Litterfall of a subtropical evergreen broad-leaved forest in Okinawa island, Japan

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ABSTRACT The seasonal patterns of litterfalls, such as leaves, woody organs, reproductive parts, insect bodies, and feces, were investigated monthly for three years from January 1999 to December 2001 in a subtropical evergreen broad-leaved forest in the northern part of Okinawa Island, Japan. The total annual litterfall was estimated at 6.66-8.28 Mg ha^{-1} yr^{-1}. The litterfall was mainly composed of leaves (52.4-54.8% of the total litterfall), about half of which were from *Castanopsis Sieboldii*. The species composition of leaf litter was almost consistently the same every month for a year. The leaf litter was separated into two groups: one group, which had a high proportion of the total leaf litter, included *C. Sieboldii, Schima Wallichii, Elaeocarpus japonicus,* and *Cinnamomum Doederleinii*; the other group included the other 44 species. The species diversity indexes of leaf litter *H*' and *J*' showed their minimum values in March, when the leaf litter reached its maximum. There was no significant difference in species rank among years in terms of the annual amount of leaf litter. The mean leaf litter per tree of a given species was significantly proportional to its corresponding basal area, regardless of species and year. The degree of overlap in the seasonal patterns of litterfall components showed that leaves, insect bodies, and reproductive parts are nearly overlapped, but woody organs and feces are more or less exclusive to the other three components. Although the seasonal patterns in leaf litter of *C. Sieboldii, S. Wallichii,* and *E. japonicus* were nearly overlapped, the seasonal pattern in leaf litter of *C. Doederleinii* was almost independent of those of the other three species.

Key words: *Castanopsis Sieboldii*, leaf litter, species diversity, species rank, subtropical evergreen broad-leaved forest

INTRODUCTION

Litter is an essential aspect for understanding nutrient cycling, energy flow, and primary production in forest ecosystems (Kira and Shidei, 1967; Jarvis and Leverenz, 1983; Cannell, 1989; Perry, 1994). Since the litter is considered to be the dominant pathway joining the living biological components to the decomposing organic matter, litterfall production has been widely studied (e.g. Bray and Gorham, 1964; Saito, 1977; Proctor *et al.,* 1983; Vitousek, 1984).

Subtropical evergreen broad-leaved forests develop under sufficiently moist climates on the Western Pacific coasts because the dry climates of the middle latitudes do not encroach. The chain of islands from Okinawa to Taiwan is within the subtropical zone, where the climate is sufficiently moist enough to allow the development of genuine rain forests (Kira, 1991). In the northern part of Okinawa Island, there is a subtropical evergreen broad-leaved forest, which is characterized by high woody species diversity (Itô, 1997) and low productivity (Kawanabe, 1977). In the forests, some short-term litterfall studies have been conducted using a small number of traps (Tokuyama *et al.,* 1996; 1997; 1999; Xu *et al.,* 1998).

Climates which have high precipitation and strong winds potentially cause a high degree of variation in annual litterfall. Although the forests have a high diversity of woody species, the seasonal changes of leaf litter, which constitutes a large amount of litterfall (Tokuyama *et al.,* 1996; 1997; 1999; Xu *et al.,* 1998), are not related to species composition and species diversity. There are also no reports that the interrelationships among litterfall components, such as leaves, woody organs, reproductive parts, insect bodies, and feces have been considered. Therefore, it is still necessary for more detailed data at monthly intervals to be taken in order to further elucidate litter production in subtropical evergreen broad-leaved forests on Okinawa Island.

The objectives of this study were to (a) observe the seasonal and annual changes and the amount of each litterfall components, such as leaves (for each species), woody organs, reproductive parts, insect bodies, and feces, (b) know the degree of overlap in the species composition of leaf litter between the same months for different years and among months in a year, (c) observe the seasonal pattern of the species diversity of leaf litter, (d) determine the species rank for leaf litter amount, (e) examine the relationship between the mean leaf litter per tree of a given species and its corresponding basal area, and (f) know the degree of overlap in the seasonal amount among litterfall components and among leaf litters of dominant species.

MATERIALS AND METHODS

Area description

This study was carried out in the Subtropical Field Science Center at Yona, University of the Ryukyus, located in the northern part of Okinawa Island at 26°45′30″N and 128°05′E. The slope, altitude, and direction of the plot were 24.5°, 250 m above sea level, and NWW, respectively. The pH of the soil resulting from silicate rock was 4.35.

The warmth index was 213.5°C mo. during the study period from 1999 to 2001 (Meteorological Station in Nago City, the northern part of Okinawa Island), indicating that this area belongs to the subtropical region. The highest temperatures were from June to September (summer season) and the precipitation was highest in May to June (rainy season) and in July to September (typhoon season). The mean annual precipitation was recorded to be 2401 mm. Strong typhoon winds were prevalent during the summer season.

As shown in Table 1, the sample plot area is covered with well-developed evergreen broad-leaved species, such as *Castanopsis Sieboldii* (Makino) Hatusima, *Schima Wallichii* (DC.) Korthals, *Distylium racemosum* Sieb. et Zucc., and so forth. Maximum DBH and height in 2001 were 52.8 cm (*C. Sieboldii*) and 16.5 m (*S. Wallichii*), respectively. Density, species diversity indexes H' and J', and mean DBH of trees, whose height H is more than 1.3 m, were 16644 ha^{-1}, 4.52 bit and 0.78, and 3.3 ± 0.1 (SE) cm, respectively (for trees having DBH ≥ 4.5 cm, density and mean DBH were 2694 ha^{-1} and 13.0 ± 0.4 (SE) cm, respectively). Stand basal area (for trees having H > 1.3 m) was 47.9 m^2 ha^{-1} in 1999, 50.3 m^2 ha^{-1} in 2000, and 51.3 m^2 ha^{-1} in 2001.

