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Successional change of forest pattern along topographical gradients in warm-temperate mixed forests in Mt Kiyosumi, central Japan

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Forest patterns along topographical gradients were compared between second- and old-growth forested watersheds in a warm-temperate zone of Mt Kiyosumi, central Japan. Three community types were distinguished depending on the topographical habitat type in each watershed, for example, conifer forest was dominated by *Abies firma* and *Tsuga sieboldii* on ridge sites, evergreen broad-leaved forest was dominated by *Quercus acuta, Q. salicina* and *Castanopsis cuspidata* var. *sieboldii* on slope sites, and deciduous forest was dominated by *Euptelea polyandra* and *Cornus controversa* in valley sites. Beta diversity and distinctiveness of each topographical community type increased with progression of secondary succession. Conifers and evergreen broad-leaved trees, which were intermingled with each other on ridges and slopes of the second-growth watershed, were in turn restricted to the ridge and slope habitat type, respectively, in the old-growth watershed. The process of this differentiation can be explained by the continuous regeneration of conifers on ridge sites, and its absence on slope sites due to different light conditions caused by progressive canopy closure of evergreen trees on the slope sites toward the old-growth watershed. In the valley type habitat, frequent soil disturbance, such as landslides and soil creep, hinder the continuous growth of late successional evergreen trees, and thus seral or pioneer deciduous trees can persist in the habitat.

Key words: beta diversity; secondary succession; temperate conifers; topographical community differentiation; warm-temperate forest.

INTRODUCTION

Vegetation patterns along topographical gradients may vary among different successional stages, because competition is expected to be more important for determining species distribution in mature communities where total biomass approaches the carrying capacity of the habitat. In early secondary succession, vegetation change locally depends on the speed of succession (Odum 1971). In primary succession in the subalpine region of Mt Fuji, Ohsawa (1984) has revealed that the vegetation pattern was derived from the differential successional communities along complex environmental gradients owing to both competition and disturbance. Beta diversity, or between habitat diversity, can manifest degree of differentiation of vegetation pattern along a gradient (Whittaker 1972). Previous studies have reported increasing beta diversity along topographical gradients during secondary succession in temperate zones of the United States (Robertson *et al.* 1978; Muller 1982; Christensen & Peet 1984). This suggests that divergence of communities along an environmental gradient progresses with succession.

Mt Kiyosumi, located at the southern part of Boso Peninsula, central Japan, has high floristic richness of woody species on a complex landform of easily erodible Tertiary sedimentary rock. Various life-forms of trees coexist, such as coniferous, evergreen broad-leaved and deciduous trees, which reflect its location near the northern margin of the warm-

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temperate zone. The three life-forms occupy characteristic niches in the matrix of both spatial and temporal patterns of vegetation of this area. To understand the mechanisms for coexistence of the three life-forms in Mt Kiyosumi, we studied the spatio–temporal pattern of life-form distribution. Ohtsuka *et al.* (1993) have recently revealed that the rate of succession differs among the early herbaceous stages of vegetation along topographical habitat gradients from the ridge, slope, to the valley.

This paper, therefore, intends to clarify: (i) the differentiation of forest pattern along topographical gradients by comparing different successional stages such as second-growth and old-growth watershed; and (ii) the process of community differentiation by examining the population structure of canopy dominants.

Study area

The study area belongs to the Tokyo University Forest in Chiba (TUFC) on Mt Kiyosumi, central Japan. This small mountain (383 m a.s.l.) belongs to the upper part of the warm-temperate zone, and has various life-forms such as evergreen broad-leaved trees of *Castanopsis cuspidata* (Thunb.) Schottky var. *sieboldii* (Makino) Nakai, *Quercus acuta* Thunb., and *Q. salicina* Blume, temperate conifers of *Abies firma* Sieb. et Zucc., *Tsuga sieboldii* Carr., and *Pinus parviflora* Sieb. et Zucc., and deciduous trees of *Euptelea polyandra* Sieb. et Zucc., *Cornus controversa* Hemsley, and *Zelkova serrata* (Thunb.) Makino. Phytogeographically, the conifers and deciduous trees have a wider range toward high altitudes reaching the cool-temperate zone beyond the upper limit of the evergreen broad-leaved trees. The coexistence of warm- and cool-temperate elements is one of the conspicuous features of this area.

A field survey was carried out in two watersheds covered with the forests of different age; Dohsawa watershed, an old-growth conifer–evergreen broad-leaved mixed forest, and Yomogisawa watershed, a second-growth forest that had been clear cut in 1952. The Dohsawa watershed is designated as a preserved area by the University Forest and there has been no human interference, at least since 1898 when this University Forest was established. According to TUFC (1988), this forest is composed of conifers (46% with number of stems larger than 20 cm diameter at breast height [d.b.h.]) and broad-leaved species (54%; mainly evergreen *Quercus* spp. and *Castanopsis cuspidata* var. *sieboldii*, with some deciduous trees). This is one of the oldest forests in Mt Kiyosumi.

The physiognomy of the Yomogisawa forest before clear cutting had been similar to that of Dohsawa in 1898 (TUFC 1988), and was composed of conifers (37% of wood volume, mainly *Abies firma* and *Tsuga sieboldii*), evergreen oaks (13%, *Quercus* spp.) and others (50%, presumably mainly evergreen broad-leaved species except oak with some deciduous species; yield record by TUFC). Thus the previous forest composition in Yomogisawa watershed may have been similar to that of Dohsawa. These two watersheds are located within a distance of 1.5 km, and have an altitudinal range between 200 m and 350 m a.s.l. We hereafter refer to these watersheds as the old-growth and the second-growth watershed.

