an important factor to maintain higher woody species diversity ([5], [13]).

The subtropical zone, which includes a chain of islands from Okinawa to Taiwan, is sufficiently moist to allow the development of subtropical evergreen broadleaf forests ([8]). The subtropical forest of Okinawa Islands is, therefore, phytogeographically precious. 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 of the area consists of limestone, where a different type of forest is developed in the absolutely absence of *C. sieboldii*. Several studies have been carried out on the woody species diversity, spatial distribution patterns of trees, woody species composition and stand stratification in silicate area ([2], [14]- [18]).

However, no studies of such kinds have been performed yet in the limestone area. The objectives of this study are, therefore, to distinguish the canopy multi-layering of a forest grown in the limestone habitat, and to quantify woody species diversity related to the multi-layering structure.

II. METHODOLOGY

A. Study Site and Sampling

The present study was conducted in a subtropical forest, located at Mt. Nekumatidi, Higashi Village, in the northern part of Okinawa Island (26°41'5"N and 128°8'19"E). The bedrock is mainly limestone and the soil pH is 8.1. This area is characterized by a humid-maritime subtropical climate. The wormth index is 212.8 ± 1.8 (SE) °C month, which is within the range of 180 to 240 °C month of the subtropical region defined by [19]. The mean annual rainfall is 2176 ± 171 mm. Typhoons frequently occur between July and October, bringing high rainfall and strong winds.

A sampling plot of area 1000 m² (40 m × 25 m) was established and divided into 160 quadrats (2.5 m × 2.5 m). The altitude of the plot, which faced to the north with a slope of 25.4°, was 235 m above sea level. All woody plants were numbered and identified to species according to the nomenclature by [20]. 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.

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B. Data Analysis

1. Canopy Multi-Layering

To determine the multi-layering structure of the forest stand, the M - w diagram ([10]) was used. Tree weight w was assumed to be proportional to $D_{0.1H}^2 H$ and was arranged in descending order. Mean tree weight M from the maximum tree weight to a given tree weight w was calculated. The M - w diagram was constructed by plotting values of M against the corresponding values of w on logarithmic coordinates. Reference [10] pointed out that segments on the M - w diagram can be expressed by either of the equations:

$$M = Aw + B \quad (1)$$

$$M = Cw^b \quad (2)$$

where A , B , C and b are coefficients. Each segment is considered to be related to the story with characteristics specific to beta-type distributions designated by [10], [21], which belong to special forms of the beta distribution (e.g. [22]). These distributions reflect some aspect of the manner of packing of trees into the three-dimensional space as realized by a forest stand.

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. The S_1 and S_2 are defined as:

$$S_1 = \frac{d \ln M}{d \ln w} \cong \frac{\Delta \ln M}{\Delta \ln w} \quad (3)$$

$$S_2 = \frac{d}{d \ln w} \left(\frac{d \ln M}{d \ln w} \right) = \frac{d S_1}{d \ln w} \cong \frac{\Delta S_1}{\Delta \ln w} \quad (4)$$

If the moving value of S_1 is plotted against the geometric mean of the corresponding values of w , points of inflection probably appear instead of points of intersection between the segments on the M - w diagram. The point of inflection has its x -coordinate at which point the second derivative S_2 has an extremum. The x -coordinate of the extremum, i.e. critical number, can be regarded as a boundary between layers ([4]).

2. Species Similarity

The similarity of species composition between layers was calculated using the following index C_{Π} ([23], [24]):

$$C_{\Pi} = \frac{2 \sum_{i=1}^s n_{Ai} n_{Bi}}{(\Pi_A + \Pi_B) N_A N_B} \quad (5)$$

$$(\Pi_A = \sum_{i=1}^s n_{Ai}^2 / N_A^2, \Pi_B = \sum_{i=1}^s n_{Bi}^2 / N_B^2)$$

where S is the total number of species, n_{Ai} and n_{Bi} are the number of individuals of the i th species respectively belonging to two layers (layer A, layer B), and N_A and N_B are respectively the number of total individuals in the two layers. 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. species composition is completely the same between the layers, and is 0.0 when no common species is found between them.