Table 1. Top ten species in order of importance value (IV) in the study plot in 2001

Rank	Species Name	Maximum DBH (cm)	Maximum H (m)	RD	RC	RF	IV
1	*Castanopsis Sieboldii* (Makino) Hatusima	52.8	16.2	17.20	61.24	3.40	81.84
2	*Schima Wallichii* (DC.) Korthals	33.0	16.5	1.95	19.13	2.76	23.84
3	*Distylium racemosum* Sieb. et Zucc.	6.9	9.8	8.86	1.22	3.18	13.26
4	*Elaeocarpus japonicus* Sieb. et Zucc.	16.6	13.0	5.18	4.47	3.40	13.05
5	*Syzygium buxifolium* Hook. et Arn.	7.4	6.6	7.51	0.69	3.40	11.60
9	*Antidesma japonicum* Sieb. et Zucc.	2.3	2.1	7.21	0.14	3.40	10.75
7	*Ardisia quinquegona* Blume	2.6	2.1	7.25	0.26	3.18	10.69
8	*Myrsine Seguinii* Lév.	6.5	9.1	4.84	0.64	3.40	8.88
9	*Randia canthioides* Champ. ex Benth.	5.0	6.3	4.39	0.28	3.40	8.07
10	*Tricalysia dubia* (Lindl.) Ohwi	5.1	6.3	3.12	0.36	0.36	6.66

The RD, RC, RF, and IV are relative density, relative coverage, relative frequency, and importance value, respectively (tree height H>1.3 m). $IV=RD+RC+RF$ or $IV=\left(\frac{n_j}{\sum_j n_j}\times 100\right)+\left(\frac{ba_j}{\sum_j ba_j}\times 100\right)+\left(\frac{f_j}{\sum_j f_j}\times 100\right)$, where n_j is the number of individuals of the jth species, ba_j is the basal area of the jth species, and f_j is the number of quadrats in which the jth species appeared.

Litterfall measurement

The sample plot (40 m x 40 m) was divided into 16 subplots (10 m x 10 m) in mid-December 1998. Litterfall was measured using 16 litter traps that were placed uniformly in each subplot. These traps had a circular opening of 1.0 m in diameter. The traps consisted of a sheet of nylon attached to a plastic hoop. The hoop was positioned approximately 1.2 m above the ground with plastic pipes firmly driven into the ground to hold the traps. The mesh size of the nylon was 1.0 mm x 1.0 mm.

Contents of the traps were collected monthly from January 1999 to December 2001. The materials collected were immediately transported to the laboratory and sorted into categories; leaves, woody organs (barks, branches, and stems), reproductive parts, insect bodies, feces, and miscellaneous fractions (fine plant fragments). In addition, the leaf litter was separated again by species. All the sorted materials were oven-dried at 85°C for 24 h, stored in desiccators until a constant weight was achieved, and weighed.

Tree census

Diameter at breast height (DBH) of all trees at a height of 1.3 m above the ground was measured using measuring tapes (for trees with DBH $\geq$ 4.5 cm) and calipers (for trees with DBH < 4.5 cm) in May 1999, 2000, and 2001. Then, the basal area and the number of trees for each species were calculated.

Statistical analysis

The significance among means was analyzed by ANOVA. Fisher's test was conducted for the comparison of seasonal changes in litterfalls among years. For the significance of regression coefficient and simple correlation coefficient the *t*-test was used. For rank correlation coefficient (r_S) in species for leaf litter amount, Spearman's test was performed.

Measure of overlap

To measure overlap, the following indexes: γ and ω (Iwao, 1977) were used.

$$\gamma = \sqrt{\frac{\overset{*}{c}_{XY}\,\overset{*}{c}_{YX}}{\overset{*}{c}_{X}\,\overset{*}{c}_{Y}}}$$

where $\overset{*}{c}_{XY}\left(= \frac{\sum_j x_j y_j}{\sum_j x_j}\right.$, where x_j and y_j are respectively the amounts of the jth class of items X and Y$\left.\right)$

is the mean concentration on item X by item Y or *vise versa* and $\overset{*}{c}_{X}\left(= \frac{\sum_j x_j^2}{\sum_j x_j}\right)$ is the mean concentration of item X. The γ -value becomes 1.0 when items X and Y are completely overlapped and 0 when both are completely exclusive with each other.

$$\omega(+) = \frac{\sqrt{\overset{*}{c}_{XY}\,\overset{*}{c}_{YX}} - \sqrt{m_X m_Y}}{\sqrt{\overset{*}{c}_{X}\,\overset{*}{c}_{Y}} - \sqrt{m_X m_Y}} \quad \text{for } \overset{*}{c}_{XY}\,\overset{*}{c}_{YX} \geq m_X m_Y$$

$$\omega(-) = \sqrt{\frac{\overset{*}{c}_{XY}\,\overset{*}{c}_{YX}}{m_X m_Y}} - 1 \quad \text{for } \overset{*}{c}_{XY}\,\overset{*}{c}_{YX} \leq m_X m_Y$$

where m_X is the mean of item X. The ω-value changes from +1 for complete overlapping, through 0 for independent occurrence, to -1 for complete exclusion.

***M-w* diagram**

The order of the annual amount of leaf litter per species was analyzed by utilizing the *M-w* diagram (Hozumi, 1975). The amount of leaf litter per species w (kg ha^{-1} yr^{-1}) was arranged in order of weight. The mean value M (kg ha^{-1} yr^{-1}) of the annual amount of leaf litter per species from the first order to a given order was calculated. Then, the values of M were plotted against the corresponding values of w on logarithmic coordinates.

Species diversity index

The following two non-parametric indexes were used.

(1) Shannon-Wiener's function H' (MacArthur, 1955).

$$H' = -\sum_j \frac{l_j}{L} \log_2 \frac{l_j}{L}$$

where l_j is the amount of leaf litter of the jth species and L is the total amount of leaf litter.

(2) Equitability index J' (Pielou, 1966).

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

The S is the total number of species in leaf litter.