Climatic data from 1960 to 1984 are available at the Fudago Camp observatory (35°12′N, 140°09′E, 206 m a.s.l.; TUFC 1976, 1987), adjoining the Dohsawa watershed. The annual mean temperature is 14.0°C, with mean temperature of the coldest month (January) of 3.7°C and mean of the warmest month (August) of 25.1°C. The warmth and coldness indices (Kira 1948) are 109.8°C·month and −2.1°C·month, respectively. The mean annual precipitation is 2412 mm with no dry month, the minimum mean monthly precipitation is 96.2 mm in January.

According to Iijima and Ikeya (1976), the bed rock of this area is Upper Tertiary sedimentary rock. They also noted that such an erodible substrate in combination with high precipitation and high uplifting velocity resulted in rapid erosion at the bottom of the streams in this area. This resulted in a steeply dissected landform. Scree slopes are often found after landslides and many alluvial banks along streams are observed in both watersheds. These topographical features demonstrate frequent soil disturbances at the valley bottom.

METHODS

Field survey

The field survey was carried out from May 1986 to September 1992. The patch sampling method

(Ohsawa 1991a) was adopted for collecting data on community composition and structure. This survey method uses the 'dynamic unit' (Ohsawa 1981) or 'eco-unit' (Oldeman 1990) as a sampling unit, where a homogeneous part of vegetation is demarcated by a structural boundary that has been created by the same causal factors of community formation. In each sampling patch, d.b.h. and species for every stem taller than 1.3 m were recorded. Patch size, slope aspect and inclination were also recorded.

Each sampling patch was assigned to one of three topographical types defined as follows: 'ridge' as a top part of water divide within 10 m for both sides; 'valley' as the lowest part of a slope along a water course; and 'slope' as a uniform slope between ridge and valley. In total, 65 patches with closed canopy were sampled, 39 from the old-growth watershed, and 26 from the second-growth watershed. Average patch sizes were 85.7 m^2 and 97.7 m^2 in the old-growth and the second-growth watershed, respectively.

In this study, five life-forms were distinguished based on their leaf type and potential stature; for example, conifers, evergreen broad-leaved trees, deciduous trees, evergreen broad-leaved subtrees and shrubs, and deciduous subtrees and shrubs. Species of which the maximum observed height never or rarely reached that of the mature canopy (roughly more than 15 m) in our study area were grouped into the 'subtrees and shrubs' category.

Data analysis

Comparisons of characteristics of community structure between two watersheds were conducted by Mann-Whittney *U*-test (Sokal & Rohlf 1972). Sørensen's coefficient of community (CC; Whittaker 1975) was calculated as a measure of floristic similarity between two watersheds. Dominant component species were objectively determined by dominance analysis (Ohsawa 1984) using relative basal area (RBA), the percentage of species' basal area (BA) to the total BA of each patch.

Two-way indicator species analysis for classification (TWINSPAN; Hill 1979) of sample patches using RBA as species importance values were conducted for each watershed separately to compare vegetational pattern within a watershed.

Alpha and beta diversities of two watersheds and their respective topographical types were compared. Alpha diversity was measured by the number of species per sample patch and Shannon-Wiener's index H' (Pielou 1977) for each sample patch using the following formulation:

$$H' = -\sum_{i=1}^{N} p_i \log_2 p_i$$

where N is the number of species in a patch and p_i is the decimal fraction of the RBA of the *i*th species. Beta diversity along the topographical gradient was measured by Whittaker's index β_w (Whittaker 1960; after Wilson & Shmida 1984) calculated as follows:

$$\beta_w = S/\bar{\alpha} - 1$$

where S is the total number of species in a watershed and $\bar{\alpha}$ is the average number of species per patch.

RESULTS

Compositional and diversity relations of the old- and second-growth watersheds

Structural parameters indicated seral status of the second-growth watershed, that is, average BA/ha and maximum d.b.h. were less than a half of those for the old-growth, and stem density was roughly twice that of the old-growth (Table 1). The average BA values, 78.6 m^2/ha on ridge and 73.3 on slope in the old-growth watershed, were comparable to values of 75.9–85.8 of the primary forest of the same formation type in Shikoku, southern Japan (Suzuki 1979, 1980), and may have approached the possible maximum biomass of conifer–evergreen broad-leaved mixed forest of Japan.

The two watersheds had nearly the same floristic composition, that is, Sørensen's coefficient of community (CC) for all species was 0.78, and the late successional species of conifers and evergreen broad-leaved trees were almost identical between the two watersheds, CC = 0.92 and 0.93, respectively (Table 1).

In spite of the floristic similarity, the topographical pattern of relative dominance of each life-form was different in the two watersheds (Fig. 1). In both watersheds, the largest BA density was of conifers on the ridge, of evergreen broad-leaved trees on the slope, and of deciduous trees in the valley (Fig. 1a, b). This tendency was remarkable in the old-

Table 1. Community structural characteristics, species richness and average composition of patches for the three topographical types of the second- and old-growth watersheds