3. Overlapping in Spatial Distributions of Trees

On the basis of the concept of mean crowding proposed by [25]; [26] derived the ω -index for analyzing of spatial association between species. The ω -index was applied as its version to a measure of the degree of overlapping in spatial distributions of trees between layers:

$$\left. \begin{aligned} \omega_{(+)} &= \frac{\sqrt{m_{AB}^* m_{BA}^*} - \sqrt{m_A m_B}}{\sqrt{(m_A + 1)(m_B + 1)} - \sqrt{m_A m_B}} \\ \text{for } m_{AB}^* m_{BA}^* &\geq m_A m_B \\ \omega_{(-)} &= \sqrt{\frac{m_{AB}^* m_{BA}^*}{m_A m_B} - 1} \\ \text{for } m_{AB}^* m_{BA}^* &\leq m_A m_B \end{aligned} \right\} \quad (6)$$

In Eq. (6), m_{AB}^* , quadrat-based mean crowding on layer A by layer B, is defined as:

$$m_{AB}^* = \frac{\sum_{j=1}^Q n_{Aj} n_{Bj}}{\sum_{j=1}^Q n_{Aj}}$$

where Q is the total number of quadrat existed in layer A and layer B, and n_{Aj} and n_{Bj} are the number of individuals belonging to the j th quadrat in layer A and layer B,

respectively. Similarly, m_{BA}^* , quadrat-based mean crowding on layer B by layer A, is defined as:

$$m_{BA}^* = \frac{\sum_{j=1}^Q n_{Aj} n_{Bj}}{\sum_{j=1}^Q n_{Bj}}$$

The interlayer quadrat-based mean crowding indicates the mean number of individuals of the other layer per individual of

the subject layer per quadrat. On the other hand, m_A^* , quadrat-based mean crowding within layer A, is defined as:

$$m_A^* = \frac{\sum_{j=1}^Q n_{Aj} (n_{Aj} - 1)}{\sum_{j=1}^Q n_{Aj}}$$

Similarly, m_B^* , quadrat-based mean crowding within layer B, is defined as:

$$m_B^* = \frac{\sum_{j=1}^Q n_{Bj} (n_{Bj} - 1)}{\sum_{j=1}^Q n_{Bj}}$$

The intralayer quadrat-based mean crowding indicates the mean number of the other individuals per individual of the

subject layer per quadrat. The symbol $m_A (= \sum_{j=1}^Q n_{Aj} / Q)$

and $m_B (= \sum_{j=1}^Q n_{Bj} / Q)$ stand for the mean density per quadrat in layer A and layer B, respectively. 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.

4. Species Diversity

The following two indices of Shannon's index ([27]) H' and Pielou's index ([28]) J' were used to measure woody species diversity or equitability (evenness):

$$H' = -\sum_{i=1}^s \frac{n_i}{N} \log_2 \frac{n_i}{N} \quad (7)$$

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

where n_i is the number of individuals of the i th species and N is the total number of individuals.

III. RESULTS AND DISCUSSION

A. Canopy Multi-Layering Structure

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 property of Eq. (1), i.e. Type I of the C-D curve tribe that contains eight types ([29]), whereas the third phase has the property of Eq. (2), i.e. a power function. As a result, it was confirmed that the forest consists of four layers. Fig. 1c shows that the extrema, represented by arrows, apparently emerged in the $S_2 - \ln w$ relationship. Their critical numbers, i.e. tree weights at boundaries between layers, were estimated to be 1640, 63.9 and 0.188 $\text{cm}^2 \text{m}$. Reference [10] found out that the number of layers distinguished by the M - w diagram increases along a latitudinal thermal gradient from unity in northern conifer forests to four in tropical rain forests. Reference [4] revealed using the M - w diagram that a subtropical evergreen broadleaf forest grown in silicate habitat near the present forest also consists of four layers.

