Plant Ecology **132:** 229–241, 1997.

Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan

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Received 15 November 1995; accepted in revised form 10 June 1997

Key words: CCA, Exposure, Forest stature, Monsoon wind, Nanjenshan, Nutrient, RDA, Vegetation classification

Abstract

Soil chemical properties for a subtropical rain forest in the Nanjenshan Reserve, southern Taiwan, were examined to determine soil-landscape and soil-vegetation relationships. Soil sampling sites were separated into four groups based on landscape features and exposure to the prevailing northeasterly monsoon winds. Corresponding vegetation types were delimited along the first DCA axis. The forest showed a drastic change both in structure and floristic composition along the wind-stress gradient. Redundancy analysis (RDA) showed that both topographic variables and vegetation types were needed to explain the variation in soil data. Soil properties that differed significantly among landforms were pH, available N, CEC, exchangeable Al, K, Ca and Mg. Levels of pH, exchangeable Ca and Mg increased in a downslope direction, and exchangeable Al tended to be higher in the upper slope soils. These trends pointed to the importance of slope processes in redistribution of soil minerals. The main differences in soil properties attributed to the influence of the occupying vegetation were apparently aspect dependent. The contents of available N, exchangeable K, and CEC in the 0–40 cm depth of soils under windward low-stature (mostly sclerophyllous) forest were consistently lower compared to those under the leeward forest. For a given catena, however, soil variability associated with vegetation differences seemed to be confounded by the slope processes.

Introduction

The majority of forest soils in the lowlands of Taiwan have been logged or cultivated. Virgin soils that remain are usually found in small isolated stands in preserved areas or steeply sloping sites. The Nanjenshan Nature Reserve of Kenting National Park in southernmost Taiwan, examined in this study, contains 2400 ha of virgin subtropical and semi-tropical forests. The area represents one of the last undisturbed remnants of the lowland forests in Taiwan. Because of its landscape diversity, varying vegetation patterns, and uniform parent material, it affords an excellent opportunity to study the effects of topographic position and vegetation on soil properties without the complications of human activities.

There have been notable attempts to describe and explain the relationships between soils and vegetation (Morison et al. 1948; Webb 1969; Goodland & Pollard 1973; Grubb 1977; Golley et al. 1978; Alban 1982; Gartlan et al. 1986; Haase 1990; Johnston 1992), although no generalities are possible. On the other hand, variation of soil properties within a defined climatic region may also result from topographic heterogeneity (Huddleston & Riecken 1973; Daniels et al. 1987; Honeycutt et al. 1990; Feldman et al. 1991; Brubaker et al. 1993). The resultant soil-vegetation and soil-landscape interrelationships therefore should be expected to be more complex than either of the two considered separately.

Apart from an initial reconnaissance (Jiang 1991), there has been no detailed information concerning soil-vegetation or soil-landscape relationships in Taiwan. The study reported here was conducted to characterize vegetation patterns and soils within a subtropical rain forest of the Nanjenshan Nature Reserve. Interpretation of this information was aimed at assessing the joint effect of topography and vegetation on chemical properties of surface soils of the region.

Study area

The study area (22°03′34″, 120°51′13″) is situated on the east side of a mountain range near the coast of the Pacific Ocean in southern Taiwan (Figure 1). It is part of the Nanjenshan Nature Reserve in the north portion of the Kenting National Park. The site has moderate relief with slopes most frequently between 10 and 30%. Its elevation varies from 300 to 335 m above sea level. The exposed geologic strata consist of interbedded strata of sandstone and shale of Miocene age. The soils have $>$ 45% clay, and are classified as fine, mixed, hyperthermic, Typic Paleudults with highly weathering and pedogenesis (Jiang 1991). Soil depth ranges from 40 to 60 cm to bedrock.