Watershed		Second-growth				Old-growth			
Topographical type		Ridge	Slope	Valley	Total	Ridge	Slope	Valley	Total
No. patches		9	9	8	26	15	15	9	39
Total BA (m^2/ha) ± 1 S.D.		32.4 ± 9.4	40.8 ± 7.7	13.7 ± 9.6	29.6 ± 14.3	78.6 ± 45.0**	73.3 ± 35.1**	43.1 ± 37.3*	68.4 ± 42.1*
Stem density (stems/ha) ± 1 S.D.		12312 ± 7809	9968 ± 3077	4128 ± 2141	8983 ± 6101	5540 ± 3238*	4813 ± 1968**	5674 ± 1091	5292 ± 2438*
Maximum d.b.h. (cm)		44.5	40.9	25.7	44.5	115.0	101.3	57.1	115.0
No. species†									
Total		56	51	46	82	50	37	40	71 (0.78)
Conifers		5	6	4	7	6	2	4	6 (0.92)
Evergreen broad-leaved trees		10	13	6	15	12	15	9	15 (0.93)
Deciduous trees		17	17	16	28	12	9	14	23 (0.71)
Evergreen broad-leaved subtrees and shrubs		9	9	9	11	10	10	7	13 (0.83)
Deciduous subtrees and shrubs		15	6	11	21	10	1	6	14 (0.69)
Conifers‡									
Abies firma	(Af)	3.1	4.8	1.2		28.2	10.3	2.4	
Tsuga sieboldii	(Ts)	2.9	0.2	0.4		26.1	16.8	3.3	
Pinus densiflora		2.3	1.3	–		0.4	–	–	
Torreya nucifera		0.0	0.1	0.2		0.0	–	2.1	
Chamaecyparis obtusa		0.4	–	–		–	–	–	
Cryptomeria japonica		–	0.0	0.0		0.0	–	–	
Cephalotaxus harringtonia		–	0.1	–		0.0	–	0.8	
Evergreen broad-leaved trees									
Quercus acuta	(Qa)	6.7	7.1	0.7		7.0	8.2	0.0	
Castanopsis cuspidata var. *sieboldii*	(Cc)	5.6	8.8	0.1		1.7	10.0	0.0	
Quercus salicina	(Qs)	1.3	0.8	0.1		0.9	8.5	0.0	
Quercus glauca		0.0	2.4	0.3		0.4	2.7	0.4	
Actinodaphne lancifolia		–	1.7	0.5		0.7	1.7	0.2	
Symplocos prunifolia		1.4	0.1	–		–	0.2	–	
Cinnamomum japonicum		0.1	0.9	0.1		0.2	0.1	0.0	
Ilex integra		0.3	0.4	–		0.6	1.3	0.7	
Dendropanax trifidus		0.3	0.3	–		0.1	0.1	–	
Daphniphyllum macropodum		0.3	–	–		–	–	–	
Prunus spinulosa		–	0.3	–		0.0	0.1	–	
Persea thunbergii		–	0.1	–		0.0	2.1	–	
Myrica rubra		0.1	–	–		–	0.4	–	
Ilex rotunda		–	0.1	–		0.2	0.0	0.0	
Quercus myrsinaefolia		–	0.0	–		0.0	0.0	0.8	
Actinodaphne longifolia		–	–	–		–	0.0	–	
Deciduous trees									
Euptelea polyandra	(Ep)	–	–	3.0		–	–	2.0	
Cornus controversa	(Cco)	–	0.2	1.4		–	–	2.2	
Acer palmatum	(Ap)	0.2	0.5	0.4		0.0	0.0	1.1	
Idesia polycarpa	(Ip)	–	–	–		–	0.9	4.6	
Zelkova serrata	(Zs)	–	0.2	–		–	–	11.7	
Sapindus mukorossi	(Sm)	–	–	–		–	–	3.5	
Diospyros japonica	(Dj)	–	0.4	0.2		–	0.5	2.3	
Quercus serrata		0.7	3.1	1.1		0.9	–	1.1	
Mallotus japonicus		–	0.7	0.5		–	–	0.3	
Carpinus tschonoskii		–	0.1	0.7		0.9	–	–	
Prunus jamasakura		1.0	–	0.0		3.1	1.1	–	
Albizia julibrissin		0.1	0.5	0.2		–	–	–	
Zanthoxylum ailanthoides		–	0.2	0.3		–	–	–	
Magnolia obovata		0.0	–	0.5		–	–	–	
Cornus kousa		0.2	–	0.1		0.5	0.2	–	
Fraxinus sieboldiana		0.4	–	–		0.3	0.1	–	
Acer crataegifolium		0.1	0.2	0.1		0.3	0.0	–	
Sapium japonicum		0.0	0.1	0.1		0.1	0.1	0.1	
Ilex macropoda		0.1	0.1	–		0.0	–	–	

Table 1. (*continued*)

