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Topographical pattern of the forest vegetation on a river basin in a warm-temperate hilly region, central Japan

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The relationship between tree distribution and topography was examined in a small river basin (3.4 ha) comprising a complex mosaic of topographical units at 10^2 to 10^3 m^2 order, each of which had a shallow valley bordered by small ridges or breaks of slopes. Twenty-five major woody species were divided into two groups (groups A and B) based on a cluster analysis using the distribution data in the basin. Group A, which mainly consisted of early-successional species, was distributed around the valley sites of the topographical units, while group B, which mainly consisted of late-successional species, was distributed around the ridge sites of the topographical units. This vegetation pattern coincided with erosional condition in the basin. That is, the valley sites were eroded more actively than the ridge sites, as soil depth tended to be thin in the valley sites and thick in the ridge sites, and because large (canopy) trees were restricted in the ridge sites. There was no tendency that group B was replacing group A, and hence it was suggested that repeated disturbance by slope failures or small-scale shallow landslides have prevented compositional change from the early-successional (group A) to the late-successional (group B) species by preventing the invasion of the latter into valley sites.

Key words: disturbance; geomorphic process; topographical unit; vegetation pattern analysis; warm-temperate forest.

INTRODUCTION

Patterns and dynamics of forest vegetation of mountainous and hilly regions are affected by erosion processes of the ground (Hack & Goodlett 1960; Drury & Nisbet 1971; Zimmermann & Thom 1982). In particular, where the erosion rate is high because of steep topography and high annual rainfall, such as in Japan, such geomorphic effects may be vital factors in determining vegetation characteristics (Swanson *et al.* 1988). Geomorphic effects on vegetation have been studied in various habitats such as landslides (Langenheim 1956; Hupp 1983; Shimokawa 1984; Shimokawa & Jitousono 1984; Miles & Swanson 1986; Guariguata 1990; Sakai & Ohsawa 1993), flood plains (Nakamura 1990; Craig *et al.* 1991; Wyant *et al.* 1991; Van der Sman *et al.* 1993), and valley heads (Miura & Kikuchi 1978; Ishizaki & Okitsu 1988). Sakai and Ohsawa (1993) have reported that in a landslide scar, repeated slope failure determined the vegetation pattern which coincided with the microtopography. In riparian vegetation, changing of the stream path destroys vegetation and provides open spaces for recolonization (Kalliola & Puhakka 1988; Tsuboi & Okitsu 1992; Hupp 1992; Shankman 1993). However, most studies are often restricted to habitats where erosion activities are currently intensive and the influence of geomorphic processes on vegetation is obvious. The disturbance regime should affect not only the vegetation within the habitats where disturbance effects are active, but also the overall forest ecosystem, which is a complex of habitats with various disturbance frequencies.

In the present paper, the relationship between vegetation and topography is studied in order to provide preliminary information of the effects of geomorphic processes on the vegetation in hilly regions. A small river basin was selected for the study. This was because the river basin is a hydrological unit, and the hills and mountains are eroded

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mainly by water (including indirect effects of water, such as landslides) in the humid temperate district. Therefore, the river basin is a reasonable research unit.

STUDY AREA

The study basin is located on the river head of the Dosawa (approximately 200 m in altitude), one of the tributaries of the Obitsu River, located in the Tokyo University Forest (compartment no. 27) on Mt Kiyosumi, Chiba Prefecture, central Japan (Fig. 1). This region is covered with a warm-temperate forest dominated by climax evergreen broad-leaved trees such as *Castanopsis cuspidata* (Thunb. ex Murray) var. *sieboldii* (Makino) Nakai, *Quercus acuta* Thunb. ex Murray and *Q. salicina* Blume, and conifers, *Abies firma* Sieb. et Zucc. and *Tsuga sieboldii* Carrière. The study basin, with an area of 34 236 m^2, has been unaffected by human activities during the past 100 years (Tokyo University Forest in Chiba 1986), and the vegetation is well developed.

The geology of the study basin is an alternation of strata of sandstone and mudstone (Iijima & Ikeya 1976). The erosion rate is high due to complex factors such as rapid uplift (Kashima 1982), loose Tertiary deposits (Iijima & Ikeya 1976) and high annual rainfall (2232 mm, Tokyo University Forest in Chiba 1987). Owing to these reasons, small-scale shallow landslide scars are common in this region (Sakura & Naruse 1980).

METHODS

Data sampling

The whole study basin was meshed at about 6 m intervals, and a 2 m × 2 m quadrat was placed for

