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Effects of micro-topographies on stand structure and tree species diversity in an old-growth evergreen broad-leaved forest, southwestern Japan

Tran Van Do [a,b,c,*], Tamotsu Sato [b], Satoshi Saito [d], Osamu Kozan [a], Hiromi Yamagawa [e], Dai Nagamatsu [f], Naoyuki Nishimura [g], Tohru Manabe [h]

[a] Center for Southeast Asian Studies, Kyoto University, Kyoto, Japan
[b] Department of Forest Vegetation, Forestry and Forest Products Research Institute, Tsukuba, Japan
[c] Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Hanoi, Viet Nam
[d] Department of Plant Ecology, Forestry and Forest Products Research Institute, Tsukuba, Japan
[e] Kyushu Research Center, Forestry and Forest Products Research Institute, Kyushu, Japan
[f] Tottori University, Tottori City, Japan
[g] Gunma University, Maebashi City, Gunma, Japan
[h] Kitakyushu Museum of Natural History and Human History, Kyushu, Japan

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ABSTRACT

Stand structure and species diversity were studied in correspondence with micro-topographies in an old-growth forest in southwestern Japan. The study was conducted in a 200×200 m^2 permanent plot, which were divided into 400 subplots using grids of 10 m $\times$ 10 m. Subplots were categorized to four micro-topographies as crest slope (CS), head hollow (HH), upper slope (US) and lower slope (LS), basing on slope of forest floor and plot position, and to two elevational zones as below 450 m and above 450 m. Tree censuses for all individuals with diameter at breast height (DBH) $\geqslant$ 5 cm were conducted in 2009 and 2013. The results indicated that CS had subplot means of living stems, dead stems, DBH, basal area (G), and basal area increment ($\triangle$G) significantly higher than that in LS. While, means of recruited stems and Shannon diversity index were significantly lower. Comparing between below and above 450 m elevational zones indicated the significantly higher parameters of stand structure and species diversity in above 450 m elevational zone. The differences of edaphic conditions led to difference of density of living stems, species density, DBH, G, and $\triangle$G among micro-topographies. Therefore, crest slope, upper slope, and higher elevational zones should be encouraged for the purposes of carbon accumulation and storage. While, the lower elevational zones should be used for the purposes of species diversity conservation.

1. Introduction

It is becoming increasingly apparent that plant communities change compositionally and structurally in response to biotic and abiotic factors. While, micro-topographies affect on edaphic conditions (e.g. fertility, depth, erosion, instability),

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* Correspondence to: Center for Southeast Asian Studies, Kyoto University, 46 Shimoadachi-cho, Yoshida Sakyo-ku, Kyoto 606-8501, Japan. Tel.: +81 75 7539645.
E-mail addresses: dotran@cseas.kyoto-u.ac.jp, dotranvan@hotmail.com (T.V. Do).

light anisotropy/availability, and biological attributes (e.g. biota, microorganism activities), leading to difference of tree's growth, crown asymmetry, and forest stand structure and diversity (Matelson et al., 1995; Clémentine et al., 1998; Clark et al., 1998; Gale, 2000; Robert, 2003; Tateno and Takeda, 2003). Therefore, micro-topography is a synthetic factor in governing stand structure and species diversity.

The regime of land surface disturbance in relation to micro-topographies has been noted as an important factor affecting stand structure and species diversity (Kikuchi and Miura, 1993; Sakai and Ohsawa, 1994; Nagamatsu et al., 2003). A relationship between vegetation characteristics and geomorphic processes was found, particularly at sites with frequent catastrophic disturbances such as land slides (Miles and Swanson, 1986; Van der Sman et al., 1993; Bellingham et al., 1996; Nakamura et al., 1997). Topographies have potential effects on species distribution, diversity, and growth through soil water availability and soil fertility (Becker et al., 1988; Silver et al., 1994; Homeier et al., 2010). Steep topography sites with high rainfall and strong typhoons mean that geomorphic processes are on occasion the critical factors determining vegetation patterns (Sakai and Ohsawa, 1993; Bellingham et al., 1996). Species richness, basal area increment, and stem density were higher in valleys than ridges in southern Ecuadorian Andes forests (Homeier et al., 2010). Enoki et al. (1996) concluded that tree species diversity was higher in lower slope than upper slope in secondary temperate forest, Japan. While, basal area was lower in lower slope than upper slope (Enoki et al., 1996).

Study on stand structure and species diversity may support us a better management strategy for each micro-topography within a climatic region. Therefore, the aims of this study were to examine changes of stand structure and species diversity and to generate the correlation of stand parameters among four micro-topographies basing on 4-year interval tree censuses of a 4-ha permanent plot in an old-growth evergreen broad-leaved forest, southwestern Japan.

2. Study site

The study was conducted in an old-growth evergreen broad-leaved forest, Aya town, southwestern Japan. Average annual rainfall and average annual temperature of study site were 2509 mm and 17.4 °C from 1981 to 2010 recorded data, respectively. The bedrock is Mesozoic shale and sandstone (Kumamoto Regional Forestry Office, 1963). A moderately moist Brown Forest soil type predominates. Climate including temperature and precipitation was known as ordinary conditions (Sato et al., 2010) and there were no strong typhoons hit the study site between 2009 and 2013, when tree censuses were conducted.

A square permanent $200 \times 200 \text{ m}^2$ plot (Fig. 1) was established in 1989 for long-term ecological research. The plot locates on a steeply inclined north-northwestern slope (32°03′N, 131°12′E), expanding from 380 to 520 m above sea level. There are two gullies and a shallow valley without surface water in the plot. More details of the permanent $200 \times 200 \text{ m}^2$ plot can be found at Sato et al. (1999).

