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Relationship between Micro-landform and Vegetation Structure in an Evergreen Broad-leaved Forest on Okinawa Island, S-W. Japan

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Abstract The relationship between micro-landform and vegetation structure was examined in a quadrat (15 m × 50 m) set up to cover a slope from the ridge to the valley bottom in an evergreen broad-leaved forest on Okinawa Island, S-W. Japan. Based on an erosion front, the slope was divided into two parts: upper slope and lower slope, each of which comprised two micro-landform units. The upper slope was composed of the crest slope and the upper side slope, and the lower slope was composed of the lower side slope and the bottomland. There were large differences in stand structure and species distribution between the upper and lower slopes. The tree density in the understorey was less and the size of the largest trees and the basal area per unit area were both considerably less on the lower slope than on the upper slope. The spatial distributions of many tree and shrub species including dominants such as *Castanopsis sieboldii* ssp. *lutchuensis* and *Distylium racemosum* were mostly restricted to the upper slope, whereas only a few species such as *Turpinia ternata* were confined to the lower slope.

Key words: micro-landform, evergreen broad-leaved forest, erosion front, vegetation structure, Ryukyu Islands, *Castanopsis*, *Distylium*.

Landform is one of the most important factors determining the vegetation pattern on a micro-spatial scale within the same climatic region. In hilly or mountainous areas particularly, complicated micro-landforms offer various habitats for plants and bring about a fine mosaic pattern of vegetation. Many studies have shown relationships between the spatial arrangement of micro-landform units and the vegetation pattern or plant species distributions (Hack and Goodlet, 1960; Miura and Kikuchi, 1978; Tamura and Takeuchi, 1980; Ishizaki and Okitsu, 1988; Kikuchi and Miura, 1991, 1993; Sakai and Ohsawa, 1993, 1994).

In recent studies, the stability of the land surface has been noted as a factor affecting the vegetation pattern in relation to micro-landform. Sakai and Ohsawa (1993, 1994) showed that the invasion of late-successional species was prevented at valley sites because of repeated disturbance of land surfaces; early-successional species persisted there. Other studies (Tanaka, 1985; Kikuchi and Miura, 1991; Shimada, 1994) have also shown that vegetation on unstable slopes, which are frequently disturbed, is often composed of pioneer or successional species. In terms of the spatial structure of micro-landforms, Kikuchi and Miura (1993) showed that a hillslope can be divided into two: the upper and lower hillslopes, whose boundary corresponds to the erosion front or the dissected front introduced by Hatano (1986). The lower hillslope, which is located below the erosion front, is characterized by relatively active processes of soil erosion, landslides and slope failure (Tamura, 1987).

Well-developed evergreen broad-leaved forest remains in the northern part of Okinawa Island. Several phytosociological studies on the vegetation of the Ryukyu Islands including Okinawa Island (Suzuki, 1979; Fujiwara, 1981, 1986) have shown that evergreen broad-leaved forests in this area are different from evergreen forests of mainland Japan in terms of floristic composition. However, there are no studies on the relationship between micro-landform and vegetation in the Ryukyu Islands.

This paper deals with the relationship between micro-landform and vegetation structure in a well-developed, evergreen broad-leaved forest of Okinawa Island. In particular, species distribution and stand structure above and below the erosion front are verified.

Study Area

The study site (26°45′N, 128°05′E) is situated in compartment 76 of the Forestry Experiment Station of University of the Ryukyus, being located in the uppermost drainage area of the Yona River, which runs through the Kunigami Mountains from the east to west in the northern part of the Okinawa Island (Fig. 1). Based on the climatic records at the office of the Forestry Experiment Station in Yona (10 m altitude and 3.0 km northwest of the study site) from 1962 to 1971 (Shinzato and Moromizato, 1972), the mean annual temperature was 21.5°C, the mean temperature of the warmest month, August, was 28.8°C, and that of the coldest month, January, was 13.5°C. The mean annual rainfall was 2630.6 mm. However, the rainfall in this area is known to increase with increase in altitude (Shimabukuro *et al.*, 1975), and thus rainfall over 3000 mm is expected at the study site. Strong winds are frequently brought by typhoons in summer and by monsoonal pressure patterns in winter.

The study area was covered with an evergreen broad-leaved forest whose canopy height was about 10 m on the windy ridge, but over 20 m at more sheltered sites. This is one of the oldest-growth forests preserved on Okinawa Island. The bedrock is composed mainly of Paleozoic slate, on which the red-yellow soil develops (Shinzato and Moromizato, 1972).