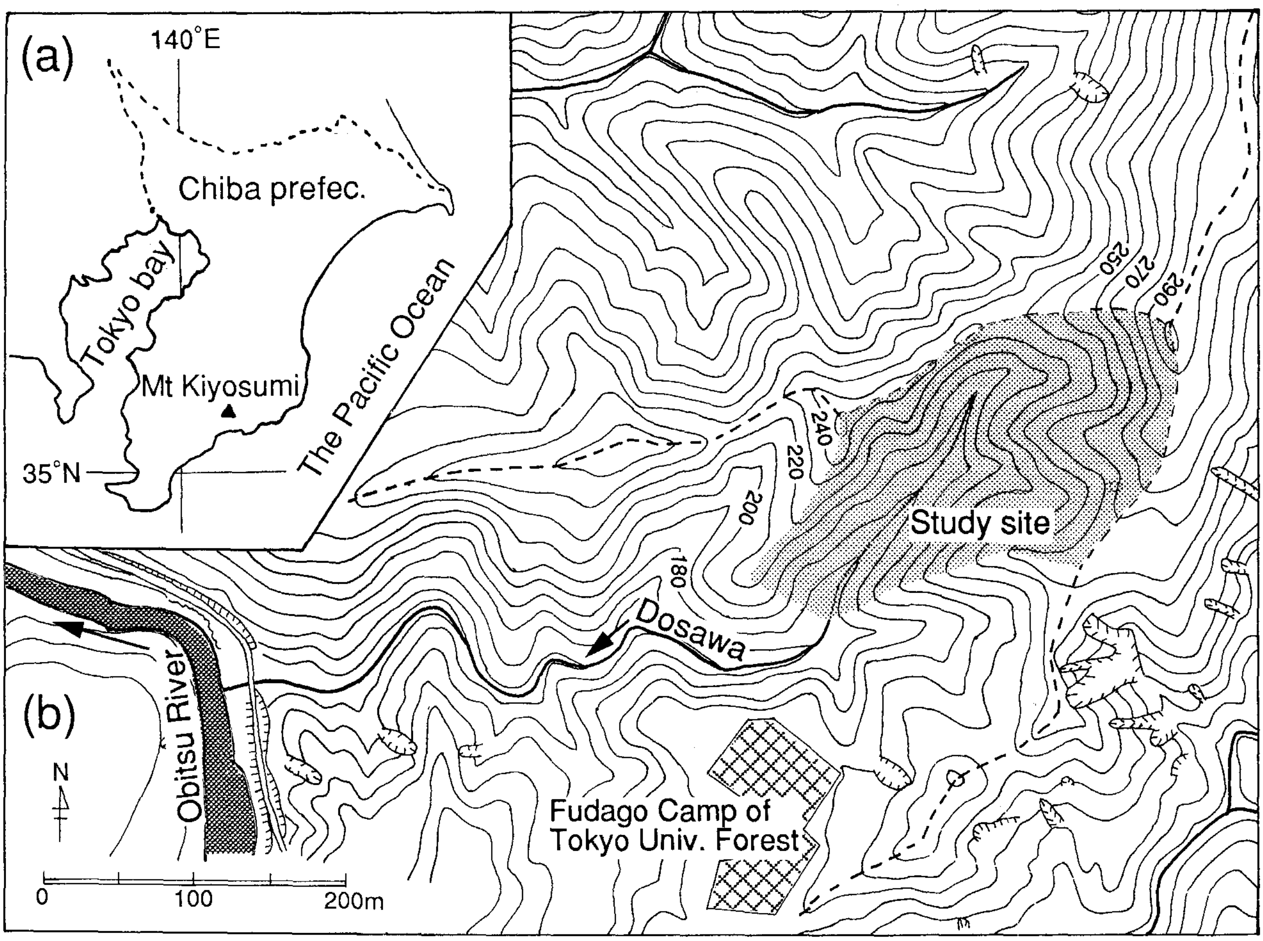

Fig. 1. Location of the study site.

each of the 840 intersection points in order to record tree and shrub individuals. Here, the positions of the quadrats were arbitrarily chosen around the intersection points in order to include much larger trees and to include trees on narrow ridge lines. In each quadrat, the size classes of diameters at 5 cm intervals were recorded at a height of 1 m for all trees and shrubs taller than 1 m. Soil depths were measured by using an iron pin of 50 cm length at 447 points to draw an isogram map. The depth was recorded if the soil at a sample point was thinner than 50 cm. Canopy types (evergreen or deciduous) were recorded from an aerial photograph at a scale of 1 : 1000. It was ascertained that the canopy layer (about 13 m to 25 m in height) of the forest in the basin consisted mainly of trees larger than 30 cm in diameter, and hence the locations of trees larger than 30 cm were recorded on the map to examine the distribution pattern of canopy trees.

Vegetation pattern analysis

There were 25 species that had a frequency of more than 3.6% (appearing in more than 30 out of the 840 quadrats). For each of these species, presence or absence data were recorded for each sampling quadrat. Cole's (1949, 1957) species association coefficient (C) was calculated using the presence or absence data for all pairs of 25 species to evaluate the similarities of distribution pattern of the species paired. The species pair concerned tend to occur in the same quadrats if their C value is large. Cole's C values (ranging from -1 to $+1$) were transformed into the values of a dissimilarity index (x) ranging from 0 to $+1$ for the cluster analysis using the equation, $x = 1 - (C + 1)/2$. The x's were adopted in the cluster analysis using average linkage method to extract species groups, in which species have a similar distribution pattern.

In order to examine the successional relationship among the species groups, a principal component analysis (PCA) was conducted at the National Grassland Research Institute using the SAS system supplied by the Computer Center for Agriculture, Forestry and Fisheries Research. For the quadrats where one or more species occurred, the PCA was computed from the covariance matrix obtained from the presence (1) or absence (0) data for each species. Component scores were calculated for each quadrat from the result of the PCA. The component scores of a quadrat indicate the location of the quadrat on the vegetational gradients obtained as the principal component axes. Trees or shrubs of each of the 25 species were grouped into two size classes, a small class (< 5 cm in diameter) and a large class (≥ 5 cm). For each size class of each species, the component scores of the quadrats where its trees or shrubs occurred were averaged to examine the location of each class of each species on the vegetational gradients. In general, size data (diameter or relative basal area, RBA) are used for PCA, and the PCA axes include size information. However, the presence or absence data were used instead of size data to clarify the shifts of the species locations with their sizes on the vegetational gradient.