Watershed	Second-growth				Old-growth			
Topographical type	Ridge	Slope	Valley	Total	Ridge	Slope	Valley	Total
Deciduous trees (continued)								
Cornus brachypoda	0.2	–	–		–	–	–	
Sorbus alnifolia	0.2	–	–		–	–	–	
Magnolia kobus	–	0.2	–		–	–	–	
Euscaphis japonica	–	0.0	–		0.3	–	–	
Rhus sylvestris	0.1	–	–		0.1	–	–	
Prunus incisa	0.0	0.1	–		–	–	0.0	
Rhus trichocarpa	0.1	–	0.0		–	–	–	
Acer mono	0.1	–	–		–	–	–	
Castanea crenata	–	–	0.1		–	–	–	
Prunus grayana	–	0.0	–		–	–	–	
Styrax japonica	0.0	0.0	–		0.6	–	0.2	
Kalopanax pictus	–	–	–		–	0.8	–	
Prunus buergeriana	–	–	–		–	–	0.2	
Acer carpinifolium	–	–	–		–	–	0.1	
Evergreen broad-leaved subtrees and shrubs								
Eurya japonica	1.1	1.3	0.3		1.0	2.0	0.1	
Cleyera japonica	0.4	1.0	0.3		1.3	3.3	1.1	
Camellia japonica	0.1	1.4	0.0		0.3	0.6	0.0	
Pieris japonica	1.0	0.1	–		0.7	0.0	–	
Illicium religiosum	0.3	0.3	0.2		1.4	1.2	0.5	
Aucuba japonica	0.0	0.1	0.2		0.0	0.0	0.9	
Osmanthus heterophyllus	0.1	0.1	0.0		0.1	0.0	–	
Neolitsea sericea	–	0.2	0.1		0.0	–	0.1	
Vaccinium bracteatum	0.1	0.0	–		0.0	0.0	–	
Skimmia japonica	–	–	–		0.0	–	–	
Ligustrum japonicum	–	–	0.0		–	0.0	–	
Ilex pedunculosa	0.0	–	0.1		–	–	–	
Fatsia japonica	–	–	–		–	0.0	–	
Elaeagnus glabra	–	–	–		–	–	0.0	
Deciduous subtrees and shrubs								
Lyonia ovalifolia var. *elliptica*	0.3	–	–		–	–	–	
Rhododendron dilatatum	0.2	–	–		–	–	–	
Pourthiaea villosa var. *laevis*	0.3	0.0	0.0		0.0	–	–	
Callicarpa japonica	–	0.0	0.0		0.0	–	0.1	
Hydrangea involucrata	–	–	0.0		–	–	0.1	
Rhododendron semibarbatum	0.1	–	–		0.0	–	–	
Viburnum erosum	0.0	0.0	–		0.0	–	–	
Euonymus alatus	0.0	0.0	–		0.0	–	–	
Deutzia scabra var. *scabra*	0.0	–	0.0		0.0	–	–	
Rhododendron kaempferi	0.0	–	0.0		0.0	–	–	
Lindera umbellata	–	0.0	0.0		0.0	–	–	
Euonymus melananthus	–	–	0.0		0.0	–	–	
Ficus erecta	–	–	0.1		0.0	0.0	0.0	
Morus bombycis	–	–	0.0		–	–	0.0	
Abelia spathulata	0.1	–	–		–	–	–	
Euonymus oxyphyllus	0.0	–	0.1		–	–	–	
Callicarpa mollis	0.0	0.0	0.0		–	–	–	
Viburnum dilatatum	0.0	–	–		–	–	–	
Vaccinium smallii var. *blabrum*	0.0	–	–		–	–	–	
Stachyurus praecox	0.0	–	–		–	–	–	
Lespedeza buergeri	0.0	–	–		–	–	–	
Sambucus sieboldiana	–	–	–		–	–	0.3	
Viburnum plicatum var. *tomentosum*	–	–	–		–	–	0.0	

*,**Significantly different from corresponding value in the second-growth watershed at $P < 0.05$ and $P < 0.01$, respectively.

†Values in parentheses are Sørensen's coefficients of community between the two watersheds.

‡Values in the table represent average BA density (m^2/ha) of each species. BA value less than 0.05 m^2/ha was represented by '0.0', and absence was represented by ' – '. Species abbreviations are given for main dominant species in the parentheses following their species name.

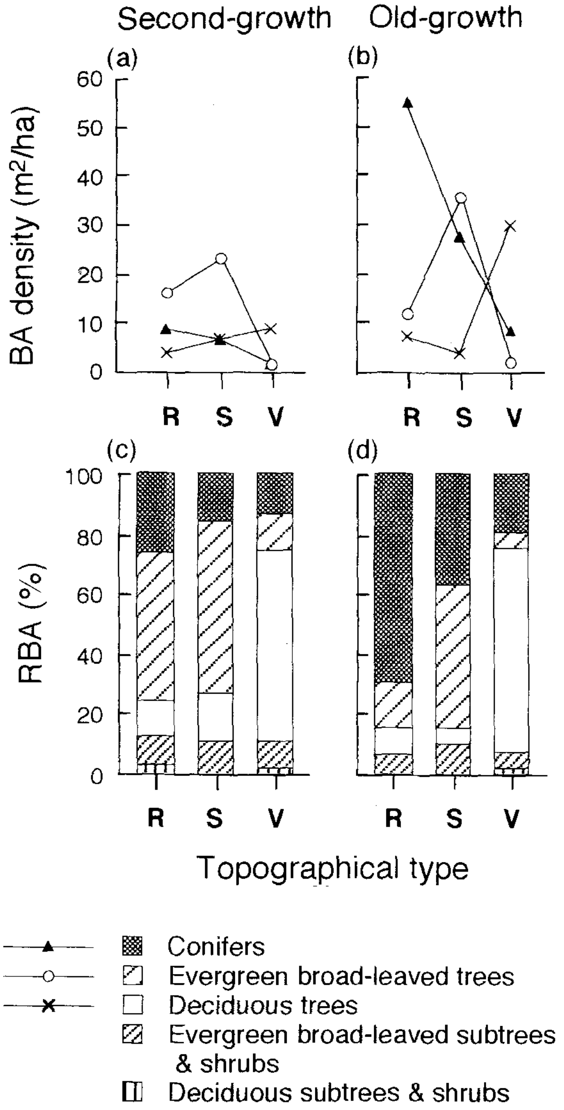

Fig. 1. (a, b) BA density of the three tree life-forms and (c, d) RBA of five life-forms including subtrees and shrubs on ridge (R), slope (S) and valley type habitat (V) in the two watersheds.