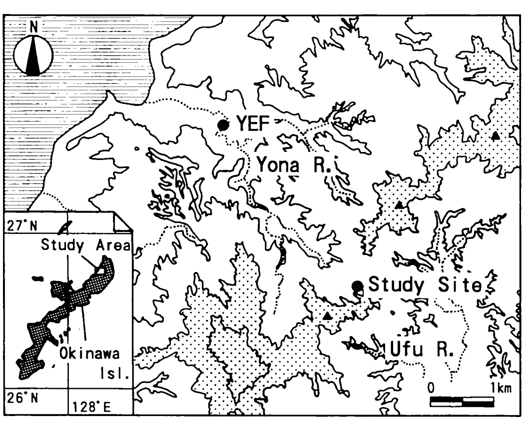

Fig. 1. Location of the study site. The contours are drawn at 100-m intervals. The area above 300 m altitude is shown as sparsely dotted, the river as a dotted line. YEF: the office of the Forestry Experiment Station, University of the Ryukyus, Yona.

Methods

The field survey was carried out in February and May 1990. A rectangular quadrat of 15 m ×50 m was set out on the slope facing south, with its longer side in the direction of the slope. Inclinations were measured with a hand level along four lines which ran at intervals of 5 m, parallel to the longer side of the quadrat. Longitudinal profiles of land surface and a contour map were drawn based on these data. For all trees taller than 2 m in height, species names, trunk diameters at breast height (DBH) and tree heights were recorded. Their locations within the quadrat were also mapped.

The whole area of the quadrat was divided into four micro-landform units: crest slope (CS), upper side slope (USS), lower side slope (LSS) and bottomland (BL), based on the form of the land surface and distribution of micro-landform elements according to the classification system of Tamura (1969, 1974, 1987). In the present paper, CS is combined with USS and called the upper slope (US) and LSS is combined with BL and called the lower slope (LS). The upper margin of LSS, i.e. the boundary between US and LS, corresponds to the line called the erosion front or dissected front introduced by Hatano (1986).

Results

1. Division of micro-landform in the quadrat

The quadrat includes a gentle broad ridge in the uppermost part, a steep slope in the middle part and a valley bottom in the lowest part (Fig. 2-a). The slope exceeds 40 degrees in the steepest part, and the elevational difference between the highest and lowest points in the quadrat reached 29.4 m. Several small cliffs occur across the lower half of the slope (Fig. 2-b). There are no streams in the valley bottom under usual conditions, but there is a small gully running through the floor.

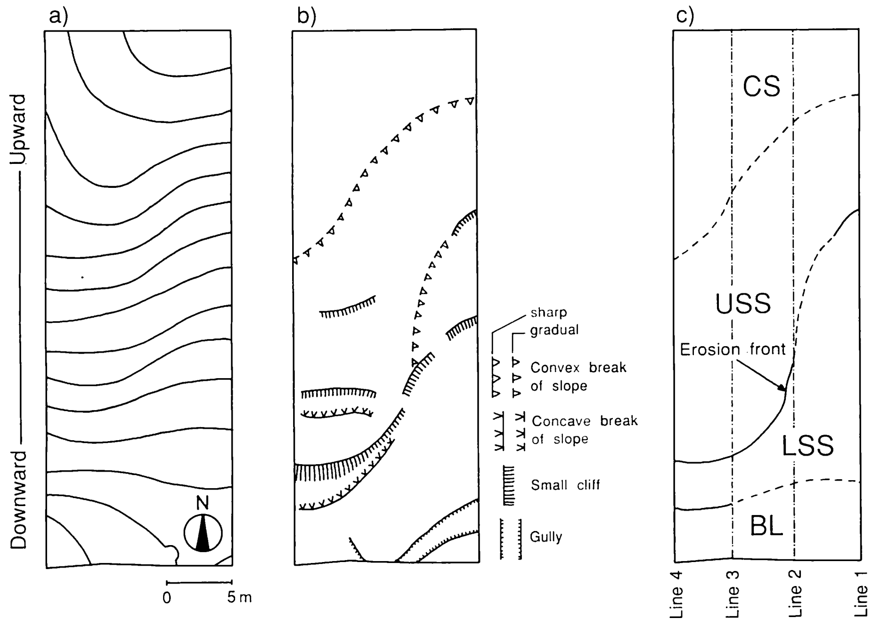

Fig. 2. Contour map (a), distribution of microlandform elements (b) and arrangement of micro-landform units (c) in the quadrat. Contour lines are drawn at intervals of 2.0 m. Sharp boundaries (in part c) are drawn as solid lines and vague boundaries as broken lines. The boundary between USS and LSS corresponds to the erosion front. Lines 1 to 4, along which longitudinal profiles of the land surface were drawn, are also shown on c as dashed and dotted lines.