RESULTS

Characteristics of topography

Figure 2a is a contour map of the study basin with a geomorphological explanation. The study basin had steep topography, and the mean inclination of slopes was about 40 degrees. There were many small cliffs on the slopes. In detail, many small ridges divided the slopes, and there were shallow valleys sometimes having an ephemeral stream between the ridges. Figure 2b shows the topographical units each of which has a shallow valley bordered by small ridges or breaks of slopes, recognized from the ridge–valley pattern. The study basin was covered with such topographical units.

In this paper, the complex of the main ridge, which bordered the study basin, and the marginal parts of the topographical units were referred to as ridge sites, and the complex of the river and the central parts of the topographical units were referred to as valley sites.

Vegetation pattern

One hundred woody species including five conifers (58.5% of the total basal area), 21 evergreen broad-leaved trees (31.3%), nine evergreen shrubs (0.7%), 34 deciduous trees (8.9%), 26 deciduous shrubs (0.5%) and five climbers (0.1%) occurred in the 840 quadrats (Table 1). Among them, 25 species, which occurred in 30 or more quadrats,

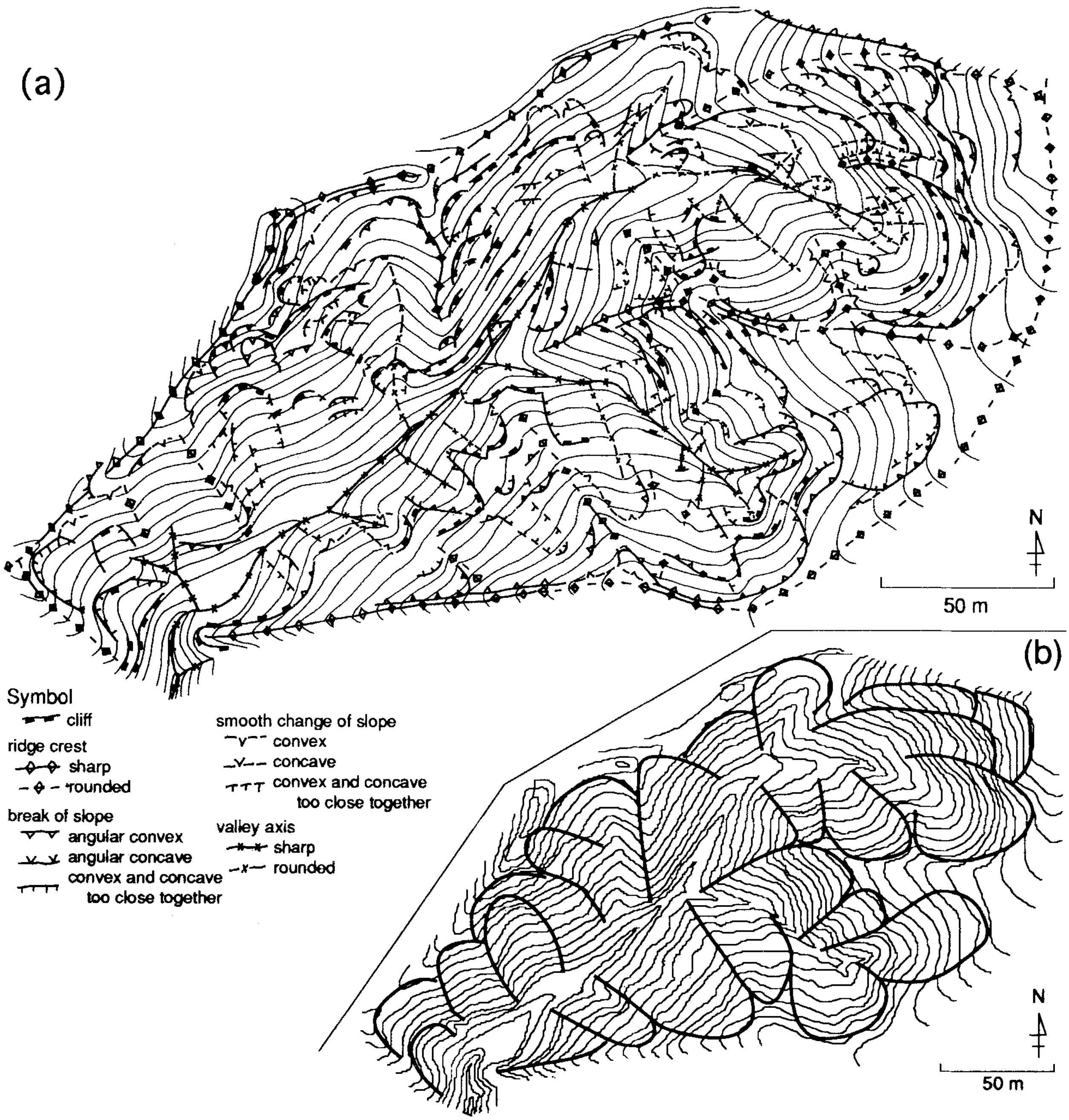

Fig. 2. Contour map with (a) geomorphological explanation and (b) topographical units (see text) of the study basin. In (a), basic morphological mapping symbols proposed by Cooke and Doornkamp (1974) are used. Counter lines are drawn at intervals of 4 m.