Weather data from a station within the plot (1992-1994) indicate that the annual rainfall varies from 2144 to 2500 mm with ca. 75% of the total falling between May and August. However, the rainy events are well spread throughout the year. The mean annual temperature is 21° with mean monthly temperature varying from 17.2 (January) to 26.4° (August). Episodes of windy weather are associated with southward extension of the Mongolian high-pressure systems during the period from November to April. These northeasterly monsoon winds usually last for several days and can reach velocities of up to 10 m s^{-1}.

The forest of the reserve was classified as monsoon rain forest (Su and Su 1988), but earlier referred to as tropical rain forest (Schimper 1903; Liu 1968). It may be categorized as the *Machilus-Castanopsis* zone in the system of Su (1984) and is a constituent of the evergreen oak-laurel forest in Taiwan.

Methods

Field and laboratory procedures

Field work was carried out between July 1989 and October 1990. A permanent 3 ha plot was established in the Nanjenshan forest. The plot measures 100 m in a north-south direction, by 300 m in an east-west direction. The plot was designed to place between two ridge crests. A small creek runs from north to south through the study plot. Preliminary field studies showed that a strong pattern of differentiation of the forest was associated with a stress gradient of northeast monsoon winds (Sun et al. 1996). This vegetation asymmetry on the windward and leeward slopes has already been reported elsewhere in the reserve (Cheng & Huang 1986; Su & Su 1988). For current study, we limited our sampling to the southwestern 1 ha of the permanent plot (Figure 2). The 1 ha plot also contained major landscape features and vegetation patterns of the reserve. Within the plot, a 10 $\times$ 10 m grid system was installed using transits, taps, and stadia rods. A topographic map was constructed from data on aspect and incline at each of the grid corners. Within each 10 $\times$ 10 m quadrat, identity and diameter at breast height (dbh) were determined for all woody stems $\geq$ 1 cm dbh. Nomenclature was taken from Flora of Taiwan (Li et al. 1975–1979).

Sampling sites of soils were separated into four groups based on topographic position and exposure to the prevailing northeasterly winds: ridge, windward slope, creek and leeward slope (Figures 2A, B). Eight to twelve quadrats, totally 40, were randomly selected on each of the four major landforms. For each sampling site, aspect, slope and elevation relative to the creek bed were determined. An aspect of 45° (the prevailing wind direction) was set to 180° and all aspects were coded 0–180° symmetrically from southwest (leeward) to northeast (windward). Within each quadrat, a soil pit was dug near the quadrat center. Samples were obtained from three horizons: 0–20 cm (layer 1), 20–40 cm (layer 2), and 40–60 cm (layer 3). These samples were then air dried and passed through a 2-mm sieve.

All procedures for soil chemical properties were performed according to the USDA-SCS (Soil Survey Staff 1984). Soil pH was measured with combined electrodes in a 1:1 soil/water suspension. Organic C was determined by a modified Walkley-Black procedure. Exchangeable K, Na, Ca, Mg and CEC were extracted using 1 M ammonium acetate (pH 7.0). Exchangeable Al was exchanged with 1 M KCl. The concentrations of K, Na, Ca, Mg and Al were measured by an atomic absorption spectroscopy (Hitachi, 180–30 type). The available N of soils, after incubation at 40 °C for two weeks, was extracted with 2 M KCl and then determined by the Kjeldahl distillation method. Available P was measured by the Bray No. 1 procedure. All chemical analyses were carried out in duplicate and the final determinations of soil properties were obtained by averaging these values.