Longitudinal land-surface profiles in the quadrat (Fig. 3) can be classified into two groups, according to whether or not a concave section occurs (Lines 1 and 2) versus (Line 3 and 4), at the middle part of the slope. Along Line 1, the convex profile in the upper part was interrupted by a small cliff at the point X = 16.0 m and changed into a concave shape downhill. There was also another, smaller cliff at the point X = 23.5 m. The opposite slope, beyond the valley bottom, started from the point X = 40.0 m. The profile along Line 2 was similar to Line 1, but the break into the concave section occurred at a lower point. On the other hand, along Line 3, the slope increased rather abruptly at X = 11.9 m, extending steeply downward. Between this straight slope and the valley bottom, another short but steeper slope intervened. The profile along Line 4 was similar to Line 3, but the shape increased more gradually in its middle part.

Based on the above longitudinal profile and distribution of micro-landform elements, the land surface in the quadrat was divided into four micro-landform units (Fig. 2-c). USS and LSS were clearly delimited, but the boundaries between CS and USS, and between LSS and BL, were only partly clear.

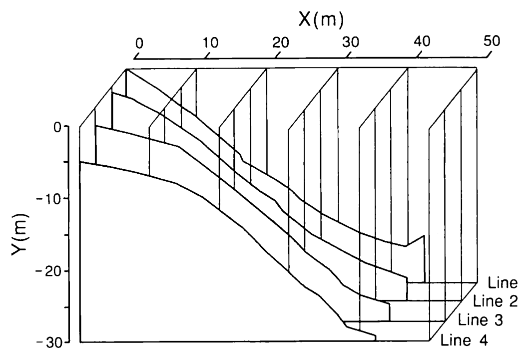

Fig. 3. Geomorphic profiles in the quadrat. For horizontal locations of each profile, refer to Fig. 2-c.

2. Floristic composition

Fifty-four woody species occurred in the quadrat (Table 1). Although the larger DBH classes were composed mainly of several large-tree species, such as *Castanopsis sieboldii* (Makino) Hatusima ex Yamazaki et Mashiba ssp. *lutchuensis* (Koidz.) H. Ohba, *Quercus miya-*

Table 1. The number of trunks in every diameter (DBH) class for all species in the quadrat.

Growth form	Species	DBH class (cm)											Total	RBA (%)
		0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55		
LT	*Castanopsis sieboldii* spp. *lutchuensis*	6	1	1	1	3	4	1	1	1		2	21	28.8
LT	*Distylium racemosum*	58	4	4	1	2	1	2	1		1		74	18.5
LT	*Schima wallichii*		1	1	4	4		2					12	11.5
LT	*Quercus miyagii*	1	1					1		1			4	6.0
ST	*Meliosma squamulata*	16	12	5	4								37	5.1
ST	*Ilex liukiuensis*	5		2	2	1		1					9	4.6
LT	*Machilus thunbergii*	4	1	3				1					8	3.0
ST	*Myrsine seguinii*	22	8	1									31	2.1
ST	*Daphniphyllum teijsmannii*	3	1		2								7	1.8
LT	*Diospyros japonica*						1						1	1.6
ST	*Neolitsea aciculata*	6		1	2								9	1.5
ST	*Dendropanax trifidus*	15	5	1	1								22	1.4
LT	*Diospyros morrisiana*				2	1							2	1.3
ST	*Tutcheria virgata*	5	3										9	1.2
ST	*Eurya osimensis*	0	1	4		1							5	1.1
ST	*Ilex warburgii*	3				1							4	1.1
ST	*Cleyera japonica*	2											3	1.0
ST	*Ilex goshiensis*	5	3		1								9	0.9
ST	*Ternstroemia gymnanthera*	23	5										28	0.7
ST	*Cinnamomun japonicum*	5	2		1								8	0.7
SH	*Tricalysia dubia*	13	1	1									15	0.6
LT	*Schefflera octophylla*	5	3										8	0.6
SH	*Rhododendron tashiori*	6	3										9	0.5
SH	*Turpinia ternata*	2	2	1									5	0.5
LT	*Litsea acuminata*				1								1	0.5
SH	*Randia canthioides*	29	1										30	0.4
ST	*Syzygium buxifolium*	17	2										19	0.4
ST	*Symplocos glauca*	2	1	1									4	0.4
ST	*Elaeocarpus japonicus*	6	1										7	0.2
LT	*Ilex integra*	2	2										4	0.2
ST	*Symplocos prunifolia*			1									1	0.2
ST	*Helicia cochinchinensis*			1									1	0.2
SH	*Ardisia quinquegona*	24											24	0.1
SH	*Psychotria rubra*	6											6	0.1
SH	*Tarenna gracilipes*	8											8	0.1
SH	*Gardenia jasminoides*	2	1										3	0.1
SH	*Symplocos microcalyx*	2	1										3	0.1
SH	*Microtropis japonica*	2											2	0.1
SH	*Eurya japonica*	2											2	0.1
SH	*Skimmia japonica* var. *lutchuensis*	3											3	0.0
LT	*Podocarpus macrophyllus*	2											2	0.0
ST	*Camellia sasanqua*	2											2	0.0
ST	*Cinnamomum doederleinii*	1											1	0.0
ST	*Camellia japonica*	1											1	0.0
SH	*Wendlandia formosana*	1											1	0.0
SH	*Viburnum japonicum*	2	1										3	0.0
ST	*Illicium anisatum*	1											1	0.0
	Total	320	65	28	22	13	6	8	2	2	1	2	469	100.0