growth, but not in the second-growth watershed. In the second-growth watershed, ridge and slope sites showed quite similar life-form spectra, and were commonly dominated by evergreen broad-leaved trees such as *Castanopsis cuspidata* var. *sieboldii* and *Quercus acuta* (Fig. 1c). In the old-growth watershed, however, each habitat type was dominated by different life-forms; for example, conifers such as *Abies firma* and *Tsuga sieboldii* (69.5% of RBA) on ridge, and evergreen broad-leaved trees such as *C. cuspidata* var. *sieboldii, Q. acuta* and *Q. salicina* (48.1% of RBA) on slope (Fig. 1d). The valley type habitats of the two watersheds were both dominated by deciduous trees (Fig. 1c, d). Thus the most clear distinction between second- and old-growth watersheds was the increasing dominance of conifers on ridge type habitat, where the BA density of evergreen broad-leaved trees was rather decreased. On the other hand, slope and valley sites were dominated by evergreen and deciduous broad-leaved trees, respectively, both in the second- and old-growth watersheds.

TWINSPAN classification clearly distinguished three community types A, B, and C at the division level two for each of the second- and old-growth watershed (Fig. 2). The main dominant species and the number of patches in which each dominant species dominated are also shown in the figure. The three floristic types A, B, and C for each growth stage (distinguished by suffixes 's' and 'o' for the second-growth and old-growth, respectively) had common characteristic physiognomic features, the similar dominant life-form in both watersheds. Types A_s and A_o were mainly composed of evergreen broad-leaved trees such as *C. cuspidata* var. *sieboldii, Q. acuta* and *Q. salicina*, type B_s and B_o of conifers such as *A. firma* and *T. sieboldii*, and type C_s and C_o of deciduous trees such as *Euptelea polyandra, Cornus controversa, Acer palmatum* Thunb., *Idesia polycarpa* Maxim., *Zelkova serrata, Sapindus mukorossi* Gaertn., and *Diospyros japonica* Sieb. et Zucc.

In the second-growth watershed, most of the ridge and slope patches were included in type A_s (Fig. 2). Type B_s was evenly scattered throughout three topographical habitat types, and type C_s was restricted to the valley type habitat. In the old-growth watershed, all three community types, A_o, B_o, and C_o, corresponded to the specific topographical habitat types; that is, type A_o to the slope type, type B_o to the ridge, and type C_o to the valley (Fig. 2). Thus, the topographical community types could be clearly distinguished in the old-growth watershed.

Table 2 compares the diversity relations of the two watersheds. The number of species per patch and the diversity index H' of the second-growth were larger than those of the old-growth for respective topographical type and also as a watershed total. The alpha diversity decreased during succession, irrespective of topographical types. This is mainly due to monopolization of the characteristic dominants at each topographical type and the exclusion of

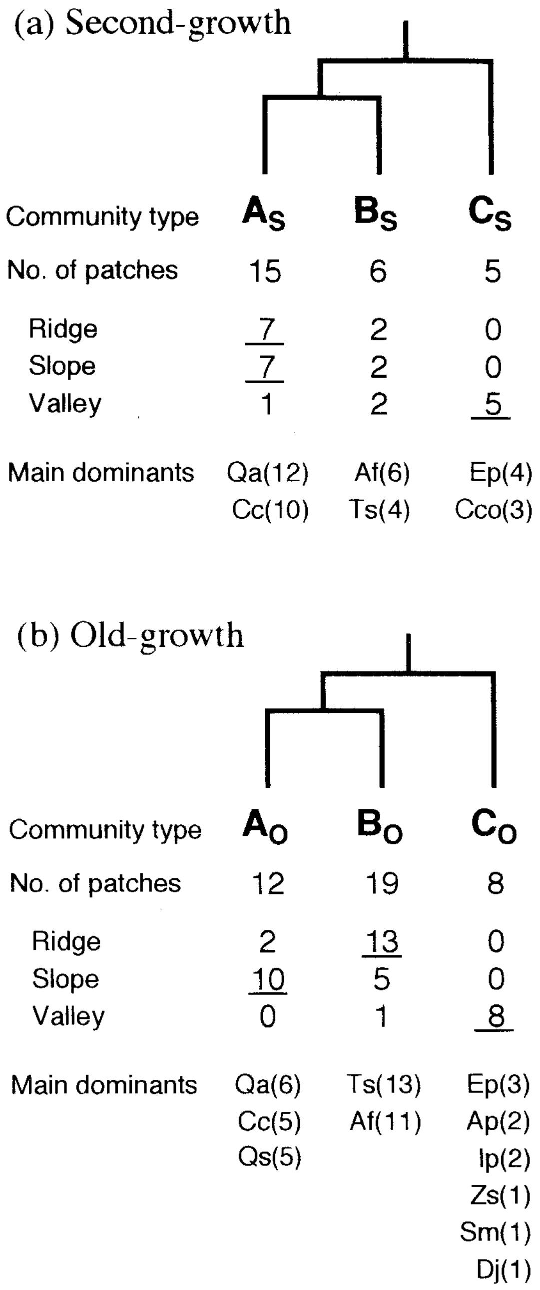

Fig. 2. TWINSPAN classification of community types for (a) the second-growth and (b) the old-growth watershed. Three types, A, B and C (with suffixes '$_s$' or '$_o$' that denote respective watersheds), were distinguished in each watershed. Number of patches classified into each community type are given in the middle, and the largest value within each topographical type is underlined. The main dominant species, which frequently dominated in a particular community type, are shown at the bottom (see Table 1 for abbreviations of species). Numbers in parentheses represent frequency of dominance determined by the dominance analysis.