Fig. 2 shows the relationship between tree height H and weight w (cf. [30]), which was formulated as:

$$\frac{1}{H} = \frac{1}{1.13w^{0.415}} + \frac{1}{11.52} \quad (9)$$

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 heights of boundaries were determined as 7.83, 4.10 and 0.53 m by substituting the critical numbers 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 $0.0 \leq H \leq 0.53$ m for the bottom layer.

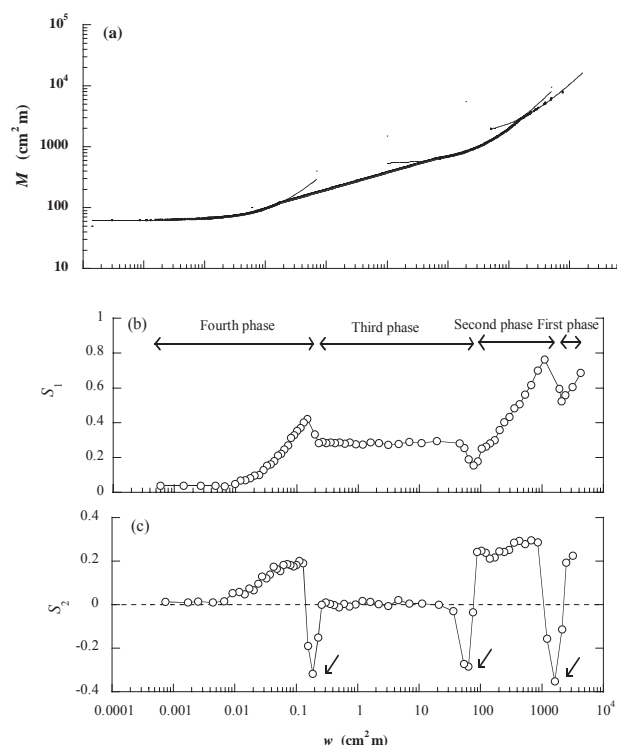


Fig. 1 Relationships of (a) mean tree weight M (b) the first derivative S_1 and (c) the second derivative S_2 to tree weight w on logarithmic coordinates. In the M - w diagram (a), the regression curves for the top, second and bottom layers are given by Eq. (1), where $A = 0.903$ and $B = 1492 \text{ cm}^2 \text{m}$ ($R^2 = 0.99$) for the top layer; $A = 1.49$ and $B = 524 \text{ cm}^2 \text{m}$ ($R^2 = 0.98$) for the second layer; $A = 332$ and $B = 61.5 \text{ cm}^2 \text{m}$ ($R^2 = 0.97$) for the bottom layer. The regression curve for the third layer is given by Eq. (2), where $C = 192 \text{ cm}^{2-b} \text{m}^{1-b}$ and $b = 0.284$ ($R^2 = 0.92$)

B. Species Similarity among the Layers

As far as the species composition among the layers concerns on the basis of the similarity index C_{Π} (Fig. 3), the forest is classified into three groups. The first group consists of the third and the bottom layers, the second group the third, bottom and the second layers, and the third group the top and the lower three layers. Among these groups, the first group showed the highest similarity in species composition with a C_{Π} -value of 0.82. The next highest similarity was in the second group with a C_{Π} -value of 0.58, indicating that species composition was

nearly the same. The lowest C_{II} -value of 0.13 was found in the third group, indicating that a few species were similar between the layers.

Species composition was almost the same between the third and the bottom layers because of the similar characteristics of the species of these lower layers, i.e. the species are mainly shade-tolerant, occupying the lower canopy layers. A few species (10% of the total species), which have a nature of facultative shade species, can grow from the bottom to the upper layers. However, the similarity in species composition in the third group was almost exclusive, i.e. different species composition, because the top layer may consist of sun and facultative shade species, whereas the lower layers may consist of shade and facultative shade species. In addition, *Rhus succedanea* L. had the highest number in the upper layers, whereas it had no saplings and seedlings in the lower layers. This result indicates the nature of shade-intolerance for *R. succedanea*, i.e. early successional species (pioneer species), and also indicates a sign of extinction. Thus, this forest is likely to be in compositional unequilibrium.