were taken as the objects of vegetation analysis. Figure 3 shows the result of the cluster analysis for the 25 species. They were divided into two species groups (group A and B) in relation to the distribution pattern in the study basin. All of the deciduous shrub species and all of the deciduous tree species, except for one species (*Sapium japonicum* [Sieb. et Zucc.] Pax et K. Hoffm), belonged to group A. On the other hand, evergreen broad-leaved trees and conifers, which were major climax members, belonged to group B.

Figure 4 shows the distribution of group A (a) and group B (b) in the study basin. Plants of group A were mainly distributed in the valley sites, while

Table 1. List of the 100 woody species that occurred in the study basin.

Species name	Abbreviation	Life-form	Frequency (%)*	Maximum diameter class (cm)†	Relative dominance (%)
Eurya japonica	Ej	et	37.9	17.5	1.8
Aucuba japonica	Aj	es	33.8	7.5	0.4
Cleyera japonica	Clj	et	30.5	17.5	4.1
Castanopsis cuspidata var. *sieboldii*	Cc	et	16.3	67.5	8.7
Hydrangea involucrata	Hi	ds	15.1	7.5	0.1
Illicium anisatum	Ia	et	11.8	17.5	1.2
Quercus salicina	Qs	et	11.8	37.5	4.7
Quercus acuta	Qa	et	9.9	47.5	5.6
Cinnamomum japonicum	Cij	et	9.5	19.5	0.3
Tsuga sieboldii	Ts	co	8.9	107.5	32.3
Quercus glauca	Qg	et	7.6	22.5	1.2
Camellia japonica	Cmj	et	7.5	12.5	0.4
Ilex integra	Ii	et	6.7	22.5	0.7
Euptelea polyandra	Ep	dt	6.4	22.5	1.0
Maesa japonica	Mj	es	6.1	2.5	0.1
Cephalotaxus harringtonia	Ch	co	6.1	17.5	0.3
Abies firma	Af	co	5.4	107.5	23.8
Neolitsea sericea	Ns	et	4.9	17.5	0.1
Callicarpa japonica	Cj	ds	4.8	7.5	0.1
Acer palmatum	Ap	dt	4.6	22.5	1.2
Stachyurus praecox	Sp	dt	4.0	7.5	0.1
Sapium japonicum	Sj	dt	3.9	12.5	0.3
Dendropanax trifidus	Dt	et	3.8	17.5	0.2
Actinodaphne lancifolia	Al	et	3.8	22.5	1.1
Callicarpa mollis	Cm	ds	3.2	7.5	0.1
Skimmia japonica	—	es	2.9	2.5	0.0
Osmanthus heterophyllus	—	et	2.6	12.5	0.1
Torreya nucifera	—	co	2.5	62.5	2.1
Ficus erecta	—	dt	2.3	7.5	0.1
Trachelospermum asiaticum	—	cl	2.0	7.5	0.0
Deutzia scabra	—	ds	2.0	2.5	0.0
Symplocos prunifolia	—	et	1.8	20.5	0.2
Mallotus japonicus	—	dt	1.7	17.5	0.3
Deutzia crenata	—	ds	1.7	7.5	0.0
Pieris japonica	—	es	1.5	17.5	0.1
Ilex rotunda	—	et	1.5	17.5	0.2
Morus australis	—	dt	1.5	12.5	0.1
Idesia polycarpa	—	dt	1.4	47.5	1.4
Diospyros japonica	—	dt	1.3	27.5	0.7
Viburnum plicatum var. *tomentosum*	—	dt	1.3	7.5	0.0
Damnacanthus macrophyllus	—	es	1.3	2.5	0.0
Zelkova serrata	—	dt	1.3	47.5	1.0
Ligustrum japonicum	—	es	1.2	2.5	0.0
Wisteria floribunda	—	cl	1.2	12.5	0.1
Pourthiaea villosa	—	ds	1.2	7.5	0.0
Acer crataegifolium	—	dt	1.2	12.5	0.1
Fraxinus sieboldiana	—	dt	1.1	12.5	0.1
Machilus thunbergii	—	et	1.1	27.5	0.4
Euonymus oxyphyllus	—	ds	1.0	7.5	0.0
Albizzia julibrissin	—	dt	1.0	22.5	0.2
Styrax japonicus	—	dt	1.0	22.5	0.3
Fatsia japonica	—	es	1.0	7.5	0.0
Rhamnella franguloides	—	dt	0.8	12.5	0.0