Table 2. Measures of alpha and beta diversity in the second- and old-growth watersheds

	Second-growth	Old-growth
No. species per watershed (S)	82	71
No. species per patch		
Ridge	20.6	14.4*
Slope	17.9	10.5‡
Valley	12.1	9.4
Watershed total ($\bar{\alpha}$)	17.0	11.8‡
Average H' (bit)		
Ridge	2.789	1.952†
Slope	2.666	1.977‡
Valley	2.200	1.748
Watershed total	2.565	1.914‡
Whittaker's β^{w}	3.82	5.02

*,†,‡Significantly different from corresponding value of the second-growth watershed at $P < 0.1$, $P < 0.05$ and $P < 0.01$, respectively.

pioneer or seral deciduous species such as *Albizia julibrissin* Durazz. and *Zanthoxylum ailanthoides* Sieb. et Zucc. in the old-growth watershed. Despite decreased alpha diversity of the old-growth watershed, beta diversity, measured by Whittaker's index β_w, was higher than that in the second-growth watershed (Table 2). Increased beta diversity reflects the progression of the differentiation of topographical communities in the secondary succession.

D.b.h.-class distributions

Figure 3 indicates d.b.h.-class distributions for both total stem and principal dominant species obtained by dumping all the patch data of each topographical type in the second- and old-growth watersheds. All the histograms of total stem showed positively skewed distribution with the mode in the smallest size-class (d.b.h. < 5 cm) corresponding to saplings. The second-growth watershed had a higher density of saplings and had no stem larger than 50 cm d.b.h. (Fig. 3). In the valley type habitat, a truncated distribution with a much smaller maximum stem size in the two watersheds indicated frequent soil or physical disturbances in the habitat.

Curvilinear regression for total stem distributions was better fitted by the negative exponential model in the second-growth, and by the negative power function model in the old-growth watershed (Table 3), indicating the constant mortality throughout size classes in the former changed to the

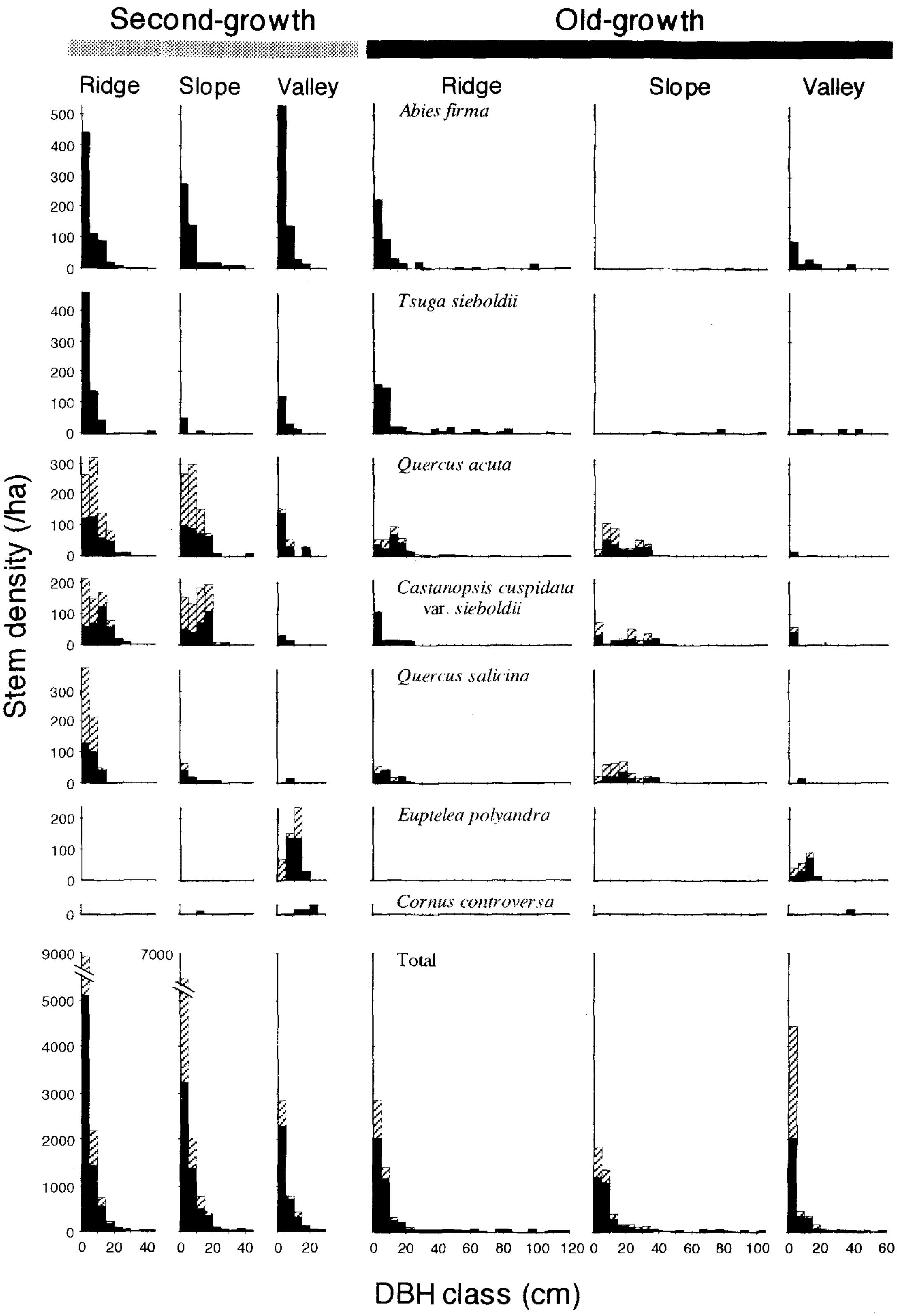

Fig. 3. D.b.h. class distribution of principal dominant tree species and total stems on the three topographical habitat types in the second-growth (left three columns) and the old-growth watershed (right three columns). Solid and hatched bars represent non-sprout and sprout stems, respectively. The class width is 5 cm. Stem frequency is transformed into density per hectare. Notice the different vertical scaling for total stem histograms.