RESULTS AND DISCUSSION

Leaf litter

Figure 1 shows the seasonal change in leaf litter from 1999 to 2001. Within the three years, the seasonal trend of leaf litter showed a similar trend every year ($P > 0.05$), in which there were two peaks. The first peak, which took place in spring (March), was associated with a leaf-shedding period, and another small peak in summer and autumn (August to October) was attributed to a defoliating period.

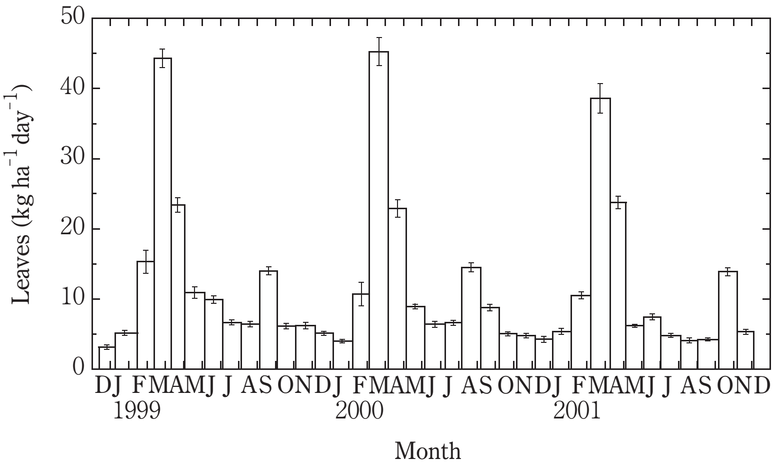

Fig. 1. Monthly change in leaf litter, from January 1999 to December 2001. Values are represented with mean ± SE (n = 16).

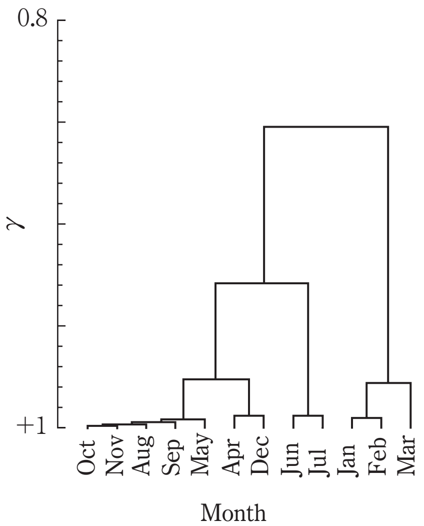

Fig. 2. An example of the dendrogram of the degree of overlap γ in species composition of leaf litter among months within a year (the second year).

Figure 2 shows the dendrogram of the degree of overlap γ in the species composition of leaf litter among months in the second year. In general, the degree of overlap was very high among months, having a minimum value of 0.85. In May and from August to November, the index was ca. +1, indicating that the species composition of leaf litter was completely overlapped among months. From January to March, the degree of overlap was relatively low indicating that the species composition tended to be exclusive to the other months. The value of the index was especially high between neighboring months, such as June and July, and January and February. In addition, the γ-value between the same months for the second and the third year showed tremendously high values, ranging from 0.93 (March) to 0.99 (May), indicating that each species showed consistently the same seasonal pattern of its leaf litter every year.

M-w diagram The diagram was characterized by two segments, as shown in Fig. 3. Each segment can be approximated by the following equation:

$$M = A \cdot w + B \quad (1)$$

where A and B are coefficients. The first segment was fulfilled by four tree species, *C. Sieboldii, S. Wallichii, Elaeocarpus japonicus* Sieb. et Zucc., and *Cinnamomum Doederleinii* Engler, and the second segment was formed by 44 species of plants, which consisted of 36 tree species, six vines, one fern, and one bamboo. The same relationships of M to w were found in each year. Therefore, it may be concluded that on the basis of the annual leaf litter per species there are two groups: one group consisting of *C. Sieboldii, S. Wallichii, E. japonicus,* and *C. Doederleinii,* whose total amount accounted for 90% of the total leaf litter; and another group consisting of the other 44 species, whose total amount was very small.

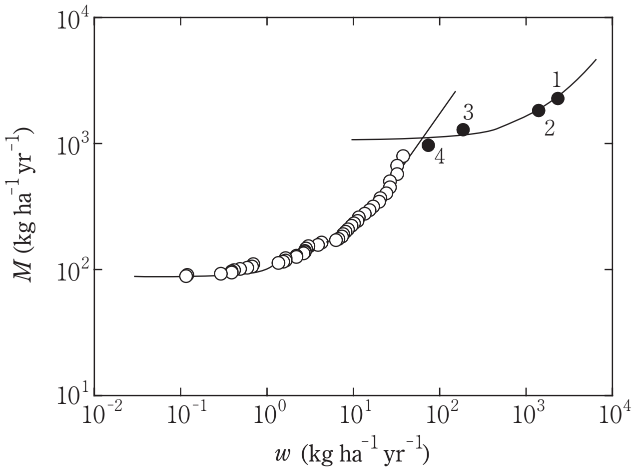

Fig. 3. An example of the relationship between mean leaf litter M and leaf litter of each species w (the first year). Symbols ● and ○ are the first and the second groups, respectively. Numerals 1, 2, 3, and 4 are *Castanopsis Sieboldii, Schima Wallichii, Elaeocarpus japonicus,* and *Cinnamomum Doederleinii,* respectively. The coefficients of Eq. (1) are A = 0.542 and B = 1068 kg ha^{-1} yr^{-1} (r^2 = 0.970) for the first group and A = 15.9 and B = 86.0 kg ha^{-1} yr^{-1} (r^2 = 0.971) for the second group.

Diversity index Figure 4 shows the seasonal trends in the species diversity indexes H' and J' of leaf litter. The seasonal trends of H' and J' have nearly identical patterns. The values of H' and J' ranged from 1.41 to 3.01 bit and 0.28 to 0.57, respectively. It shows that H' and J' values, in the first year, decreased sharply from December to March, increased until May, and reached a more or less constant value which was maintained until December. The H' and J' trends in the second year were similar to those in the third year, showing that the minimum value was reached in March when the amount of leaf litter was highest and the maximum in May when the amount of leaf litter sharply decreased. The diversity indexes H' and J' negatively correlated with the percentage of *C. Sieboldii's* leaf litter to the total leaf litter ($P < 0.05$), indicating that the ratio affects the values of H' and J' indexes. The diversity indexes were lowest when the ratio was highest, which means the decline of equitability for the species composition of leaf litter in March.