Table 1. *(continued)*

Species name	Abbreviation	Life-form	Frequency (%)*	Maximum diameter class (cm)†	Relative dominance (%)
Weigela coraeensis	—	ds	0.8	7.5	0.0
Prunus verecunda	—	dt	0.7	37.5	0.8
Vaccinium bracteatum	—	et	0.7	12.5	0.1
Sapindus mukorossi	—	dt	0.7	32.5	0.3
Hydrangea macrophylla var. *acuminata*	—	ds	0.7	2.5	0.0
Elaeagnus multiflora f. *orbiculata*	—	dt	0.6	2.5	0.0
Myrica rubra	—	et	0.6	32.5	0.4
Rubus palmatus	—	ds	0.6	2.5	0.0
Lindera umbellata	—	ds	0.6	2.5	0.0
Zanthoxylum piperitum	—	ds	0.6	7.5	0.0
Prunus spinulosa	—	et	0.5	2.5	0.0
Alangium platanifolium var. *trilobum*	—	ds	0.5	2.5	0.0
Zanthoxylum ailanthoides	—	dt	0.5	17.5	0.1
Benthamidia japonica	—	dt	0.4	22.5	0.1
Helwingia japonica	—	ds	0.4	2.5	0.0
Actinidia polygama	—	cl	0.4	2.5	0.0
Ligustrum obtusifolium	—	ds	0.4	2.5	0.0
Ardisia crenata	—	es	0.2	2.5	0.0
Clerodendrum trichotomum	—	dt	0.2	12.5	0.0
Aphananthe aspera	—	dt	0.2	22.5	0.1
Ilex macropoda	—	dt	0.2	12.5	0.0
Actinodaphne longifolia	—	et	0.2	7.5	0.0
Quercus myrsinaefolia	—	et	0.2	7.5	0.0.
Cornus controversa	—	dt	0.2	22.5	0.1
Kalopanax pictus	—	dt	0.2	27.5	0.1
Rhus javanica var. *roxburgii*	—	dt	0.2	7.5	0.0
Rhus trichocarpa	—	dt	0.2	7.5	0.0
Rosa multiflora	—	ds	0.2	2.5	0.0
Prunus incisa	—	dt	0.2	7.5	0.0
Pinus densiflora	—	co	0.2	17.5	0.1
Stauntonia hexaphylla	—	cl	0.1	7.5	0.0
Meliosma myriantha	—	dt	0.1	2.5	0.0
Rhus ambigua	—	cl	0.1	7.5	0.0
Rhododendron obtusum var. *kaempferi*	—	ds	0.1	2.5	0.0
Quercus serrata	—	dt	0.1	12.5	0.0
Vaccinium smallii var. *versicolor*	—	ds	0.1	2.5	0.0
Clethra barbinervis	—	dt	0.1	2.5	0.0
Lyonia ovalifolia var. *elliptica*	—	dt	0.1	2.5	0.0
Lespedeza bicolor	—	ds	0.1	2.5	0.0
Aralia elata	—	ds	0.1	2.5	0.0
Acanthopanax spinosus	—	ds	0.1	2.5	0.0
Deutzia gracilis	—	ds	0.1	7.5	0.0
Acer palmatum var. *amoenum*	—	dt	0.1	12.5	0.0
Euonymus alatus f. *ciliato-dentatus*	—	ds	0.1	2.5	0.0
Viburnum erosum var. *punctatum*	—	ds	0.1	2.5	0.0
Philadelphus satsumi	—	ds	0.1	2.5	0.0
Viburnum dilatatum	—	ds	0.1	2.5	0.0
Total					100.0

*The % occurrence in the 840 quadrats.
†The medians of the diameter size classes at 5 cm intervals.
Co, conifer; et, evergreen broad-leaved tree; es, evergreen shrub; dt, deciduous tree; ds, deciduous shrub; cl, climber.

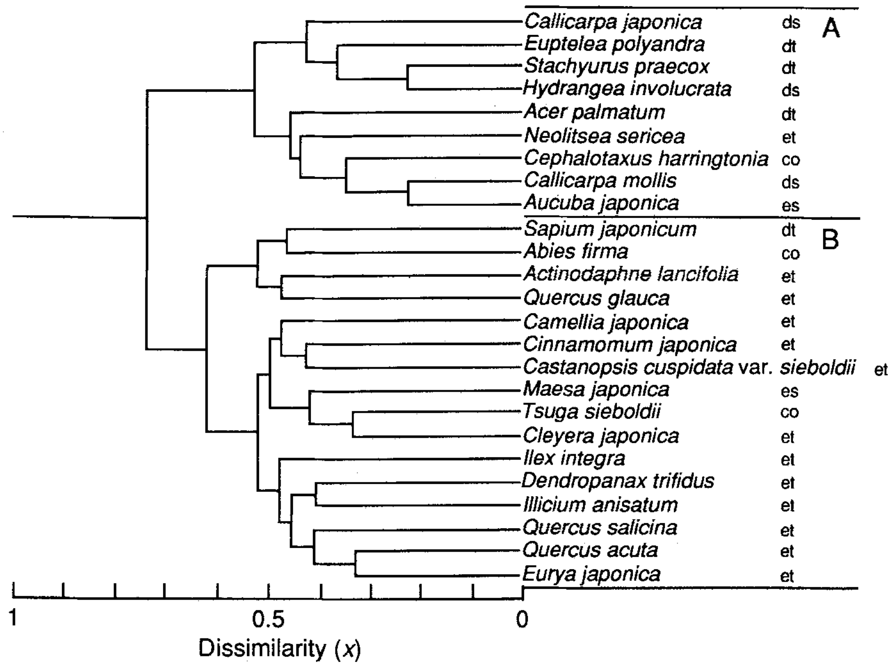

Fig. 3. A dendrogram obtained by cluster analysis using the dissimilarity index (x) values, which represent dissimilarity of spatial distribution pattern (see text) of the 25 major species. In the figure, co = conifer; et = evergreen broad-leaved tree; es = evergreen shrub; dt = deciduous tree; ds = deciduous shrub.