Table 3. Coefficients of determination (R^2) for the negative exponential and the negative power regressions of d.b.h.-class distributions for total stems in each topographical type of the two watersheds

Topographical habitat type	n*	Model Negative exponential	Negative power
Second-growth			
Ridge	8	0.948	0.943
Slope	9	0.922	0.887
Valley	6	0.989	0.888
Old-growth			
Ridge	20	0.623	0.906
Slope	17	0.777	0.886
Valley	11	0.609	0.878

*Number of classes.

increasing mortality as tree size decreased in the latter. This suggests that sapling mortality due to suppression from upper layers is not so severe in the second-growth watershed as in the old-growth.

D.b.h.-class distribution patterns of principal dominants varied depending on life-form group, the developmental phase of vegetation, and the topographical habitat type (Fig. 3). In the second-growth watersheds, *Abies firma* showed an inverse J-shaped distribution in all the three topographical types, indicating its abundant recruitment throughout the topographical gradient, although the maximum size was small in the valley type habitat (Fig. 3). *Tsuga sieboldii* also showed an inverse J-shaped distribution on ridge sites, but it was poorly represented in slope and valley sites. In the old-growth watershed, they were represented by the different d.b.h.-class distributions depending on topographical habitat types. On ridge type habitat, the two conifers persisted as having an inverse J-type distribution, with additional large emergent trees. All the stems larger than 50 cm on ridge and slope patches were of these conifers. The most drastic change was found on slope-type habitat. In the second-growth watershed, there were abundant small trees of these conifers, but in the old-growth watershed, only emergent trees were found above evergreen broad-leaved canopy. These conifers cannot regenerate under the deep shade of a closed canopy of evergreen broad-leaved trees. All of the five slope patches of the old-growth watershed, which belonged to community type B_0 (Fig. 2), were dominated by such emergent conifers. In the valley type habitat of the old-growth watershed, the two conifers were poorly represented. Only *A. firma* had a small peak in the smallest d.b.h.-class. Moreover, their maximum d.b.h. was considerably smaller than those on ridge and slope sites.

Average annual d.b.h. growth rate was estimated by linear regression analysis (Table 4) using the stem analysis data for three individuals of *A. firma* cut in one of the old-growth forests of this area (Kabaya *et al.* 1976). The estimated age of the largest *A. firma* tree in the valley of the old-growth watershed was 68 years old, and it was roughly one-third the age of those in the ridge and slope habitat (Table 5). This may be due to the frequent disturbance, which interrupts further growth of *A. firma* in the valley-type habitat.

The three evergreen broad-leaved trees, *Quercus acuta, Castanopsis cuspidata* var. *sieboldii* and *Q. salicina*, also had similar d.b.h.-class distribution. On ridge and slope sites of the second-growth watershed, they had abundant stems including many sprouts up to 20 cm d.b.h. (Fig. 3). These sprouts constituted multi-stemmed individuals which usually have a stump at their base. This indicates that these species have been vegetatively regenerating mainly by sprouting after clear cutting. On the other hand, in the old-growth watershed, they showed sporadic d.b.h.-class distributions both on ridge and slope sites. The only difference between the two habitat types was a relatively higher density in the smallest d.b.h.-class on ridges, especially for *C. cuspidata* var. *sieboldii* which has the highest sapling density among the three evergreen broad-leaved dominants (Fig. 3). Except for this minor difference, as opposed to conifers, no remarkable change in size structure between the two habitat types was found for the evergreen broad-leaved

Table 4. Estimated annual d.b.h. growth rate of *Abies firma* by regression analysis using stem analysis data by Kabaya *et al.* (1976).

Tree no.	D.b.h. (cm)	Age at 1.3 m	Annual d.b.h. growth rate (cm/year)	R^2
1	61.0	118	0.54	0.996
2	51.3	94	0.58	0.996
3	46.8	109	0.48	0.991
Average			0.53	

Table 5. Estimated age at 1.3 m for the largest tree of *Abies firma* in each habitat type of the old-growth watershed

Topographical habitat type	Max d.b.h. (cm)	Age
Ridge	115.0	216
Slope	94.0	177
Valley	36.0	68

dominants. Moreover, they are the only dominants that have saplings under the closed canopy of the slope patches in the old-growth watershed. The three evergreen broad-leaved trees were poorly represented or nearly absent from the valley habitat both in the second- and old-growth watersheds.

In both watersheds, deciduous trees, such as *Euptelea polyandra, Cornus controversa, Acer palmatum, Idesia polycarpa, Zelkova serrata, Sapindus mukorossi* and *Diospyros japonica*, become dominant only in the valley type habitat. *Euptelea polyandra* had unimodal d.b.h.-class distribution, and other deciduous dominants such as *C. controversa* showed emergent type distribution in both watersheds (Fig. 3). No saplings of these deciduous trees were found under closed canopy, indicating their regeneration only after a relatively large canopy opening was created, for example, by riparian disturbances.