Rank correlation The rank correlation of leaf litter per species is shown in Fig. 5. The four dominant species, *C. Sieboldii, S. Wallichii, E. japonicus,* and *C. Doederleinii,* had exactly the same rank all three years. About 80% of the total species were placed within the difference of ±4 in rank. It may be concluded from a high value of the rank correlation coefficient (r_S = 0.988) that the rank of the leaf litter was more or less stable over the years.

Litterfall of non-photosynthetic organs

Figure 6 shows the seasonal changes in litter components. In the first year (1999), the litterfall of woody organs showed four

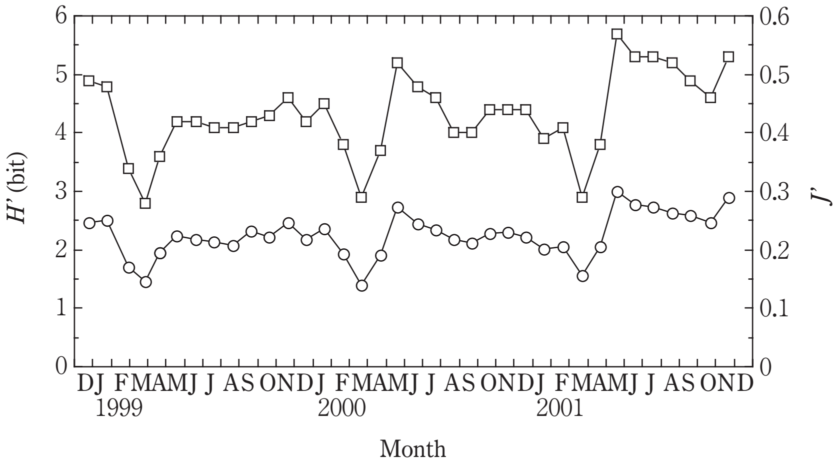

Fig. 4. Monthly trends in species diversity indexes *H'*(○) and *J'*(□).

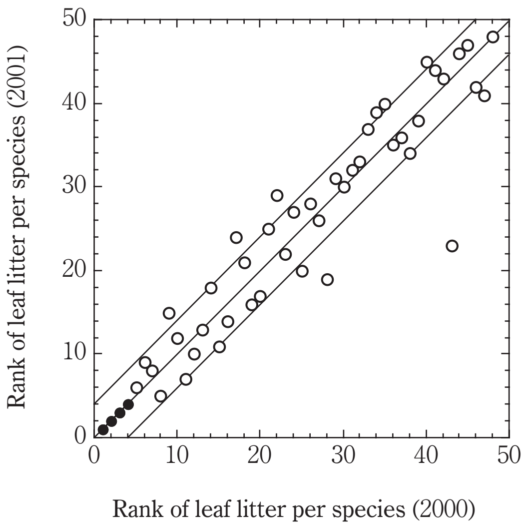

Fig. 5. An example of the rank correlation of the annual leaf litter per species between the second year (2000) and the third year (2001) (r_s = 0.948, P < 0.01). Symbols ● and ○ are the four dominant species (*C. Sieboldii, S. Wallichii, E. japonicus,* and *C. Doederleinii*) and the other species, respectively.

extreme peaks in January, May, July, and September (Fig. 6a). In the second year (2000), the litterfall was negligible from January to July, increased rapidly to form a peak in August, decreased swiftly in October, and again was negligible in both November and December. In the third year (2001), there were a small peak in May and a large peak in October. However, no significant difference was recognized in seasonal change among the years ($P > 0.05$). The different peaks of the woody organs in every year coincided with dead and living branches dropped by strong winds. During this study, strong winds were recorded to be 28.8 m s^{-1} in September 1999, 25.2 m s^{-1} in August 2000, and 22.5 m s^{-1} in October 2001. Within the litterfall components, only the woody organs were significantly correlated with the strong winds ($r = 0.622$, $P < 0.05$ in 1999; $r = 0.930$, $P < 0.01$ in 2001). Xu *et al.* (1998) and Tokuyama *et al.* (1996; 1997; 1999) also reported that strong winds influenced the intensity of branch fall.

The fall of reproductive parts, including seeds, flowers, buds, and fruits, was usually high in March for all three years (Fig. 6b) with the exception of the second year that had three peaks in March, June, and October. There was no significant difference in seasonal change between the first and the second years ($P > 0.05$), but there was a significant difference in seasonal change between the second and the third year ($P < 0.01$). A high contribution to these components was fruit and seed fall from both *C. Sieboldii and S. Wallichii*.