3. Methods

3.1. Field surveys and data collection

Most studies of vegetation–geomorphology relationship have been based on topographic elements, such as ridges, slopes, and valleys (Harrison et al., 1989; Basnet, 1992; Ashton et al., 1995; Nagamatsu et al., 2003). Each micro-topography has a different geomorphic process, which refers to the interactions between erosion and deposition of soil materials by overland flow and mass movements. Therefore, slope degree and position are the main parameters used to classify micro-topographies (Harrison et al., 1989; Basnet, 1992; Ashton et al., 1995; Yamakura et al., 1995; Nagamatsu et al., 2003). The range of slope degree in each micro-topography is different site by site based on the difference of soil type, rainfall, and soil erosion level. In this study, micro-topography classification was inherited from Ohnuki et al. (1998), who classified the present study plot to four micro-topographies and found the significant difference of amount of soil erosion among micro-topographies. Crest slope (CS) has a gentle slope of approximate 0°–25°, locating in uppermost area of slopes. Upper slope (US) locates adjacent to CS and has slope of less than 32°. Head hollow (HH) including both head hollow and head wall is a concave slope of less than 42°. Lowe slope (LS) including both lower slope and flat foot slope has slope of less than 49° (Ohnuki et al., 1998). CS had lowest soil erosion, which equaled to 20% of that in HH. LS equaled 40% soil erosion in HH. US equaled 48% soil erosion in HH. The highest soil erosion belonged to HH.

A $200 \times 200 \text{ m}^2$ permanent plot was divided into 400 subplots by using 10 m × 10 m grids (Fig. 1). Each subplot was classified to one of four micro-topographies. If a subplot locates in more than one micro-topography, it was classified to a micro-topography which has highest area ratio. For analyzing the effects of elevation on stand structure and species diversity, subplots were divided into two groups of above 450 m elevational zone and below 450 m elevational zone. The 4-ha plot expands from 380 to 520 m above sea level with a range of 140 m elevation. Contour 450 m was selected as it is the middle of plot, which divides plot to two equal elevation ranges of 70 m and more or less similar number of 100 m² plots for two elevational zones. In Septembers 2009 and 2013, tree censuses were conducted for all stems with diameter at breast height (DBH) ≥ 5 cm. All stems were identified to species, mapped, tagged, and measured for DBH. In addition, recruited and dead stems were recorded in 2013 census.
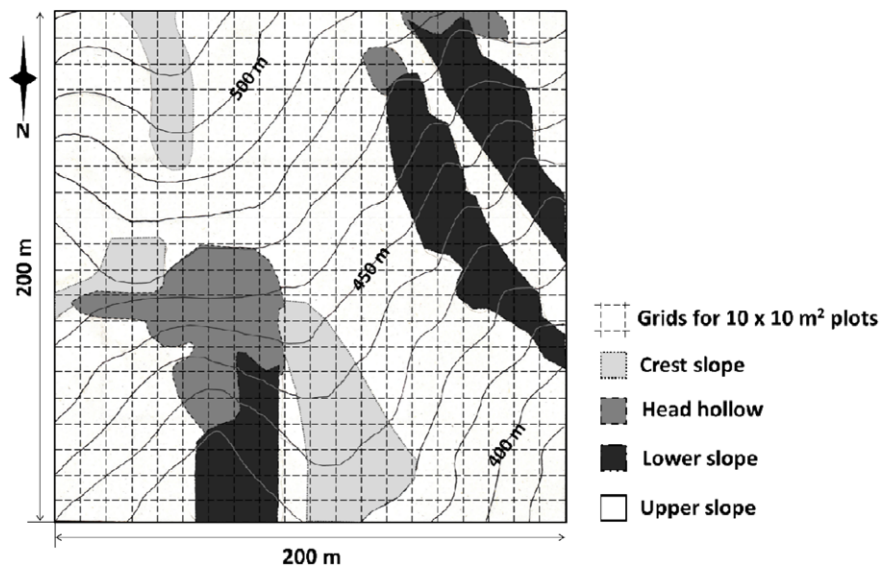
Fig. 1. Layout of a 200 × 200 m^2 plot and 10 × 10 m^2 subplots.

3.2. Data analysis

Basal area increment (ΔG) was estimated as

$$\Delta G = \sum_{i=1}^{n} (G_{\text{living stem } i \text{ in } 2013} - G_{\text{living stem } i \text{ in } 2009}) + \sum_{j=1}^{m} (G_{\text{recruited stem } j \text{ in } 2013} - G_{\text{stem } j \text{ at DBH=5 cm}}) \tag{1}$$

where, $G_{\text{living stem } i \text{ in } 2009}$ and $G_{\text{living stem } i \text{ in } 2013}$ are basal areas of stem i in 2009 and 2013, respectively. n is number of living stems, which had DBH in 2009 $\geq$ 5 cm and were still alive in 2013. $G_{\text{stem } j \text{ at DBH=5 cm}}$ is basal area of stem j, when it had DBH equal 5 cm or basal area of 0.00196 m^2. $G_{\text{recruited stem } j \text{ in } 2013}$ is basal area of recruited stem j in 2013. m is number of recruited stems, which had DBH in 2009 < 5 cm but ≥5 cm in 2013.

Shannon diversity index (Magurran, 1988, H) was estimated as

$$H = -\sum_{i=1}^{n} p_i \operatorname{Ln}(p_i) \tag{2}$$

where, p_i is stem proportion of species ith in plot. n is species number in plot.