Growth form: LT = large tree; ST = small tree; SH = shrub. RBA: relative values of basal area.

gii Koidz., *Distylium racemosum* Sieb. et Zucc. and *Schima wallichii* (DC.) Korthals, many other species occurred in the smaller DBH classes. Many of them were small-tree or shrub species which rarely reached the canopy layer. The proportion of basal area shared with the first dominant species (*C. sieboldii*) was limited to 28.8% total basal area of the stand and the remainder was shared with many other species. Based on the number of trunks, there was no dominant species.

3. Species distributional pattern

The occurrence of every species in areas US and LS was compared using a binomial test (Table 2). The expected number of each species in US or LS was calculated as the total number of plants of each species in the quadrat multiplied by the ratio of the area of US or LS to the total area of the quadrat. The expected numbers were compared statistically with the real number of plants in US or LS. Ten species showed densities significantly higher in US, at the 0.5% or 1.0% level. Most were higher-rank species in the species order viewed from the number of plants occurring in the quadrat (Table 1). Many other species also showed higher densities in US, although this was not statistically significant.

On the other hand, only one species, *Turpinia ternata* Nakai, showed significantly higher densities in LS. *Ardisia quinquegona* Blume and several other species showed distributions skewed to LS, but the differences were not statistically significant.

Examples of tree spatial distributions in the quadrat are shown in Fig. 4 for several species. The first and second dominant species, *Casta-*

Table 2. Binomial test for the distribution of plants in slope portion US versus LS.

Species	Relative no. of plants (%)		Total no. of plants
	US	LS	
Distylium racemosum	93.2**	6.8	74
Meliosma squamulata	83.3*	16.7	36
Myrsine seguinii	96.7**	3.3	30
Randia canthioides	83.3*	16.7	30
Ternstroemia gymnanthera	100.0**	0	28
Ardisia quinquegona	52.2	47.8	23
Dendropanax trifidus	95.2*	4.8	21
Syzygium buxifolium	89.5*	10.5	19
Castanopsis sieboldii spp. *lutchuensis*	80.0	20.0	15
Tricalysia dubia	100.0*	0	14
Schima wallichii	90.9	9.1	11
Ilex liukiuensis	100.0*	0	9
Tutcheria virgata	88.9	11.1	9
Ilex goshiensis	88.9	11.1	9
Rhododendron tashiori	88.9	11.1	9
Machilus thunbergii	75.0	25.0	8
Schefflera octophylla	100.0*	0	8
Tarenna gracilipes	71.4	28.6	7
Daphniphyllum teijsmannii	100.0	0	7
Elaeocarpus japonicus	100.0	0	7
Neolitsea aciculata	66.7	33.3	6
Cinnamomum japonicum	33.3	66.7	6
Psychotria rubra	80.0	20.0	5
Eurya osimensis	80.0	20.0	5
Turpinia ternata	0	100.0*	5
Area (%)	70.8	29.9	—
Area (m^2)	422.0	225.2	—

** and * indicate significantly larger values at the level of 0.5% and 1.0%, respectively. For test procedures, refer to the main text. Only those species having more than four individuals in the quadrat are shown.

nopsis siebodii ssp. *lutchuensis* and *Distylium racemosum*, particularly their larger individuals, were mostly restricted to US. Many other species also showed scattered distributions over CS and USS, but rarely occured below the erosion front, the upper margin of LSS. *Turpinia ternata* was mostly confined to BL.