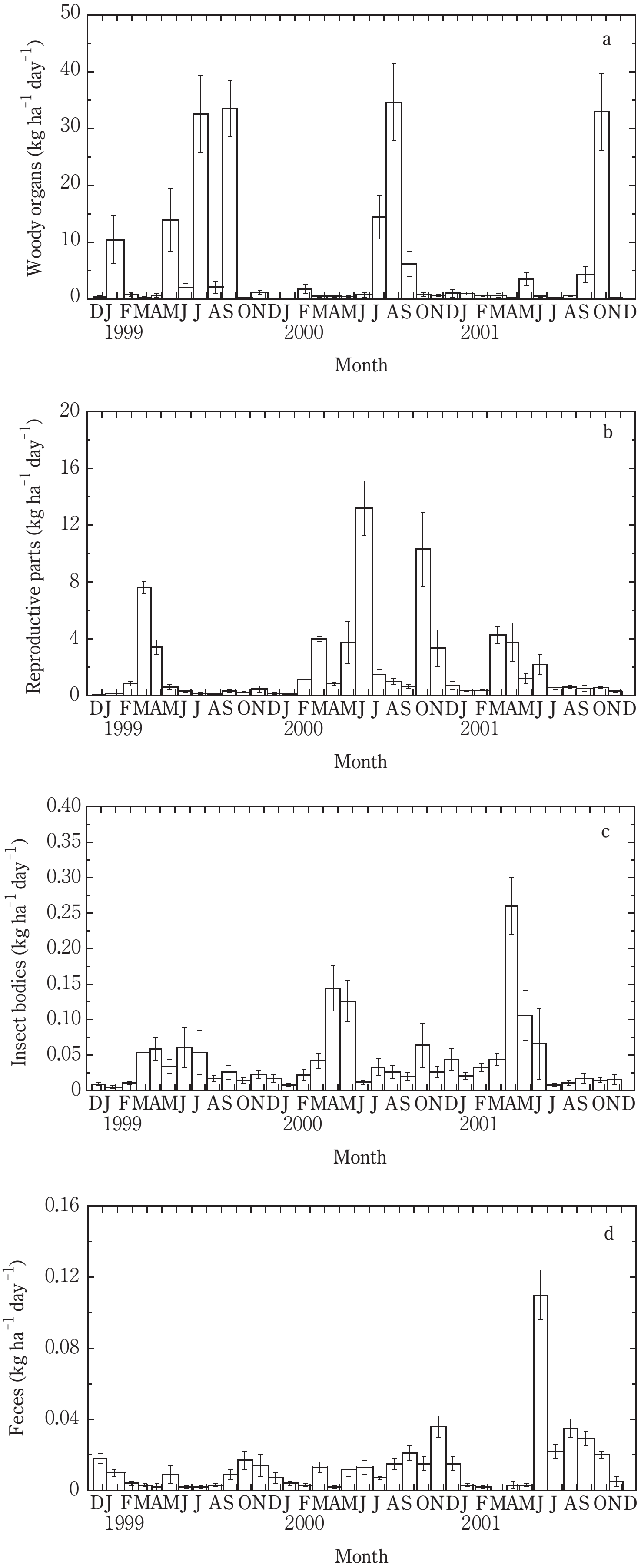

Fig. 6. Monthly changes in litterfall of woody organs (a), reproductive parts (b), insect bodies (c), and feces (d), from January 1999 to December 2001. Values are represented with mean ± SE (*n* = 16).

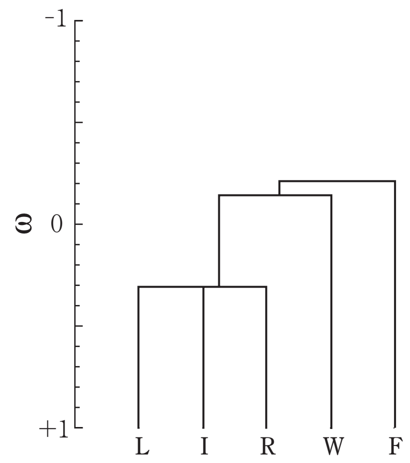

Fig. 7. Dendrogram of the degree of overlap ω in seasonal pattern among litterfall components over the three years. Symbols L, I, R, W, and F are leaves, insect bodies, reproductive parts, woody organs, and feces, respectively.

The fall of insect bodies increased gradually in February, formed a peak in April, indicating the high activity of insects, and then decreased to small values from summer to winter (Fig. 6c). The fall of feces exhibited an irregular trend and a short-term fluctuation over the three years, though a tremendous peak was found in June 2001 (Fig. 6d). There were no significant differences in both the seasonal changes of insect bodies and feces over the three years ($P > 0.05$).

A dendrogram of the degree of overlap, ω, in the seasonal patterns of litterfall components over the three years is shown in Fig. 7. It illustrates that the seasonal patterns of leaves, insect bodies, and reproductive parts were nearly overlapped. The seasonal changes of leaves, insect bodies, and reproductive parts to that of woody organs, and the seasonal changes of leaves, insect bodies, reproductive parts, and woody organs to that of feces were more or less exclusive. It can be concluded that the seasonal patterns of leaves, insect bodies, and reproductive parts are different than those of woody organs and feces.

Annual amount of litterfall

The total annual litterfall was calculated to be 8.28 ± 0.52 (SE), 8.34 ± 0.39 (SE), and 6.66 ± 0.29 (SE) Mg ha^{-1} yr^{-1} for the first, second, and third year, respectively (Table 2). The leaf litter accounted for the greatest amount ranging from 3.89 ± 0.14 (SE) (58.4%) to 4.39 ± 0.12 (SE) Mg ha^{-1} yr^{-1} (52.6% of the total litterfall) over the three years. The woody organs, including branches, twigs, and barks, were 1.43 ± 0.24 (SE) (21.5%) to 3.04 ± 0.52 (SE) Mg ha^{-1} yr^{-1} (36.7% of the total litterfall) and the reproductive parts accounted for 0.39 ± 0.03 (SE) (4.71%) to 1.23 ± 0.20 (SE) Mg ha^{-1} yr^{-1} (14.7% of the total litterfall). Although the total litterfall amount was significantly different between the second and the third year ($P < 0.01$), there were no significant differences between the first and the second year ($P > 0.05$) and between the first and the third year ($P > 0.01$).