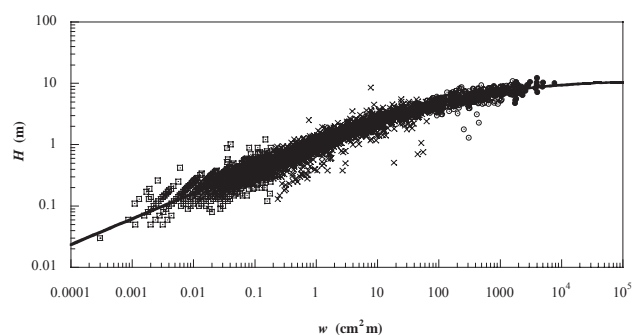


Fig. 2 Relationship between tree height H and weight w . The regression curve is given by Eq. (9), where $R^2 = 0.95$. Filled circles, top layer ($7.83 < H \leq 12.3$ m); open circles, second layer ($4.10 < H \leq 7.83$ m); crosses, third layer ($0.53 < H \leq 4.10$ m); open squares, bottom layer ($0.00 < H \leq 0.53$ m)

C. Overlapping in Spatial Distributions of Trees among the Layers

A dendrogram of the degree of overlapping in spatial distributions of trees among the layers is shown in Fig. 4. It shows that the ω -index between the third layer and the bottom layer was 0.38, indicating that the spatial distributions of trees were overlapped between the two layers. The ω -index between the second layer, and the third and bottom layer was 0.17, indicating that the spatial distributions of trees were nearly independent between the layers. However, the spatial distributions of the top layer and the lower three layers were independent or slightly exclusive with a value of -0.06 . Thus, sufficient light would penetrate into the lower layers, where trees can catch light necessary to photosynthesize.

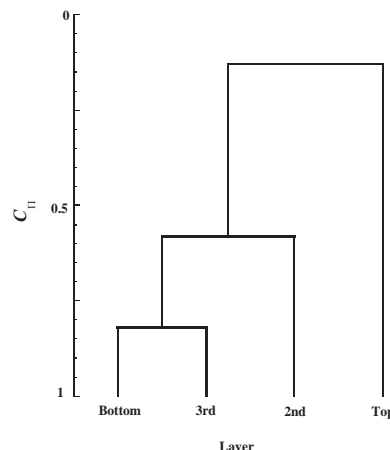


Fig. 3 Dendrogram of the degree of similarity C_{II} in species composition among layers

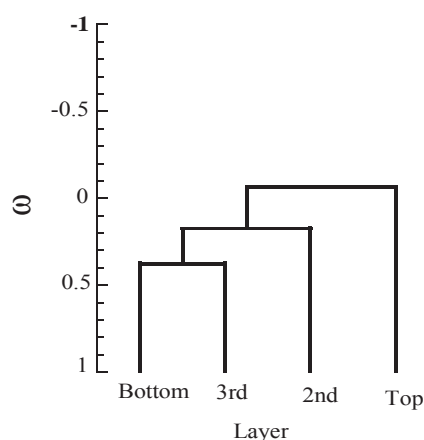


Fig. 4 Dendrogram of the degree of overlapping ω in the spatial distributions of trees among layers

D. Woody Species Diversity and Evenness in the Stratified Forest Stand

Fig. 5 shows that the values of H' and J' (evenness) tended to increase from the bottom layer upward, except for H' -value of the top layer. The highest value of H' occurred in the second layer, though species richness (44) and evenness were the second highest. The lowest value of H' was in the top layer. This is ascribed to quite low species richness (11) as compared with those in other layers. 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.

In the present forest, the values of H' and J' for $H > 1.3$ m and $DBH \geq 4.5$ cm were higher than values of H' and J' for the total stand, though the species richness was low for $H > 1.3$ m and $DBH \geq 4.5$ cm (Table I). This may be caused by a high evenness for large trees in the upper layers. This trend of increasing diversity with increasing layer height becomes much clear in Fig. 5, where the values of H' and J' increased upward. In the subtropical evergreen broadleaf forest in silicate area in Okinawa Island, however, the values of diversity

indices H' and J' increased downward, indicating that the high-species diversity depends on small trees in the lower layers ([4]). In the present forest, it is undoubted that the high woody species diversity depends on large trees in the upper layers, especially in the second layer. Thus, an increase of woody species diversity with an increase of layer height may be a characteristic of young-aged subtropical forests in limestone habitats in the northern part of Okinawa Island.