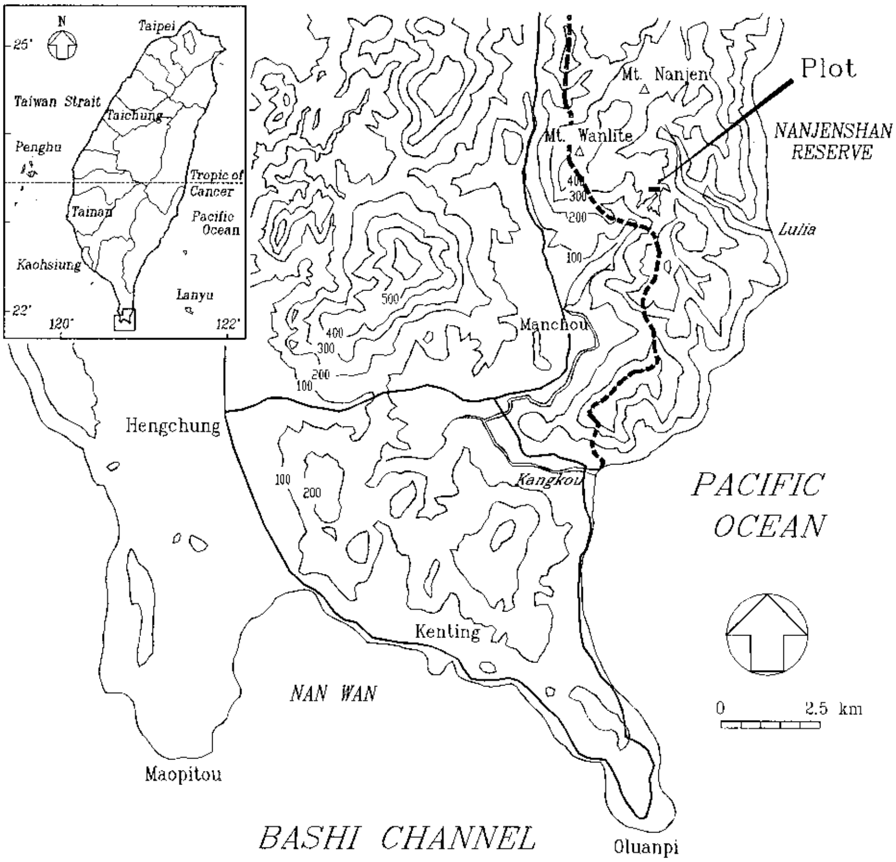

Figure 1. Map of the Hengchung Peninsula with the location of the study plot (denoted by a black square) in Nanjenshan Reserve.

Data analysis

An importance value (IV) for each species in each quadrat was calculated as one-half the sum of the relative density and relative basal area. To reveal vegetation and species patterns, both correspondence analysis (CA) and detrended correspondence analysis (DCA) were carried out. All species were included. Species richness (number of species) and species diversity were measured at site scale. Species diversity values were calculated as Simpson's index, the Shannon index and Hill's N1 index (Hill 1973), where N1 measured the number of abundant species in the sample.

Differences in soil properties among landforms were examined by ANOVA and Duncan's test (GLM procedure; SAS Institute Inc. 1988). In order to obtain a display of the soil-landscape and soil-vegetation relationships, redundancy analysis, RDA was applied to the soil data with topographic properties (aspect, slope and elevation) and vegetation types as external variables. RDA is a linear multivariate technique for relating two sets of variables (here the set of soil properties and the set of topographic properties or vegetation types). To corroborate and assist the interpretation of the soil-landscape relationship found in RDA, Pearson's correlation coefficients were calculated between soil properties and topographic variables. To test which variables best explained the soil data, a forward selection of the variables was carried out by means of a Monte Carlo permutation test (ter Braak 1990). To test if the topographic variables alone are sufficient to explain the soil variation, a partial RDA was applied with topographic variables as covariables and vegetation types as variables of interest. Similarly, to determine the variance explained by vegetation types, vegetation types were treated as covariables. In addition, constrained ordination with canonical correspondence analysis (CCA) was applied to summarize variation in species composition related to soil properties and topographic variables. All ordinations, including DCA,