Table 2. Annual fall of each component collected from January 1999 to December 2001

Components	Litterfall						Mean	
	1999		2000		2001			
	Mg ha^{-1} yr^{-1}	%	Mg ha^{-1} yr^{-1}	%	Mg ha^{-1} yr^{-1}	%	Mg ha^{-1} yr^{-1}	%
Leaves	4.34 ± 0.14 A, a	52.4	4.39 ± 0.12 A, a	52.6	3.89 ± 0.14 a	58.4	4.21	54.2
Woody organs	3.04 ± 0.52 A	36.7	1.86 ± 0.27 A, B	22.3	1.43 ± 0.24 B	21.5	2.11	27.2
Reproductive parts	0.39 ± 0.03 A	4.71	1.23 ± 0.20	14.7	0.46 ± 0.06 A	6.91	0.69	8.92
Insect bodies	0.011 ± 0.002 a	0.13	0.016 ± 0.001 A, a	0.22	0.018 ± 0.002 A, a	0.27	0.015	0.19
Feces	0.0029 ± 0.0006 A	0.04	0.0045 ± 0.0004 A	0.08	0.0074 ± 0.0007	0.12	0.0049	0.06
Miscellaneous litter	0.50 ± 0.04	6.02	0.84 ± 0.04 A	10.1	0.85 ± 0.06 A	12.8	0.73	9.43
Total	8.28 ± 0.52 A, a	100	8.34 ± 0.39 A	100	6.66 ± 0.29 a	100	7.76	100

Values are represented with mean ± SE (n=16). Values with the same letter in a row are not significantly different; A, B ($P > 0.05$) and a ($P > 0.01$).

Relationship between leaf litter and basal area

Figure 8 shows the relationship between the mean leaf litter per tree of a given species l (g yr^{-1}) and the corresponding basal area ba (dm^2). The l proportionally increased with increasing ba. The relationship can be expressed in the form, regardless of species and year:

$$l = k \cdot ba \qquad (2)$$

where the proportional constant k was 852 ± 65 (SE) g dm^{-2} yr^{-1}. There was no significant difference between 1.0 and the regression coefficient (= 0.962) for the regression of log l on log ba ($P > 0.05$). A similar relationship between the variables l

and *ba* was also found for evergreen and deciduous trees, but the relationship was not proportional (Sumida, 1991). The annual amount of leaf litter in the forest was tentatively estimated using the proportional constant *k* in Eq. (2). Since the mean basal area on a stand basis over the three years was 49.8 m^2 ha^{-1}, the annual amount of leaf litter was estimated to be 4.24 Mg ha^{-1} yr^{-1}, which was quite similar to 4.21 Mg ha^{-1} yr^{-1} of the mean value observed over the three years (Table 2).

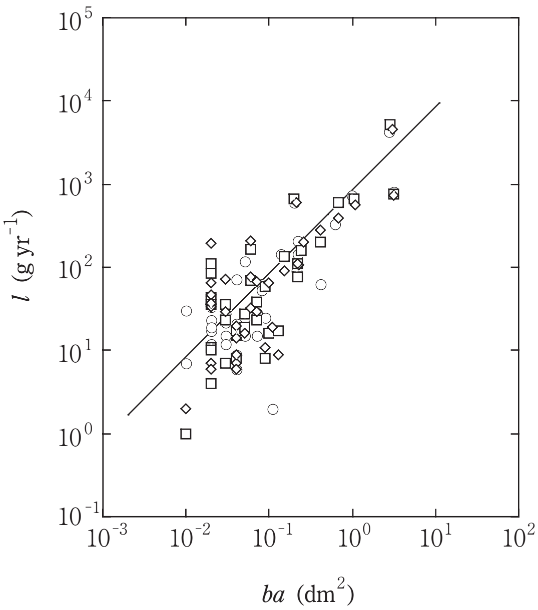

Fig. 8. Relationship between the leaf litter per tree of each species *l* and the corresponding species basal area *ba*. Symbols ○, □, and ◇ are 1999, 2000, and 2001, respectively. The straight line is based on Eq. (2) (r^2 = 0.578).

Table 3. Annual litterfall rates in several types of evergreen broad-leaved forests

Forest Types	Location	Total (Mg ha^{-1} yr^{-1})	Authors
Warm-temperate forests			
Castanopsis cuspidata	Kumamoto, Kyushu, Japan	*ca.* 3.75 - 6.13	Tadaki and Kagawa (1968)
Mixed species	Minamata, Kyushu, Japan	7.52	Kawahara (1971)
Mixed species	Minamata, Kyushu, Japan	4.37 - 6.43	Nishioka and Kirita (1978)
Subtropical forests			
Mixed species	Yona, Okinawa, Japan	5.58 - 12.70	Xu *et al.* (1998)
Mixed species	Genka, Okinawa, Japan	5.8	Tokuyama *et al.* (1996)
Mixed species	Kayou, Okinawa, Japan	10.5	Tokuyama *et al.* (1996)
Mixed species	Genka, Okinawa, Japan	4.24 - 9.51	Tokuyama *et al.* (1997)
Mixed species	Yona, Okinawa, Japan	6.66 - 8.34	Present study
Tropical forests			
Albizia falcata	Aras-asan, Philippines	10.13	Kawahara *et al.* (1981)
Gmelina arborea	Aras-asan, Philippines	7.29	Kawahara *et al.* (1981)
Dipterocarp	Aras-asan, Philippines	8.73	Kawahara *et al.* (1981)
Mixed species	Khao Chong, Thailand	23.3	Kira *et al.* (1964)
Eucalyptus camaldulensis	Somdet, Thailand	6.1-9.1	Thoranisorn *et al.* (1991)
Mixed species	West Java, Indonesia	5.96	Yamada (1976)
Mixed species	Pasoh, Malaysia	10.55	Ogawa (1978)
Dipterocarpus baudii	Kepong, Malaysia	*ca.* 9.30 - 12.80	Yamashita *et al.* (1995)
Dipterocarp	Pasoh, Malaysia	8.6	Yamashita and Takeda (1998)