4. Stand structure in each micro-landform unit

As shown in Table 3, the sizes and densities of trees differed among the various micro-landform units, in particular between US (CS and USS) and LS (LSS and BL). There were trees of larger DBH in US. Basal area values were nearly twice as high in US as in LS.

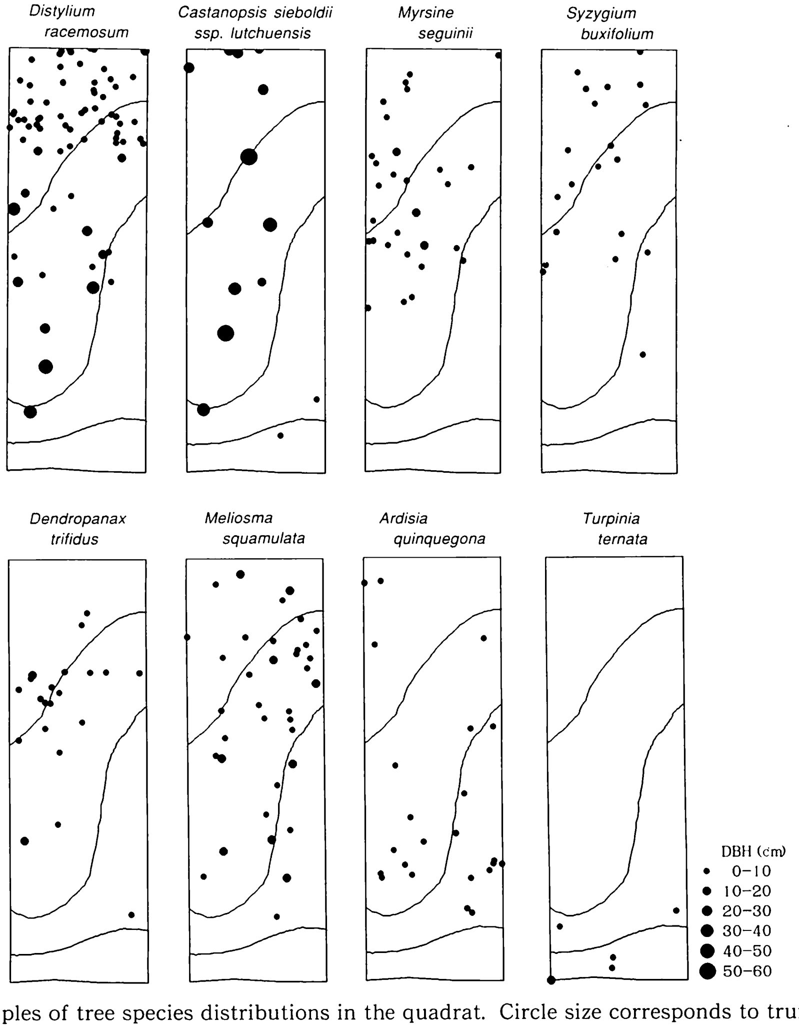

Fig. 4. Examples of tree species distributions in the quadrat. Circle size corresponds to trunk diameter.

Table 3. Comparison of max. DBH, basal area and trunk density among micro-landform units.

Micro-landform unit		Area (m^2)	Max. DBH (cm)	Basal area (m^2/ha)	Trunk density (/100 m^2)
US	CS	159.6	52.6	67.6	119.7
	USS	267.1	50.6	77.1	76.4
LS	LSS	142.2	34.0	36.5	34.5
	BL	79.2	28.4	41.1	31.6

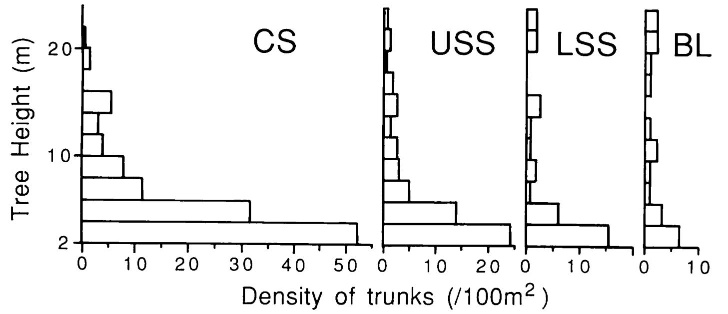

Fig. 5. Height-class distribution of trunks in each micro-landform unit. For abbreviations of micro-landform units (CS, USS, LSS and BL), refer to the main text.