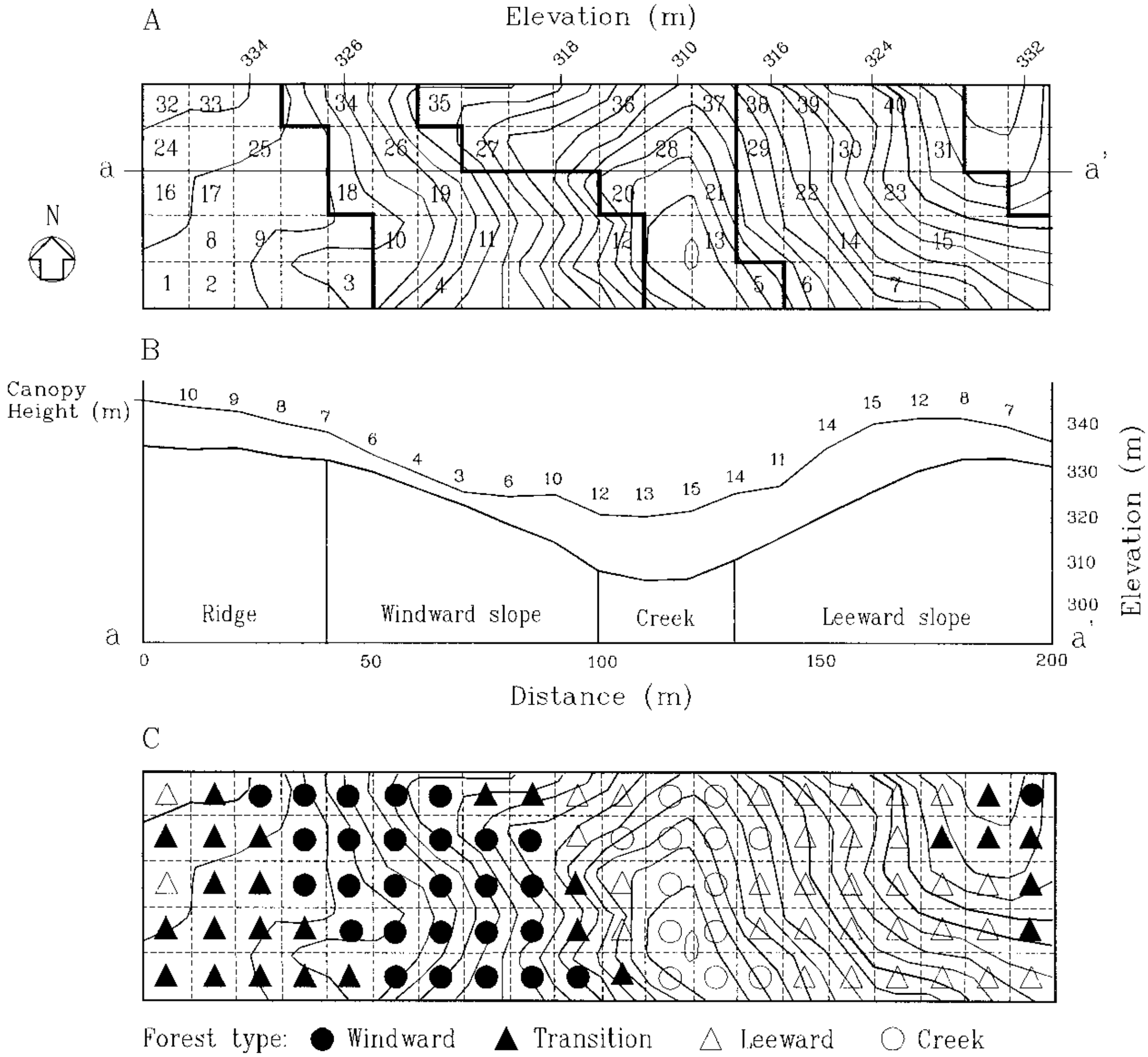

Figure 2. Topographic map of the 1-ha plot. (A) Location of the 40 soil sampling sites. Landforms are delimited by solid lines. (B) Cross-section profile across the study plot. (C) Distribution of four vegetation types based on the quadrat groups delimited along the first DCA axis.

CA, RDA and CCA, were performed using CANOCO version 3.1 (ter Braak 1990). Due to a low content of organic C, ten samples in layer 3 were omitted from the analysis.