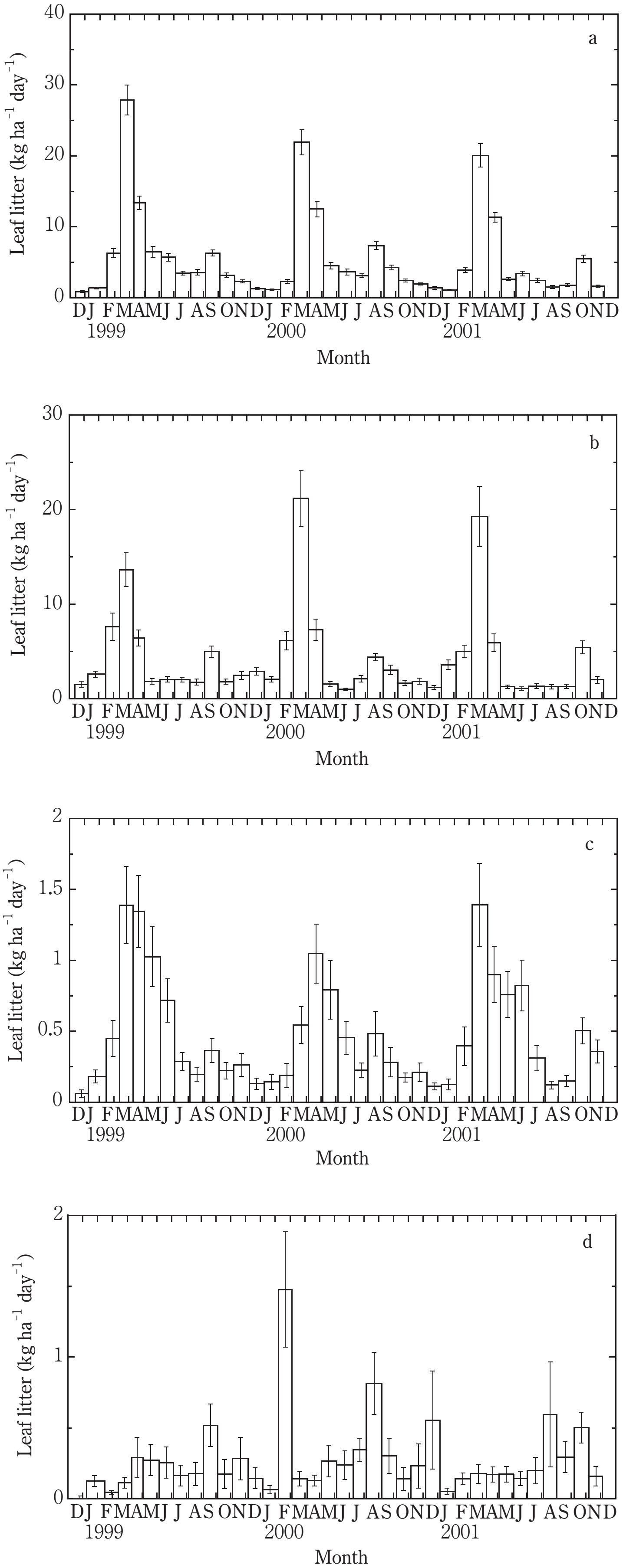

Fig. 9. Monthly changes in the leaf litter of main species, such as *C. Sieboldii* (a), *S. Wallichii* (b), *E. japonicus* (c), and *C. Doederleinii* (d), from January 1999 to December 2001. Values are represented with mean ± SE (*n* = 16).

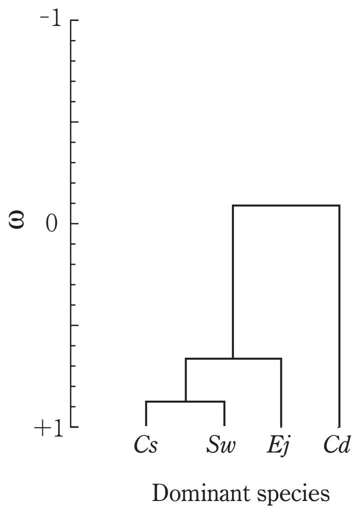

Fig. 10. Dendrogram of the degree of overlap ω in seasonal pattern among the four dominant species of leaf litter over the three years. Symbols *Cs, Sw, Ej,* and *Cd* are *C. Sieboldii, S. Wallichii, E. japonicus,* and *C. Doederleinii,* respectively.

Comparison among three types of evergreen broad-leaved forests

To compare the amount of litterfall in other forests, Table 3 summarizes several types of evergreen broad-leaved forests. The amount of litterfall ranged from 3.75 to 7.52 Mg ha^{-1} yr^{-1} in warm-temperate forests (Tadaki & Kagawa, 1968; Kawahara, 1971; Nishioka & Kirita, 1978), 4.24 to 12.70 Mg ha^{-1} yr^{-1} in subtropical forests (Tokuyama *et al.,* 1996; 1997; Xu *et al.,* 1998) and 5.96 to 23.3 Mg ha^{-1} yr^{-1} in tropical forests (Kira *et al.,* 1964; Yamada, 1976; Ogawa, 1978; Kawahara *et al.,* 1981; Thoranisorn *et al.,* 1991; Yamashita *et al.,* 1995; Yamashita and Takeda, 1998). The annual litterfall of the present study ranged from 6.66 to 8.34 Mg ha^{-1} yr^{-1}, which is considerably lower than that of tropical forests, with the exception of a montane forest (Yamada, 1976), in which the amount of litterfall was 5.96 Mg ha^{-1} yr^{-1}, and it seems to be significantly higher than those in warm-temperate forests. Our values were fairly similar to those of other subtropical evergreen broad-leaved forests, in which tree species were mainly composed of *C. Sieboldii* and *S. Wallichii* in Genka and *Rhaphiolepis indica* Lindl. var. *insularis* Hatusima, *Cinnamomum pseudo-pedunculatum* Hayata, and *Gardenia jasminoides* f. *grandiflora* Makino in Kayou (Tokuyama *et al.,* 1996); *C. Sieboldii and Distylium racemosum* in Yona (290-310 m above sea level) (Xu *et al.,* 1998). Tokuyama *et al.* (1997) also reported that the annual litterfall in Genka was 4.24 Mg ha^{-1} yr^{-1} in the lowlands (90 m above sea level), where were mainly composed of *C. Sieboldii, Quercus Miyagii* Koidzumi, and *E. japonicus,* 9.51 Mg ha^{-1} yr^{-1} in the mid-elevations (105 m above sea level), where were mainly composed of *C. Sieboldii* and *S. Wallichii,* and 6.28 Mg ha^{-1} yr^{-1} in the highlands (130 m above sea level), where were mainly composed of *C. Sieboldii, S. Wallichii,* and *C. Doederleinii*.