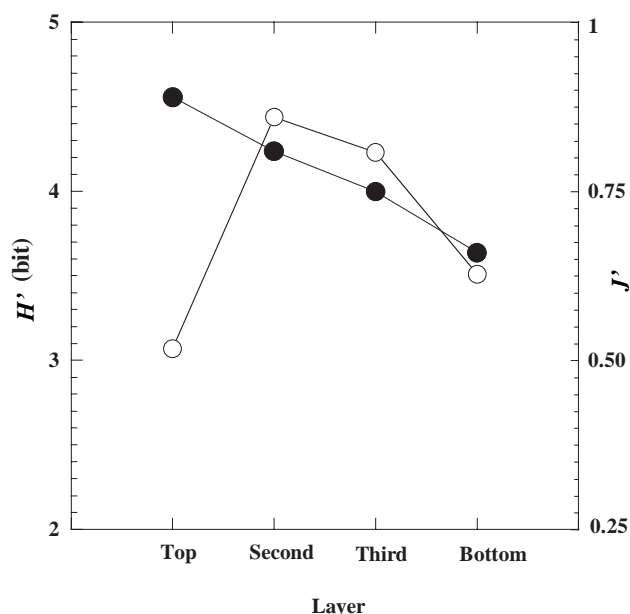


Fig. 5 Relationships of Shannon's index H' and Pielou's index J' to layer. Open circle, H' ; filled circle, J' . The number of species is 11 for the top, 44 for the second, 53 for the third and 41 for the bottom layers

E. Mean Tree Weight and Density among the Layers

As shown in Fig. 6, mean tree weight \bar{w}_i of the i th 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 i th layer. This trend was well expressed in the form ([4]):

$$\bar{w}_i = K\rho_i^{-\alpha} \left(1 - \frac{\rho_i}{\rho_0} \right) \quad (10)$$

where the values of coefficients K , α and ρ_0 were 86697 $\text{cm}^2 \text{m ha}^{-\alpha}$, 0.599 and 22327 ha^{-1} , respectively. This relationship is analogous to the process of self-thinning plant populations ([31]). This relationship in the present forest was the same trend as that in the subtropical evergreen broadleaf forest in silicate area ([4]). This may be a general phenomenon for subtropical forests.

TABLE I
COMPARISON IN SPECIES DIVERSITY AND EVENNESS BETWEEN DIFFERENT TREE SIZES

Stand age	No. of trees	No. of species	H' (bit)	J'
Total stand	47980	62	4.21	0.73
$H > 1.3 \text{ m}$	16730	58	4.82	0.82
$\text{DBH} \geq 4.5 \text{ cm}$	3330	40	4.35	0.82

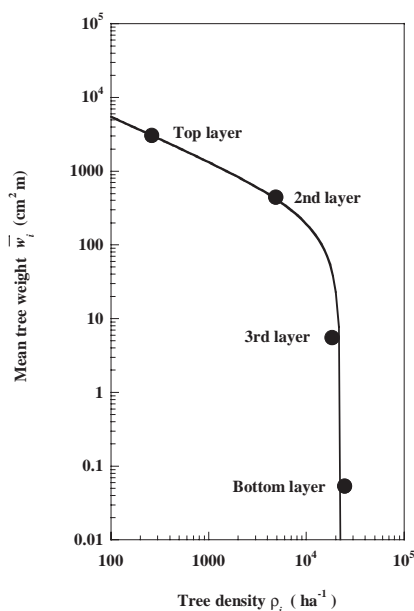


Fig. 6 Relationship between mean tree weight \bar{w}_i and tree density ρ_i . The curve is given by Eq. (10), where $R^2 \cong 1.0$

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