Jaccard's similarity coefficient or species similarity index (SI) between pairs of micro-topographies and that of elevational zones was calculated as

$$SI = \frac{\text{no. of species shared by two micro-topographies or elevational zones}}{\text{total species found in two micro-topographies or elevational zones}}. \tag{3}$$

Species/area curve is applied to generate relationship between survey area (A) and number of species (S) in the form of Eq. (4).

$$S = a * A^b \tag{4}$$

where, a and b are constant and estimated through linear logarithmic transform as $\log(S) = \log(a) + b * \log(A)$. Randomly picked up subplots (10 × 10 m^2 plot) for species aggregation was used. The process was repeated 30 times. Then mean, upper limit, and lower limit ($\pm$ SE) of species/area curve was regenerated.

Stand parameters including number of living stems, number of dead stems, number of recruited stems, mean DBH, basal area (G), basal area increment (ΔG during 2009–2013), species density (number of species/subplot), and Shannon diversity index were calculated for each subplot (10 × 10 m^2 plot) separately. ΔG and number of dead stems were calculated basing on data recorded in 2009 and 2013, while other stand parameters were calculated basing on data recorded in 2013.

The effects of four micro-topographies on stand parameters were assessed by univariate analysis of variance (ANOVA) and post-hoc Tukey's test. Meanwhile, pair-comparison using t-test ($p = 0.05$) was applied to find out the effect of two elevational zones on stand parameters for combination of all micro-topographies and for each micro-topography separately.

Correlations between pair of stand parameters were generated. It usually results in a correlation matrix showing correlation values of all pairs in the form of table, including significant correlations ($R > 0.7$) and non-significant correlations. For simplification, only significant correlations were shown in the form of correlation circle. Mathematically, significant correlation indicates the change of a parameter leads to change of other positively or negatively.
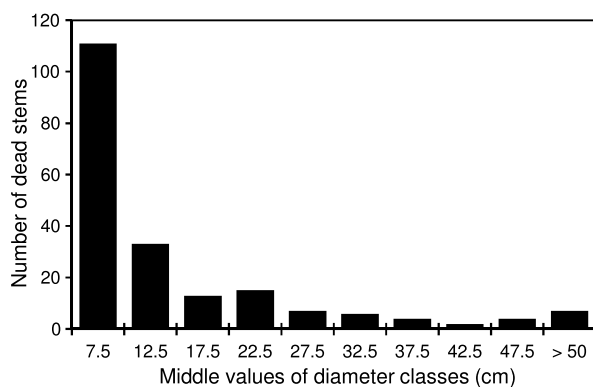
Fig. 2. Number of dead stems in different diameter classes (5 cm DBH intervals were used). The largest DBH dead stem was 111.7 cm, belonging to species *Persea thunbergii.*

4. Results

4.1. Vegetation in a 4-ha plot

A total of 5268 stems (DBH $\geq$ 5 cm) was recorded in a 4-ha plot in 2013 census. These individuals belong to 55 species of 28 families. There were 13 singleton species, six doubleton species, and four tripleton species (Appendix). Ninety four stems with DBH larger than 70 cm, in which 15 stems had >100 cm DBH, were recorded. Plot had a total basal area (G) of 207.5 m^2. Of which five most abundant species (*Distylium racemosum, Persea thunbergii, Quercus salicina, Quercus acuta,* and *Cleyera japonica*) accounted for 69.8% G and 54.3% stems. During 2009–2013, 254 stems were found to recruit into $\geq$5 cm DBH classes, belonging to 28 species of 15 families. Of which, 12 species recruited one stems, one species recruited two stems, and two species recruited three stems. Species with most abundant recruited stems were *Cinnamomum insularimontanum* (87 stems), *Distylium racemosum* (28 stems), and *Actinodaphne longifoli*a (24 stems; Appendix). There were 200 stems found dead in 2013 census, belonging to 26 species of 14 families. In which, eight species had one stem dead, four species had two stems dead, and four species had three stems dead. Species with the numerous dead stems were *Cleyera japonica* (48 stems), *Distylium racemosum* (38 stems), and *Persea japonica* (32 stems; Appendix). DBH of dead stems extended to 117.8 cm (*Persea thunbergii*). Of 200 dead stems, there were 144 stems in DBH classes <15 cm and seven stems with DBH > 50 cm measured in 2009 (Fig. 2).

4.2. Micro-topographies

In total 400 subplots from a 4-ha plot, there are 36 subplots classified to lower slop (LS), 305 subplots of upper slope (US), 23 subplots of head hollow (HH), and 36 subplots of crest slope (CS). Species richness was different among micro-topographies, the highest species richness belonged to US (55), following LS (27), HH (24), and CS (23). ANOVA analysis indicated that micro-topographies had no significant effect on species density ($df = 3$, 396; $F_{crit} = 2.63$; $F = 0.70$, $p = 0.55$). While, it had significant effect on other stand parameters ($df = 3$, 396; $F_{crit} = 2.63$; number of living stem, $F = 3.45$, $p = 0.02$; number of dead stems, $F = 3.90$, $p = 0.009$; number of recruited stems, $F = 6.88$, $p = 0.0002$; DBH, $F = 2.63$, $p = 0.04$; G, $F = 4.25$, $p = 0.006$; ΔG, $F = 2.65$, $p = 0.05$; Shannon diversity index, $F = 3.67$, $p = 0.013$). Post-hoc Tukey's test for mean stand parameters of 10 × 10 m^2 plot (Table 1) indicated that CS had highest number of living stems (15.3) and dead stems (0.9), while the lowest belonged to LS (10.5 living stems and 0.3 dead stem). As result of lowest number of living stems, LS had highest number of recruited stems (1.7). While the lowest number of recruited stems belonged to CS (0.5; Table 1). Lowest number of living stems led to significantly lowest mean G (0.35 m^2) and ΔG (0.018 m^2) in LS. While CS, US, and HH had much higher G (0.64, 0.53 and 0.51 m^2, respectively) and ΔG (0.026, 0.027 and 0.025 m^2, respectively). The highest number of living stems (15.3) but lowest Shannon diversity index in CS (1.25) resulted from lowest species density (5.1 species 100 m^{-2}). The difference of mean of Shannon diversity index between CS and other three micro-topographies was significant (Table 1).