plants of group B were mainly distributed in the ridge sites. Basal areas of the two groups were calculated using the median of the diameter class of each tree or shrub individual. Vegetation types, type A, where plants of group A dominated, and type B, where plants of group B dominated, were determined for each quadrat, based on the RBA of the two groups (Fig. 4c). Table 2 shows the RBA of life forms for the vegetation type. Coinciding with the composition of each group (Fig. 3), the deciduous trees and the shrubs had high RBA in type A, while the conifers and the evergreen broad-leaved trees had high RBA in type B. The total basal areas was smaller in type A, and larger in type B (Fig. 4c, Table 2).

Habitat conditions

Figure 5 shows the distribution patterns of soil depth, canopy types and canopy trees in the study basin.

There was a tendency for soils to be thick around the ridge sites and thin in the valley sites (Fig. 5a). In the ridge sites, thick accumulated aeolian volcanic deposits (Kanto loam) around the main ridge were left behind erosions. On the other hand, in the valley sites, alluvial deposits were less accumulated due to active erosion, and bedrock was exposed in large areas.

Figure 5b shows canopy types of the study basin. While evergreen closed canopies were developed around the ridge site, there were many more deciduous canopies and there was a large area around the valley site where there was a lack of canopy (gap). In the order of evergreen, deciduous and gap, the soils were significantly deeper ($P < 0.05$, Kolmogorov–Smirnov test).

The canopy distribution pattern was decided by the distribution pattern of canopy trees. Figure 5c shows the distribution of trees larger than 30 cm in diameter. They were distributed mainly along ridges. They were *Tsuga sieboldii* (32.5% of total), *Abies firma* (23.2%), *Castanopsis cuspidata* var. *sieboldii* (16.6%), *Quercus acuta* (7.3%), *Quercus salicina* (6.4%), other evergreen trees (4.5%), and deciduous trees (9.5%). The dominant species of canopy trees, which are listed here, all belonged to group B.

The distribution of the vegetation types mentioned above had a close relationship with the distribution of the soils and the canopies (Table 2, Figs 3, 5). The quadrats of type A were located on thinner soils than the quadrats of type B ($P < 0.001$, Kolmogorov–Smirnov test). In gaps, there were more quadrats of type A than quadrats of type B, while under closed canopies, there were more quadrats of type B than quadrats of type A ($P < 0.005$, G test).

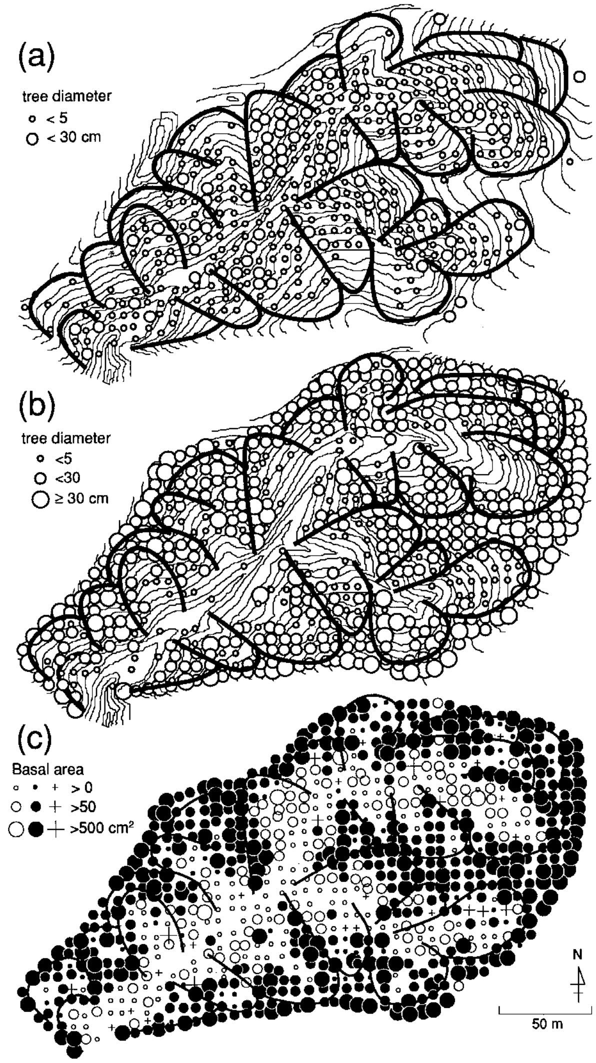

Fig. 4. Distribution of (a) species group A and (b) species group B obtained from the cluster analysis (Fig. 3). The circles in the figure show the diameter class of the largest tree of the group in each quadrat. In (c), vegetation type based on the relative basal areas of the two species groups in each quadrat is shown. The basal areas of the groups were calculated using the median of the diameter class of each tree or shrub. Vegetation type was determined for each quadrat as type A or B, when the plants of group A or B dominated, respectively. If the two groups have the same value, the vegetation type is none. In the figure, open circle, solid circle or cross show that vegetation type is A, B or none, respectively. Total basal areas are indicated as the mark sizes.