Results

Vegetation pattern

A total of 10894 stems of 104 woody species, representing 70 genera and 36 families, were found in the plot. The largest family was Lauraceae (11 species), followed by Fagaceae (10), Rubiaceae (8), Theaceae (8), Euphorbiaceae (7) and Aquifoliaceae (6). The dominant species were, in order, *Castanopsis carlesii* (Fagaceae), *Illicium arborescens* (Illiciaceae), *Daphniphyllum glaucescens* subsp. *oldhamii* (Daphniphyllaceae), *Ilex cochinchinensis* (Aquifoliaceae) and *Schefflera octophylla* (Araliaceae). In general, the forest showed a high density and an intermediate basal area (38.9 m^2 ha^{-1}).

As expected, the first eigenvalues of DCA and CA are quite high (0.55 for both DCA and CCA), relative

Table 1. Composition and species diversity of the Nanjenshan forests. Density (DEN) is given in stems ha^{-1} and basal area (BA) in m^2 ha^{-1}. Importance value (IV) is one-half of the sum of the relative density and relative basal area. Only the 52 species with overall IV $\geq$ 0.4 are given (in parentheses are the values of the 40 quadrats for soil sampling). Species order is based on species scores along the first DCA axis.

	Windward forest			Transition forest			Leeward forest			Creek forest		
	DEN	BA	IV	DEN	BA	IV	DEN	BA	IV	DEN	BA	IV
Cyclobalanopsis championii	332	6.04	6.89	0	0	0	3	0	0.02	8	0.01	0.11
Rhaphiolepis indica var. *hiiranensis*	936	3.45	6.34	4	0.06	0.11	0	0	0	0	0	0
Syzygium buxifolium	1604	2.45	6.68	73	0.18	0.61	3	0	0.03	8	0	0.08
Eurya hayatai	2032	2.09	7.48	165	0.35	1.38	3	0.01	0.02	54	0.02	0.53
Ilex triflora kanehirai	693	1.25	3.17	54	0.79	1.22	9	0.04	0.08	0	0	0
Microtropis japonica	1261	0.65	3.64	104	0.11	0.67	55	0.1	0.55	8	0	0.08
Gordonia axillaris	379	1.07	2.3	65	0.58	1.07	0	0	0	0	0	0
Ilex matsudai	1300	1.28	4.6	158	0.58	1.48	48	0.27	0.74	0	0	0
Pasania formosana	118	2.15	2.48	15	0.16	0.29	0	0	0	0	0	0
Podocarpus philippinensis	471	0.47	1.72	123	0.36	1.19	15	0.05	0.16	0	0	0
Garcinia multiflora	400	0.33	1.38	77	0.4	0.93	45	0.09	0.35	15	0.06	0.24
Osmanthus marginatus	911	2.24	4.99	254	2	3.9	79	0.41	0.98	31	0	0.28
Illicium arborescens	2300	2.12	9	1223	3.33	10.75	179	0.69	2.05	15	0	0.15
Lithocarpus amygdalifolius	171	0.76	1.46	46	0.83	1.57	27	0.31	0.65	0	0	0
Castanopsis carlesii	493	5.83	8.64	273	9.66	12.62	161	5.49	6.86	8	0.1	0.25
Antidesma hiiranense	439	0.09	1.39	377	0.1	2.1	179	0.04	1.25	23	0	0.25
Daphniphyllum glaucescens ssp. *oldhamii*	825	1.6	4.24	269	2.59	4.48	215	1.92	3.58	115	0.42	2.05
Schima superba var. *kankoensis*	243	0.65	1.38	77	0.52	1.12	30	0.4	0.66	54	0.3	1.35