Trunk densities were also considerably higher in US than in LS. Differences between CS and USS and between LSS and BL were relatively smaller. The comparison of tree height-class distributions among micro-landform units revealed that trunk densities in height classes lower than 10 m were considerably lower in LSS and BL than in CS or USS, although the canopy heights and the trunk densities in higher classes were similar (Fig. 5).

Discussion

Clear differences of stand structure and species distribution between the upper slope (US), above the erosion front, and the lower slope (LS) were recognized in this study. Tree density, particularly that of the understorey, was lower in LS than in US. Furthermore, the size (DBH) of the largest plants and the basal area per unit area were considerably smaller in LS. These results suggest that the establishment of plants is more severely hindered in LS than in US, and that the growth or longevity of established plants also differs between the two parts of the slope. Viewed from the distributions of the species, many species were mostly confined to US. In particular, the two dominant species, *Castanopsis sieboldii* and *Distylium racemosum* showed this pattern, which was responsible for the differences in size of the largest trees and basal area in both units.

The importance of the erosion front in dividing habitats within a slope, from ridge to valley bottom, as observed in this study, seems to be common to many forest types in various region, Japan. Kikuchi and Miura (1993) reported extreme differences in species composition of the plant comminity across the erosion front, in a hilly region near Sendai, N-W. Japan. Sakai and Ohsawa (1994) reported that the distribution of late-successional species, including canopy species such as *Castanopsis cuspidata* var. *sieboldii* (synonym of *C. sieboldii*), was restricted to ridge sites, whereas only early-successional species were seen on valley sites in the Boso Peninsula, central Japan. Valley sites in the Boso Peninsula were characterized by repeated disturbance due to slope failures or small-scale shallow landslides, and thus the upper margin of the valley sites seems to correspond to the erosion front.

In this study, only one species, *Turpinia ternata*, was found to characterize the vegetation on LS, although many species showed a distribution which are strongly biased to US. Other species occurring on LS, except for *Turpinia ternata*, were either those which occurred also in US at higher densities or "rare" species which occurred in the quadrat only as a few individuals. Some species such as *Machilus japonica* Sieb. et Zucc., *Diospyros japonica* Sieb. et Zucc., and *Ficus bengutensis* Merrill, however, occur with relatively high frequency along the valley floor adjacent to the plot (Oono, unpublished data). They were not included in the quadrat because of the low plant density. Although the LS is characterized by frequent land-surface disturbances, pioneer species which are common in secondary forests such as *Macaranga tanarius* (L.) Muell. Arg. and *Mallotus japonicus* (Thunb.) Muell. Arg. (Ohsawa and Ohtsuka, 1989) were usually absent or scarce.

In addition to stability of the land surface, many other factors, particularly soil fertility may cause differences in vegetation structure between US and LS. It is known that poor soil fertility on landslide scars, where the mineral soil is often exposed, limits the growth of seedlings there (Guariguata, 1990; Dalling and Tanner, 1995). The growth of trees might be similarly limited, particularly in LSS, because this micro-landform unit is characterized by the most active processes of soil erosion and the most frequent occurrence of landslides or slope failures (Tamura, 1987). Further study is necessary, however, because there has been almost no study of soil fertility in each micro-landform unit or its effect on the growth of trees.

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沖縄本島の照葉樹林における微地形と植生構造の関係

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沖縄本島北部，琉球大学与那演習林内の照葉樹林において，尾根から谷底にかけて 15 m×50 m の調査区を設置し，微地形と植生の関係を調べた．調査区内には，頂部斜面と上部谷壁斜面，下部谷壁斜面，谷底面の 4 つの微地形単位が認められ，それらは侵食前線を境に，上部斜面（頂部斜面と上部谷壁斜面）と下部斜面（下部谷壁斜面と谷底面）にまとめられた．上部斜面と下部斜面では，林分構造や，分布する種に顕著な違いが認められた．すなわち上部斜面に比べると下部斜面では，下層木の密度が低く，また最大個体の胸高直径と単位面積あたりの胸高断面積合計値は小さかった．オキナワジイやイスノキなど林分の優占種を含め，多くの高木種および低木種の分布は上部斜面に偏っていた．一方，分布が下部斜面に偏っていた種はショウベンノキのみであった．