Species/area curves indicated that at the same area equal to 23 subplots, US had highest species richness, following by HH, LS, and CS (Fig. 3(a), (b), (c), (d)). LS and HH had highest species similarity index (Table 2), following by pair of CS and LS (0.52), US and LS (0.49). The lowest species similarity belonged to pair of CS and US (0.42). J shape best described the stem proportion/DBH relationship in all micro-topographies (Fig. 4(a), (b), (c), (d)). However, the diameter diversity index (DI) indicated that CS was highest (1.79), following US (1.75), HH (1.67), and LS (1.56). The largest DBH stem found in CS was 101.8 cm, it was 93.1 cm in HH, 110.6 cm in LS, and 133.6 cm in US.

Table 1
General stand structure and species diversity of four micro-topographies and two elevational zones in a 4-ha plot.

	Number of 10 × 10 m² plots	Species richness	Mean ± SE (10 × 10 m² plot)							
			Number of living stems	Number of dead stems	Number of recruited stems	DBH (cm)	Basal area (G; m²)	ΔG (m²)	Species density	Shannon diversity index
Micro-topographies										
Lower slope	36	27	10.5 ± 0.9[a]	0.3 ± 0.1[a]	1.7 ± 0.7[a]	15.0 ± 0.80[a]	0.35 ± 0.05[a]	0.018 ± 0.003[a]	5.2 ± 0.4	1.46 ± 0.08[a]
Head hollow	23	24	12.5 ± 1.1[b]	0.2 ± 0.2[a]	0.8 ± 0.2[b]	17.3 ± 0.79[b]	0.51 ± 0.06[b]	0.025 ± 0.003[b]	5.7 ± 0.3	1.51 ± 0.07[a]
Crest slope	36	23	15.3 ± 1.3[c]	0.9 ± 0.1[b]	0.5 ± 0.3[c]	17.6 ± 0.85[b]	0.64 ± 0.07[c]	0.026 ± 0.004[b]	5.1 ± 0.5	1.25 ± 0.08[b]
Upper slope	305	55	13.8 ± 0.4[b]	0.5 ± 0.1[c]	0.6 ± 0.1[c]	16.5 ± 0.27[c]	0.53 ± 0.02[b]	0.027 ± 0.002[b]	5.7 ± 0.1	1.45 ± 0.02[a]
Elevational zones										
Above 450 m	207	39	15.6 ± 0.5[d]	0.52 ± 0.06	0.72 ± 0.13[d]	15.9 ± 0.30[d]	0.55 ± 0.02[d]	0.029 ± 0.002[d]	6.2 ± 0.2[d]	1.52 ± 0.02[d]
Below 450 m	193	52	11.4 ± 0.36[e]	0.48 ± 0.06	0.51 ± 0.07[e]	17.3 ± 0.37[e]	0.48 ± 0.02[e]	0.023 ± 0.002b[e]	5.2 ± 0.15[e]	1.36 ± 0.03[e]
Combination of micro-topographies and elevational zones										
Lower slope — Above 450 m	18	22	12.7 ± 1.45[f]	0.1 ± 0.08	2.9 ± 1.24[f]	14.1 ± 1.34	0.39 ± 0.01	0.022 ± 0.005	6.8 ± 0.65[f]	1.72 ± 0.09[f]
Lower slope — Below 450 m	18	22	8.0 ± 0.09[g]	0.6 ± 0.03	0.3 ± 0.02[g]	16.0 ± 0.08	0.31 ± 0.01	0.014 ± 0.000	4.3 ± 0.04[g]	1.22 ± 0.01[g]
Head hollow — Above 450 m	6	13	20.3 ± 1.66[f]	0.9 ± 0.36	0.8 ± 0.41	15.5 ± 0.83	0.72 ± 0.09	0.035 ± 0.005[f]	6.6 ± 0.39[f]	1.48 ± 0.09[f]
Head hollow — Below 450 m	17	21	11.8 ± 0.78[g]	0.9 ± 0.27	0.2 ± 0.13	19.1 ± 1.12	0.58 ± 0.07	0.019 ± 0.003[g]	4.3 ± 0.36[g]	1.07 ± 0.08[g]
Crest slope — Above 450 m	15	19	14.3 ± 1.58[f]	0.2 ± 0.10	1.0 ± 0.40[f]	16.7 ± 0.87	0.56 ± 0.08	0.029 ± 0.005[f]	6.1 ± 0.62	1.50 ± 0.11
Crest slope — Below 450 m	21	21	7.5 ± 1.20[g]	0.3 ± 0.34	0.0 ± 0.00[g]	19.2 ± 2.11	0.35 ± 0.09	0.014 ± 0.04[g]	5.2 ± 0.61	1.48 ± 0.12
Upper slope — Above 450 m	168	37	15.4 ± 0.62[f]	0.6 ± 0.07	0.4 ± 0.06	16.0 ± 0.36	0.55 ± 0.03	0.028 ± 0.002	6.1 ± 0.15[f]	1.50 ± 0.36
Upper slope — Below 450 m	137	52	11.9 ± 0.44[g]	0.4 ± 0.06	0.6 ± 0.09	17.1 ± 0.42	0.50 ± 0.03	0.026 ± 0.003	5.4 ± 0.18[g]	1.41 ± 0.04