Principal component analysis

Figure 6 shows the location of each size class (< 5 cm or ≥ 5 cm in diameter) of each species on the vegetational gradient given by PCA. The shifts of the locations from the small classes (open circles) to the large classes (solid triangles) are shown as lines in the figure. The directions of growth (small to large classes) tended to be opposite between group A and group B in relation to the first axis, while the directions tended to be the same within each group. This indicated that group A was not being replaced by group B in this basin, because, if group A was being replaced by group B, the small size trees of group B tend to co-occur with the large size trees of group A, and there should be continuity in the direction of growth (lines) between group A and group B.

Table 2. Vegetation composition, soil depth and canopy type for groups A and B.

Vegetation type	A	B
Sampling quadrats	247	531
Basal area per quadrat (cm^2)	101.3	856.2
Relative basal area (%)		
Conifer	7.0	60.5
Evergreen broad-leaved tree	7.7	33.4
Evergreen shrub	7.7	0.5
Deciduous tree	69.2	5.3
Deciduous shrub	8.2	0.2
Climber	0.2	0.1
Total	100.0	100.0
Soil depth average (cm)*	14.6	30.1
(Number of cases deeper than 50 cm)	(11)	(80)
Canopy type (%)		
Closed	63.0	94.2
(Evergreen)	(47.0)	(90.1)
(Deciduous)	(16.0)	(4.1)
Gap	37.0	5.80

* In the case where soil depth was deeper than 50 cm, 60 cm was used for calculation, so the averages are underestimates.

DISCUSSION

There were two species groups (groups A and B) in terms of distribution patterns in the basin (Fig. 3). Group B included dominant members of the late-successional communities in this region such as *Castanopsis cuspidata* var. *sieboldii* and *Abies firma*, which formed the canopy of this basin. Although this forest is regarded as a well-developed older one in this region, the distribution range of group B,

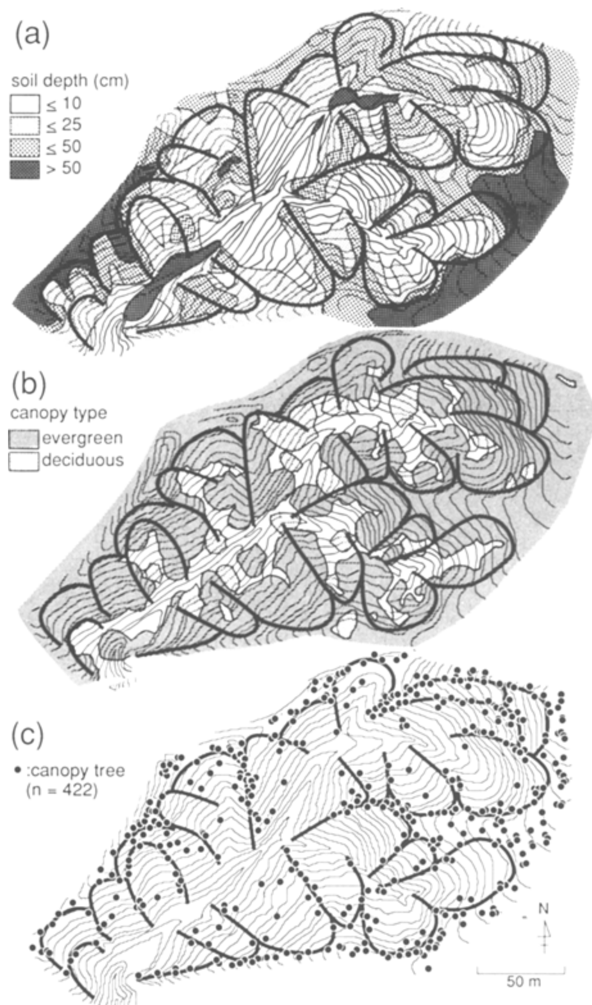

Fig. 5. (a) Soil distribution, (b) canopy distribution and (c) canopy tree distribution in the study basin. The bold lines in the figure show the topographical units shown in Fig. 2b. Counter lines are drawn at intervals of 4 m.

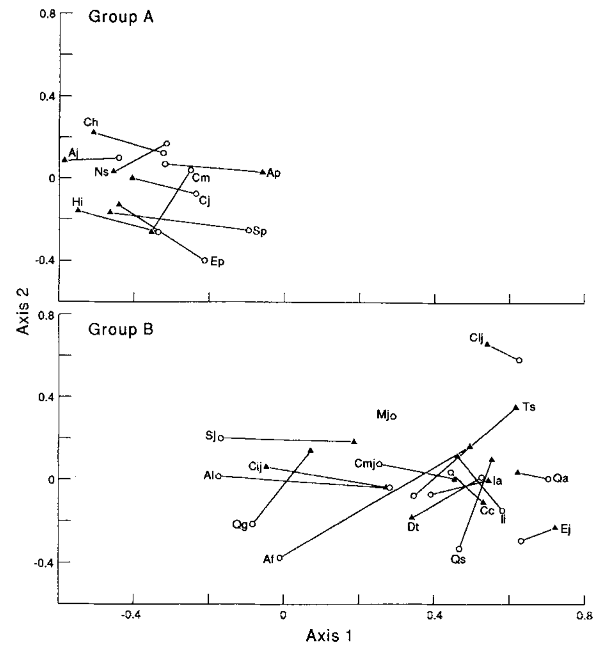

Fig. 6. The position of each species of group A (upper) and group B (lower) on principal component area. The abbreviation in the figure is the species name, shown in Table 1. For each species, an open circle and solid triangle indicate the mean position of individuals which are not more than 5 cm and more than 5 cm in diameter, respectively.