Leaf litter of the dominant species

The four dominant species, *C. Sieboldii* (Fig. 9a), *S. Wallichii* (Fig. 9b), *E. japonicus* (Fig. 9c), and *C. Doederleinii* (Fig. 9d), contributed to the majority of the leaf litter. The leaf litter of *C. Sieboldii, S. Wallichii,* and *E. japonicus* had two peaks, one of which was large in March or April and another was small in August and October. The leaf litter of *C. Doederleinii* showed a different seasonal pattern with a peak in August to September and an extreme peak in February (2000). It was recognized that the leaf litter of each dominant species was not seasonally significantly different over the three years ($P > 0.05$).

The dendrogram of the degree of overlap ω of the seasonal patterns in the dominant species is shown in Fig. 10. It explains that the seasonal patterns of three species, such as *C. Sieboldii, S. Wallichii,* and *E. japonicus,* were nearly overlapped, while the degree of overlap of *C. Doederleinii* was in the vicinity of zero, indicating that its seasonal change was almost independent of the other three species. This is because *C. Doederleinii* defoliates mainly in summer (Fig. 9d), whereas the shedding season of the other three species is in spring (Figs. 9a, 9b, and 9c).

Annual amounts As shown in Table 4, *C. Sieboldii* had the greatest amount of leaf litter ranging from 1.71 ± 0.12 (SE) (44.0%) to 2.29 ± 0.16 (SE) Mg ha^{-1} yr^{-1} (52.8% of the total leaf litter) over the three years, followed by 1.39 ± 0.18 (SE)

(52.8%) to 1.69 ± 0.20 (SE) Mg ha^{-1} yr^{-1} (38.4% of the total leaf litter) for *S. Wallichii,* 0.14 ± 0.03 (SE) (3.3%) to 0.19 ± 0.03 (SE) Mg ha^{-1} yr^{-1} (4.3% of the total leaf litter) for *E. japonicus,* and 0.09 ± 0.02 (SE) (2.0%) to 0.13 ± 0.06 (SE) Mg ha^{-1} yr^{-1} (2.9% of the total leaf litter) for *C. Doederleinii*. The contribution to the total leaf litter by the other 44 species was less than 1.0%. A significant difference in the amount of leaf litter between the first and the third year was detected only for *C. Sieboldii* ($P < 0.01$).

Table 4. Annual fall of leaves by species collected from January 1999 to December 2001

Species	Leaf litter					
	1999		2000		2001	
	Mg ha^{-1} yr^{-1}	%	Mg ha^{-1} yr^{-1}	%	Mg ha^{-1} yr^{-1}	%
C. Sieboldii	2.29 ± 0.16 A	52.8	2.05 ± 0.14 A, B	46.7	1.71 ± 0.12 B	44.0
S. Wallichii	1.39 ± 0.18 A	32.0	1.69 ± 0.20 A	38.4	1.46 ± 0.20 A	37.6
E. japonicus	0.19 ± 0.03 A	4.3	0.14 ± 0.03 A	3.3	0.18 ± 0.03 A	4.6
C. Doederleinii	0.09 ± 0.02 A	2.0	0.13 ± 0.06 A	2.0	0.10 ± 0.04 A	2.5

Values are represented with mean ± SE (n=16). Values with the same letter in a row are not significantly different; A, B (P > 0.05) . The percentage stands for the ratio of the leaf litter of each species to the total leaf litter.

CONCLUSION

In this study, seasonal patterns of litterfall components were found to be similar over three years ($P > 0.05$). However, there was a significant difference in seasonal change of reproductive parts between the second and the third year ($P < 0.01$). The annual amount of total litterfall ranged from 6.66 to 8.34 Mg ha^{-1} yr^{-1}, and the contribution of leaf litter was 3.89 (58.4%) to 4.39 Mg ha^{-1} yr^{-1} (52.6% of the total litterfall). The leaf litter was greatest in the shedding period in the spring season and the defoliating period in the autumn season.

The γ index indicates the species composition of leaf litter among months in a year and between the same months in different years. In a year, the γ values in May and in August to November were approximately +1, indicating that the species composition of leaf litter was completely overlapped among these months. The species composition of leaf litter from January to March tended to be somewhat exclusive to that of the other months. In different years, the γ-value was very high (0.93 - 0.99), indicating that the species composition was completely overlapped among the same months.

The *M-w* diagram of leaf litter per species was characterized by two segments, the first segment of which was fulfilled by four species, such as *C. Sieboldii, S. Wallichii, E. japonicus,* and *C. Doederleinii,* and the second segment was formed by the other species. It was concluded that the four species in the first segment contributed a quite high amount to the total leaf litter compared to the other species, and the ranks of the four species in terms of the amount of leaf litter were the same over the three years.

The *H'* and *J'* indexes were used to know the species diversity of leaf litter. Their values ranged from 1.41 to 3.01 bit and 0.28 to 0.57, respectively. Their minimum values in March were concluded to be attributed to a large amount of leaf litter of both *C. Sieboldii* and *S. Wallichii,* whose shedding peaks were in March. The mean leaf litter per tree of a given species was proportional to its corresponding basal area. The estimated value obtained from the proportional relationship was almost equal to the observed value.

The ω index was used to examine the degree of overlap of the seasonal patterns of litterfall components and of leaf litter of the four dominant species. In the litterfall components, the seasonal patterns of leaves, insect bodies, and reproductive parts were nearly overlapped, and were more or less exclusive to those of woody organs and feces. In the leaf litter, the seasonal patterns of *C. Sieboldii, S. Wallichii,* and *E. japonicus* were almost overlapped, and were closely independent of that of *C. Doederleinii*. This was due to the difference in shedding or defoliating season between the former three species and the last species.

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