[a,b,c] Indicate significant difference of means for micro-topographies.
[d,e] Indicate significant difference of means for elevational zones.
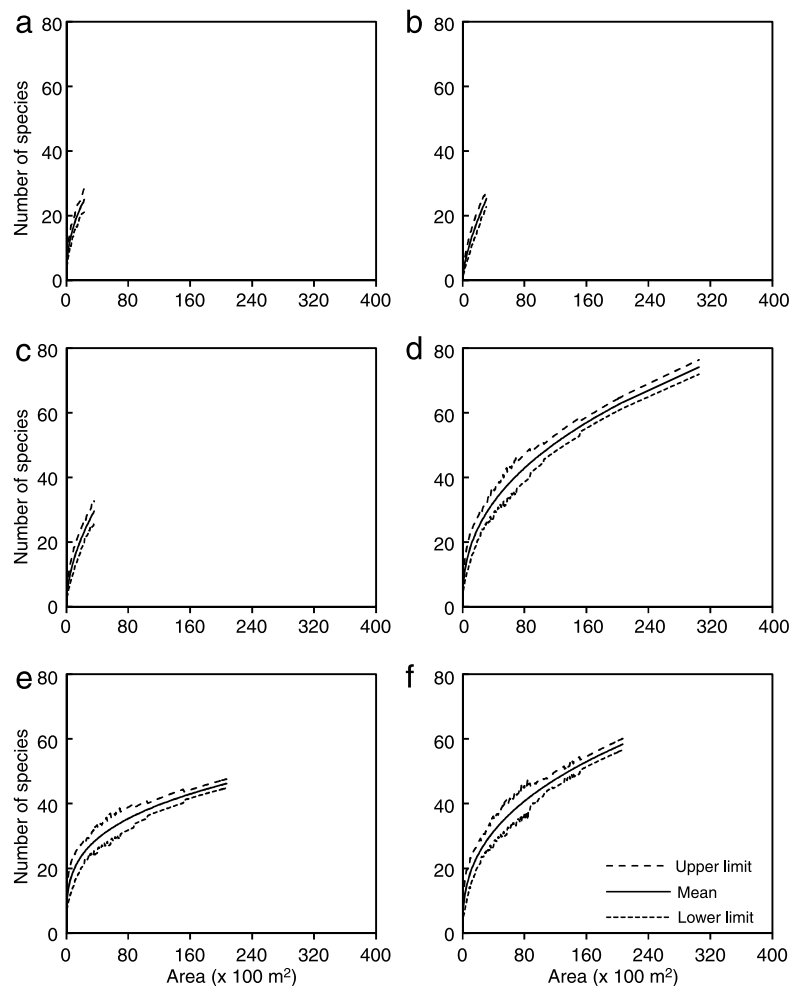[f,g] Indicate significant difference of means for combination.

Fig. 3. Species/area curves for head hollow (a), crest slop (b), lower slope (c), upper slop (d), above 450 m elevational zone (e), and below 450 m elevational zone (f).

Table 2
Species similarity index among micro-topographies in a 4-ha plot.

	Upper slope	Lower slope	Crest slope	Head hollow
Upper slope	1	0.49	0.42	0.44
Lower slope		1	0.52	0.70
Crest slope			1	0.47
Head hollow				1

4.3. Elevational zones

A little smaller area in a 200×200 m^2 plot was allocated to below 450 m (193 subplots) elevational zone (Table 1), while 207 subplots were allocated to above 450 m elevational zone. However, species richness was much different. There were 52 species found in below 450 m elevational zone with ten singleton species. While only 39 species were found in above 450 m elevational zone with three singleton species (Appendix). Above 450 m elevational zone had significantly higher means of number of living stems and recruited stems, species density, G, $\triangle G$, and Shannon diversity index than that in below 450 m elevational zone (Table 1). Conversely, above 450 m elevational zone had smaller DBH than that in below 450 m elevational zone. While, the difference of number of dead stems between two elevational zones was not significant (Table 1).

Species/area curves indicated that at equal area, below 450 m elevational zone had higher species richness than that in above 450 m elevational zone (Fig. 3(e), (f)). Both elevational zones shared 36 species in total of 55 species found, leading to species similarity index of 0.65. J shape was well describing the stem proportion/DBH relationship in both elevational zones (Fig. 4(e), (f)). However, diameter diversity index was higher (1.85) in below 450 m elevational zones compared to that (1.67) in above 450 m elevational zone.
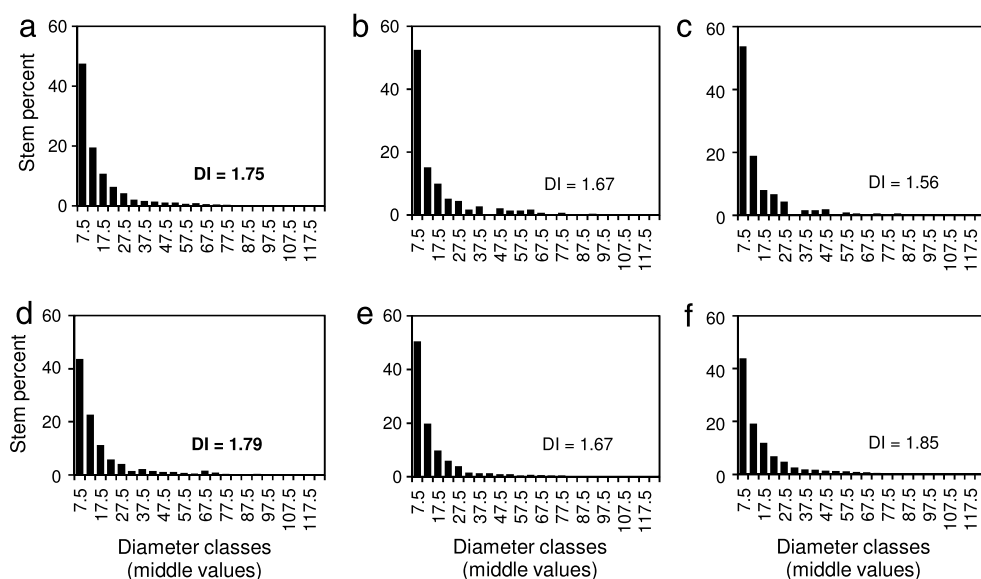
Fig. 4. Stem abundance/DBH relationship in upper slope (a), head hollow (b), lower slope (c), crest slope (d), above 450 m elevational zone (e), and below 450 m elevational zone (f). DI was estimated using Eq. (2), where p_i is stem proportion of diameter class i. 5 cm DBH intervals were used.