especially of the canopy trees, was limited to a narrow area around the ridge sites (Figs 4b, 5c). There were few plants of group B in the valley sites, and instead, group A plants prevailed. Group A mainly consisted of deciduous trees and shrubs, which are early successional species in the warm-temperate evergreen forests.

The vegetation pattern had a close relationship with the geomorphic process of the study basin. The steep slopes with many small cliffs are actively eroded; however, the erosion activity is not homogeneous throughout the basin, and small-scale ridge–valley structure (the topographical units) develops at 10^2 to 10^3 m^2 order (Fig. 2b). The ground surfaces around valleys are unstable (Basnet *et al.* 1992; Hunter & Parker 1993). In this basin, the valley sites of the topographical units, where group A dominated, coincided with the axes of steep concave slopes which are most susceptible to small-scale landslides (Tsukamoto *et al.* 1982; Swanson *et al.* 1988), and more exposed to slope failures or small-scale landslides than the ridge sites. The soil was very thin in the valley sites but thick in the ridge sites (Fig. 5a, Table 2). Coinciding with this, the basal areas were smaller in the valley sites than in the ridge sites (Fig. 4c, Table 2). Tsukamoto *et al.* (1982) and Tsukamoto and Ohta (1988) also recognized a similar topographical pattern as an erosional unit, and named it 'zero-order basin' in similar Japanese hilly and lower mountainous regions. The topographical unit in this basin is probably equivalent to the zero-order basin, and hence, it may be an erosional unit of this basin.

The distributions of two species groups were separated topographically (Fig. 4). The result of PCA indicates that group A (early-successional species) is not replaced by group B (late-successional species). Thus the separation of the two groups correlates with the erosional condition of this basin as mentioned above; repeated disturbance by slope failures or small-scale shallow landslides may prevent invasion of the species of group B in the valley sites. On the other hand, the species of group A are regarded as members of a topographical community, which persist for a long time under such disturbed conditions. It is well known that exogenous disturbances sometimes prevent the proceedings of successions (e.g. Oliver & Larson 1990). For example, in northern hardwood and coniferous forests of north America, some shade-intolerant tree species such as *Betula papyrifera* var. *cordifolia* (Leak 1975) and *Betula papyrifera* (Leak 1991) persist for a long time on unstable sites due to repeated ground surface disturbances which prevents the establishment of shade-tolerant species, and Leak (1991) named them 'persistent successional species'. In this basin, the species of group A are regarded as persistent successional species. The persistent successional species are sometimes highly resistant to physical disturbance (Langenheim 1956; Basnet *et al.* 1992) with abilities such as vegetative regrowth from damaged stems (Langenheim 1956). In this study basin, *Euptelea polyandra* Sieb. et Zucc. and *Hydrangea involucrata* Sieb., which belong to group A, are suggested to be such species (Sakai & Ohsawa 1993). *Aucuba japonica* Thunb., the most abundant evergreen shrub species among group A, may also be such a species because it can maintain the genets by vegetative reproduction on unstable ground surfaces of valley heads (Isobe & Kikuchi 1989).

The distribution pattern of canopy trees (Fig. 5c) is controlled by the erosional condition in the basin as mentioned above; in the valley sites, large areas lacked canopy cover, while a closed canopy was developed in the ridge sites. In other words, the distribution pattern of the canopy gaps is subjected to the erosional condition of the basin. The distribution patterns and frequencies of the canopy gaps are studied in detail in the cases where the causes of gaps are mainly senescence of trees (e.g. Pickett and White 1985; Yamamoto 1992). However, the role of geomorphic processes in the distribution pattern of canopy gaps has not yet been fully studied. Ohsawa (1981) reported that deciduous trees invade under canopy gaps which developed along the concave slopes at the river heads in an evergreen, lower subalpine coniferous forest of Japan. Hunter and Parker (1993) revealed that in an old-growth, mixed evergreen forest in California, the main causes of the canopy gaps are slope failures, and the canopy gaps occupy larger areas in concave slopes than convex and plane slopes. They discussed that the appearances and the distribution of canopy gaps depend on the disturbance regime governed by erosional conditions of the area. Also in this study basin, many of the canopy gaps seem to have resulted from slope failures or small-scale shallow landslides.

In a previous paper (Sakai & Ohsawa 1993), it was shown that the vegetation pattern in a landslide scar, which was located in a neighborhood basin of the present one, was determined by the ground-surface disturbance regime within the landslide scar. The present results also revealed a similar relationship between the vegetation and topography. Thus, in this hilly region on two levels of a topographical hierarchy, one at a single landslide scar, and the other a river basin, the geomorphic process is suggested to be important as a causal mechanism which determines the vegetation pattern.

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