DISCUSSION

Distinctiveness of topographical communities increased with the succession from the second- to the old-growth watershed as indicated by high beta diversity of the old-growth watershed. Decreased alpha diversity suggested that such differentiation was caused by the monopolization of each topographical habitat type by a few dominants in the old-growth watershed. This trend agrees with Muller's (1982) result for the second- and old-growth watersheds in mixed-hardwood forest region in Kentucky, USA. Robertson *et al.* (1978) also found a similar pattern for the second- and old-growth floodplain forest including topographical gradient at the middle reaches of the Mississippi River, USA. Christensen and Peet (1984) found that beta diversity increased through the old-field succession on various topographical types in North Carolina, USA. The increasing beta diversity and decreasing alpha diversity along topographical gradients could be common to arboreal stages of secondary succession (Margalef 1968; Matthews 1979).

The increasing distinctiveness of community types during secondary succession has occurred mainly between ridge and slope sites, because the valley type had more specific floristic composition compared to the ridge and slope type habitats. Deciduous trees persisted in the habitat and both broad-leaved and needle-leaved evergreen trees were poorly represented compared to ridge and slope throughout the secondary succession. Therefore, different mechanisms may control the differentiation of slope community from both ridge and valley communities.

The differentiation of community type between ridge and slope was caused through the reversal of relative dominance of conifers and evergreen broad-leaved trees. On ridge sites of the old-growth watershed, the BA density of conifers increased but that of evergreen broad-leaved trees decreased (Fig. 1). On the other hand, on slope sites of the old-growth watershed, the BA density of both life-forms increased but conifers reached only a half of that on ridge sites. On Mt Kiyosumi, when compared to slope and valley habitats, the ridge has drier, shallower soil associated with a lower pH and a lower concentration of nutrients such as P and K (Tange *et al.* 1989). This infertility of the ridge soil may limit the growth of evergreen broad-leaved trees. Considerable increase of conifers BA on ridge indicates their tolerance of poor soil conditions.

The change of the total stem d.b.h.-class distribution from the negative exponential type to the negative power type during the succession (Table 3) indicates that constant mortality among classes changed to increasing mortality as tree size decreased (Harcombe 1987). Stem density of the smallest d.b.h. class was decreased on ridge and slope sites of the old-growth watershed. This may be caused by decreasing light on the forest floor due to the increase of BA density. Along with this process, the population structure of the two dominant conifers drastically changed, reflecting their regeneration state (Fig. 3). *Abies firma* showed vigorous recruitment both on ridge and slope sites with abundant light conditions in the second-growth watershed. Abundant recruitment of *A. firma* under the deciduous canopy of the second-growth forest irrespective of topographical habitat types was also reported in the upper warm-temperate zone of Shikoku, southern Japan (Ninomiya *et al.* 1985). Recruitment of *Tsuga sieboldii* was also abundant on ridges of the second-growth watershed but less abundant on slopes, suggesting that the species prefer a soil condition of ridge habitat. Nevertheless, these factors indicate that the two conifers can regenerate not only on ridges but also on slopes when enough light is available.

In the old-growth habitat, however, emergent type or unimodal d.b.h.-class distribution of conifers on slope indicated intermittent regeneration after large-scale disturbance such as clear cutting (Ohsawa 1991b). Increased BA density of evergreen broad-leaved trees on slope seemed to exclude conifer recruitment on the forest floor. The regeneration of conifers were restricted to ridges, where their saplings were more abundant than those of evergreen broad-leaved trees. This enabled the conifers to persist in the ridge habitat. These facts suggest that the light condition beneath the canopy is better on the ridge than on the slope, though the total BA density similarly increased in both habitat types. This may be due to the different canopy structure between the two dominant life-forms. It is likely that a compact, continuous canopy of evergreen broad-leaved trees on a slope site intercepts more irradiation compared to uneven, discontinuous canopy of emergent conifers on a ridge site. In addition, the protruding situation of the ridge type landform may allow more lateral irradiation than on the slope. A thorough assessment of light condition beneath the canopy is needed to clarify the seedling establishment pattern of dominant tree species in different topographical habitat types.

Population structure of the dominant evergreen broad-leaved trees also changed during secondary succession (Fig. 3). In the old-growth watershed, the dark shade of the canopy on slope sites seemed to reduce the sapling density, but the difference between ridge and slope sites was not so remarkable when compared with that of the conifers. Sporadic or multi-modal d.b.h.-class distribution of evergreen broad-leaved trees on ridge and slope sites of the old-growth watershed indicated their regeneration after relatively small-scale disturbance such as single or several tree-fall gaps through advance regeneration by seedling or sprouting (Ohsawa 1991b). Abundant sprouting stems of small sizes may contribute to the maintenance of evergreen broad-leaved trees even under the deep shade of their own canopy. This and the lack of conifer regeneration facilitate the monopolization by evergreen broad-leaved trees on slope sites.

In the case of the valley–slope boundary, a gradational change of disturbance regime is important for community differentiation. Smaller BA density and d.b.h. of trees in the valley habitat may be due to frequent soil disturbance such as landslides and washouts. Shade-intolerants, or pioneer trees, often invade such sites along a topographical gradient (Peet & Locuks 1977; Romme & Knight 1981; Stewart & Harrison 1987). *Euptelea polyandra* and *Cornus controversa* are typical early colonizers on landslide scars in Mt Kiyosumi (Sakai & Ohsawa 1993). No deciduous trees had saplings under their own canopy in the valley habitat of the two watersheds. Frequent soil disturbances that hinder growth of late-successional shade-tolerant tree species, however, may provide an opportunity for their invasion.

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