4.4. Combination of micro-topographies and elevational zones

ANOVA analysis indicated that combination of micro-topographies and elevational zones had no significant effect on stand parameters ($p > 0.07$). Meanwhile, pair-comparison between above 450 m elevational zone and below 450 m elevational zone in each micro-topography indicated significant difference of stand parameters (Table 1). In LS, number of living stems and recruited stems, species density, and Shannon diversity index were significantly higher in above 450 m elevational zone. In HH, number of living stems, $\triangle G$, species density, and Shannon diversity index were significantly higher in above 450 m elevational zone. In CS, number of living stems and recruited stems, and $\triangle G$ were significantly higher in above 450 m elevational zone. While, in US the significant difference between two elevational zones was only found for number of living stems and species density. In all micro-topographies, significant difference between two elevational zones was not found for number of dead stems, mean DBH, and basal area (Table 1).

4.5. Correlation among stand parameters

Among eight concerned parameters of stand structure and species diversity, number of living stems had positive correlations with two parameters (number of dead stems and species density) and negative correlations with three others (number of recruited stems, DBH, and $\triangle G$). While it had no correlation with basal area and Shannon diversity index (Fig. 5). Number of dead stems, species density, DBH, and $\triangle G$ had six significant correlations with others. Number of living stems and number of recruited stems had five correlations with others. Basal area had four correlations with others. Meanwhile, Shannon diversity index had only two significant correlations with basal area and species density (Fig. 5).

5. Discussion

Twenty canopy species accounted for 46.2% stems and 81.4% basal area in a 4-ha plot (Appendix). Meanwhile, ten of 13 singletons are under-canopy species and accounted for <0.2% basal area. Of 13 singleton species, five had DBH < 10 cm, three had DBH of 10–20 cm, and five had DBH of 20–60 cm. These indicated less importance of singleton species in stand structure. Small size-stems of singleton species are vulnerable by typhoons (Sato et al., 1999), which usually happen in the present study site and cause the large and big trees falling, leading to its disappearance. The falling of big trees may cause singleton species dead. A comparison is that there were 60 species (DBH $\geq$ 5 cm) recorded in 1991 tree census (Sato et al., 1999), while only 55 were found in 2013 tree census (Appendix). Five species (DBH $\geq$ 5 cm) disappeared in a duration of 22 years.

The differences of parameters of stand structure and species diversity in the present study (Table 1) resulted from the differences of edaphic conditions, soil erosion degree, and light availability in each micro-topography (Ohnuki et al., 1995; Tanouchi and Yamamoto, 1995; Enoki et al., 1996; Clark et al., 1998; Robert, 2003; Tateno and Takeda, 2003). Ohnuki et al. (1998) indicated in the present 4-ha plot there was lowest soil erosion in CS and highest in HH. In addition, US and HH have porosity in higher suction range, leading to less water retention. The highest density of living stems, dead stems, larger
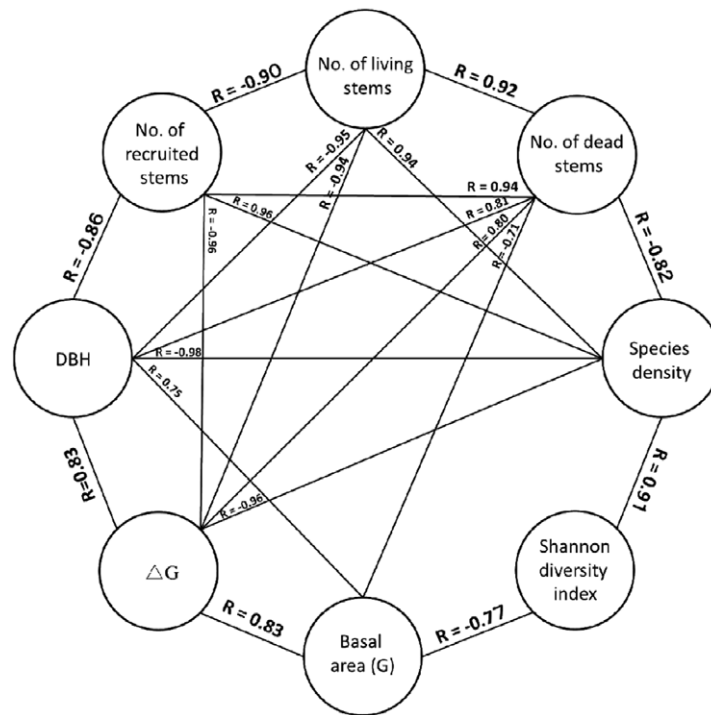
Fig. 5. Correlation circle of parameters of stand structure and species diversity. $\triangle G$ is basal area increment. Negative value of R indicates negative correlation between two stand parameters. Only correlation (R) > 0.7 is shown.

DBH, G, and $\triangle G$ (Table 1) in CS in the present study site may result from low soil erosion (Ohnuki et al., 1998) and sunlight availability (Bailey, 1996; Tanouchi and Yamamoto, 1995). The same patterns of highest living stem density and G in CS were observed in an evergreen broad-leaved forest on Amami Ohshima Island, southwestern Japan (Hara et al., 1996), which resulted from the differences of soil disturbance regime. The numerous density of living stems in CS (15 stems 100 m^{-2}) may lead to high competition among stems, which resulted in highest number of dead stems in this micro-topography (Table 1). Opposite pattern was found in LS, where there were lowest number of living stems and dead stems (Table 1). Lowest living stem density of canopy species was also reported in LS in the present study plot (Tanouchi and Yamamoto, 1995). Recruited stems were highest in LS among four micro-topographies. Lower number of living stems (Table 1) with smaller size-stems (Fig. 4(c)) in LS led to less competition among individuals. In addition, soil in LS had high water retention (Ohnuki et al., 1998). These favored seed germination and stem recruitment in LS compared to other three micro-topographies (Table 1). Again, less sunlight availability (Tanouchi and Yamamoto, 1995) and poor and/or unstable edaphic condition (Ohnuki et al., 1998) in LS responded for smaller DBH, and lower G and $\triangle G$ compared to that in CS, HH, and US.

Mathematically, Fig. 5 shows increase number of living stems leads to increasing number of dead stems but decreasing number of recruited stems; increase mean DBH leads to increasing $\triangle G$ and G, but reducing number of recruited stems; increase species density leads to increasing Shannon diversity index, but reducing DBH and $\triangle G$. However, ecologically changes of stand structure and species diversity are mainly governed by climates, edaphic conditions, and fauna itself (Gao et al., 2014; Suratman, 2012). The differences of natural conditions among micro-topographies lead to differences of stand structure and species diversity, and to significant correlations among them. Correlation is not just for only two parameters, it is a matrix of correlations in which parameters have cross-correlations with many others. In the present study, the significant correlations between stand parameters resulted from micro-topographies, which have different soil conditions as soil erosion and water retention (Tanouchi and Yamamoto, 1995; Ohnuki et al., 1998). Therefore, it is obvious that flat land areas, which have homogeneous soil and natural conditions, are preferably selected for timber plantation to ensure fair growth of all stems. While, for purpose of diversity conservation areas with diversity of micro-topographies are usually selected, since those are suitable for co-existence of many species and stem sizes.

In a quite narrow elevation range (380–520 m) in the present 200 × 200 m^2 plot, the difference of stand structure and species diversity between two elevational zones of 380–450 m and 450–520 m was significant (Table 1). Regardless of micro-topography, below 450 m elevational zone had much larger DBH but lower number of living stems and recruited stems, basal area (G), $\triangle G$, species density, and Shannon diversity index than that in above 450 m elevational zone. If considering each micro-topography separately, number of living stems, number of recruited stems, species density, and Shannon diversity index in above 450 m elevational zones were also significantly higher than that in below 450 m elevational zone (Table 1). This may be explained by the differences of light availability (Tanouchi and Yamamoto, 1995) and edaphic conditions as soil

Table A.1
List of species, their stems, and basal area in four micro-topographies and two elevational zones in a 4-ha plot.

No	Species	2013 No. of stems — Dead	Recruited	Elevational zones — Below 450 m	Above 450 m	Micro-topographies — Upper slope	Lower slope	Crest slope	Head hollow	2013 Total stems	2013 Basal (m²)	2009 Total stems	2009 Basal (m²)	1995 Total stems	1995 Basal (m²)	1991 Total stems	1991 Basal (m²)
1	*Distylium racemosum*[c]	38	28	722	812	1204	51	240	39	1534	56	1544	55	1507	47	1508	46
2	*Persea thunbergii*[c]	3	1	45	48	63	6	20	2	92	28	94	29	122	32	142	36
3	*Quercus salicina*[c]	3	4	74	69	111	6	14	10	142	25	141	23	137	21	152	26
4	*Quercus acuta*[c]	3	1	19	55	55	1	14	2	73	23	75	23	86	28	101	35
5	*Cleyera japonica*	48	22	439	579	814	72	74	58	1018	13	1044	13	1043	13	1056	13
6	*Castanopsis cuspidata*[c]	8	7	64	75	110	15	2	12	139	11	140	11				
7	*Persea japonica*[c]	32	11	112	148	207	29	2	25	260	10	281	10	337	10	337	11
8	*Quercus gilva*[c]	1		21	16	30	3	2	2	36	9	37	9	38	7	38	7
9	*Cinnamomum insularimontanum*	10	87	134	572	573	30	60	42	706	7	629	5	155	2	139	2
10	*Camellia japonica*	8	11	122	220	270	16	18	36	342	6	339	6	354	6	357	6
11	*Actinodaphne longifolia*	3	24	94	78	126	38	7	7	171	4	150	4	103	3	144	4
12	*Pasania edulis*[c]	10	4	41	31	64	3	9	1	72	2	78	2	84	2	97	2
13	*Neolitsea aciculata*	5	15	44	138	143	15	17	7	181	2	171	2		1		2
14	*Cornus controversa*[c]			5	1	1	4		1	6	1	6	1			14	1
15	*Podocarpus macrophyllus*[c]	2		7	5	8	2	4		12	1	14	1	14	1	13	1
16	*Carpinus tschonoskii*[c]			1	3	1	2		1	4	1	4	1	6	1	6	2
17	*Idesia polycarpa*[c]		1	1	2	1	1		1	3	1	2	1	3	1	3	1
18	*Diospyros japonica*[c]		1	4	3	5			2	7	1	6	1	6	1	6	1
19	*Diospyros morrisiana*	2	3	14	12	15	2	10	1	26	1	25	1				
20	*Eurya japonica*	13	15	63	133	154	13	16	8	195	1	193	1	140		129	
21	*Actinodaphne lancifolia*	1		11	5	15		1		15	1	16	1	114		125	
22	*Meliosma rigida*	1	3	20	10	24		6		29	1	27	1				
23	*Ternstroemia gymnanthera*	1	1	7	14	17	1	3		20		20			3		
24	*Daphniphyllum macropodum*[c]	2	6	5	32	22	17			37	1	33	1	17		24	2
25	*Prunus jamasakura*[c] [e]			1		1				1		1					
26	*Cinnamomum camphora*[c] [e]			1		1				1		1					
27	*Zanthoxylum ailanthoides*	1		2	16	10	1	6		17		18					
28	*Ilex integra*	1		3	3	6				5		6	1				
29	*Sapindus mukurossi*[c]		1	2		1			1	2		1					
30	*Acer rufinerve*[e]		1	1		1				1							
31	*Neolitsea sericea*	1	7	11	26	27	8	1	1	36		30					

Table A.1 (continued)

No	Species	2013 No. of stems Dead	Recruited	Elevational zones Below 450 m	Above 450 m	Micro-topographies Upper slope	Lower slope	Crest slope	Head hollow	Basal (m²)	Total stems	2009 Basal (m²)	2009 Total stems	1995 Basal (m²)	1995 Total stems	1991 Basal (m²)	1991 Total stems
32	Daphniphyllum teijsmannii			11		11					11		11				
33	Illicium religiosum		1	6	6	10		2			12		11				
34	Elaeocarpus japonicus[e]			1	3	1					1		1				
35	Premna japonica			4	3	6	1				7		7				
36	Symplocos prunifolia	2		7	2	9		2			9		11				
37	Michelia compressa			1	1	1		1			2		2				
38	Ficus erecta			1	7	5	1		2		8		8				
39	Acer nipponicum[c]	1	1	3	7	10					9		9				
40	Mallotus japonicus[e]				1	1					1		1				
41	Ilex goshiensis[e]			1		1					1		1				
42	Stewartia monadelpha[e]				1	1					1		1				
43	Ilex rotunda[c]			2		2					2		2				
44	Symplocos theophrastaefolia		1	1	2	3					3		2				
45	Osmanthus insularis			1	1	1		1			2		2				
46	Quercus sessilifolia[c] [e]				1	1					1		1				
47	Dendropanax trifidus[e]			1							1		1				
48	Symplocos lancifolia			3		3					3		3				
49	Syzygium buxifolium			1	1	1			1		2		2				
50	Symplocos glauca		2	3		2	1				3		3				
51	Viburnum odoratissimum var. awabuki		1	2		1	1				2		1				
52	Ficus erecta var. sieboldii[e]			1		1					1		1				
53	Randia cochinchinensis[e]			1		1					1		1				
54	Symplocos lucida[e]			1		1					1		1				
55	Myrsine seguinii[e]		1	1		1					1						
56	Unidentified species		2	3	1	4					4		2				
	Total	200	254	2136	3132	4150	519	262		207.5	5268	203.7	5207	181.2	4275	201.1	4058
	Species with one stem	8	12	17	7	21		3	6								
	Species with two stems	4	1	3	3	2	1	2	2								
	Species with three stems	4	2	2	3	2											
	Singleton species			10	3	13	1	1	1								

Data in 1995 and 1991 were cited from Sato et al. (1999) and only dominant species were listed. While total stems and basal area were of 4-ha plot. Singleton species are species with only one stem in a 4-ha plot. [c] indicates canopy species (Tanouchi and Yamamoto, 1995). [e] indicates singleton species.

erosion, fertility, and water retention (Ohnuki et al., 1998) between two elevational zones. Higher species density (species number 100 m^{-2}) in above 450 m elevational zone (Table 1) indicates higher species holding capacity (Rosenzweig, 1995; Mitchell and Ryan, 1998) of this zone compared to below 450 m elevational zone, resulting from higher availability of energy and more stability of soil surface in upper elevational zone (Ohnuki et al., 1998). While, higher species richness as a total of 52 species appeared in below 450 m elevational zone resulted from more diversity of micro-topographies in lower zone. Since there are more number of 100 m^2 plots of HH and CS in below 450 m elevational zone (Table 1), compared to that in above 450 m elevational zone. However, studies on vegetation zonation in the present study site should be conducted for further understanding.

6. Conclusion

Results from the present study indicated that crest slope, upper slope, and high elevational zone are most suitable for biomass accumulation and carbon storage in forests. While, for the purposes of species conservation lower elevational zones are encouraged since they have much diverse micro-conditions favoring the growth and coexistent of many species. However, the successful forest management for low elevational zones is much challenging as higher vulnerability on species establishment compared to that in crest slope, upper slope, and higher elevational zones.

Appendix A

See Table A.1.

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