Elaeocarpus sylvestris	61	0.4	0.84	42	0.94	1.59	33	0.78	1.32	8	0.08	0.23
Symplocos theophrastaefolia	157	0.15	0.69	212	0.57	1.81	73	0.33	1.01	23	0.16	0.5
Decaspermum gracilentum	79	0.15	0.48	73	0.44	0.86	42	0.31	0.59	38	0.05	0.39
Ilex uraiensis	368	0.77	1.75	415	1.09	3.37	264	1.14	3	77	0.21	1.18
Tricalysia dubia	104	0.11	0.44	227	0.31	1.56	112	0.29	1.22	8	0	0.07
Magnolia kachirachirai	114	0.1	0.44	119	0.55	1.42	58	0.88	1.29	15	0.07	0.39
Cyclobalanopsis longinux	104	0.55	1.1	258	2.5	4.59	227	3.18	5.12	23	0.16	0.58
Ilex cochinchinensis	479	0.39	1.81	654	1.18	4.88	815	1.5	7.6	223	0.21	3.61
Adinandra formosana	86	0.2	0.47	88	0.33	0.94	124	1.28	2.4	77	0.4	1.46
Beilschmiedia erythrophloia	18	0.02	0.12	154	0.39	1.4	133	0.89	1.97	46	0.15	0.69
Syzygium euphlebium	46	0.15	0.42	127	0.55	1.43	124	1.49	2.58	123	0.21	1.54
Sapium discolor	14	0.08	0.17	92	1.18	2.11	55	1.86	2.26	8	0.25	0.45
Psychotria rubra	132	0.02	0.5	846	0.3	4.66	779	0.32	5.74	262	0.18	3.05
Mallotus paniculatus	29	0.01	0.19	115	0.03	0.71	42	0.17	0.73	15	0.01	0.47
Cyclobalanopsis pachyloma	25	0.25	0.32	27	0.44	0.76	55	1.34	1.9	8	0.1	0.39
Pasania brevicaudata	18	0.14	0.26	38	0.67	1.11	30	1.09	2.19	8	0.01	0.26
Diospyros eriantha	36	0.02	0.16	112	0.22	0.91	136	0.54	1.73	46	0.03	0.67
Litsea acutivena	32	0.01	0.16	277	0.29	2.01	306	0.4	2.68	77	0.22	1.46
Neolitsea hiiranensis	14	0	0.06	142	0.16	0.96	194	0.63	2.13	92	0.11	1.47
Melastoma candidum	89	0.01	0.28	31	0	0.17	91	0.11	0.86	54	0.03	0.88
Machilus thunbergii	39	0.01	0.19	108	0.3	1.08	158	0.71	2.04	62	0.47	1.67
Astronia ferruginea	139	0.58	1.29	58	0.55	0.93	64	0.61	1.6	215	2.24	6.14
Beilschmiedia tsangii	79	0.04	0.29	227	0.28	1.61	200	0.97	2.54	85	0.52	3.38
Sloanea formosana	4	0	0.01	35	0.08	0.26	88	1.18	2.11	23	0.04	0.38
Prunus phaeosticta	14	0.02	0.1	38	0.06	0.26	97	0.29	1.1	54	0.06	0.75
Ardisia quinquegona	4	0	0.01	65	0.01	0.34	161	0.04	1.26	92	0.04	1.37
Castanopsis stellato-spina	4	0	0.01	69	0.19	0.69	70	1.03	1.76	54	1.79	3.74
Schefflera octophylla	46	0.16	0.42	162	0.61	1.75	173	4.3	6.2	238	6.09	15.01
Helicia formosana	0	0	0	42	0.04	0.33	124	0.14	1.14	262	0.43	4.6
Ficus fistulosa	4	0.01	0.03	19	0.02	0.17	42	0.1	0.56	162	0.33	2.62
Pithecellobium lucidum	0	0	0	0	0	0	100	0.63	1.58	146	1.59	5.67
Wendlandia formosana	0	0	0	23	0.04	0.21	103	0.38	1.2	323	1.29	7.56

Table 1 continued.

Alniphyllum pterospermum	0	0	0	4	0.03	0.07	6	0.27	0.26	69	3.76	8.22
Evodia merrillii	0	0	0	4	0	0.03	42	0.04	0.32	131	0.43	3.65
Subtotal	17243	38.9	90.8	8262	37.0	90.5	6173	39.0	90.0	3485	22.6	89.8
Total	19993	41.0	100	9358	39.9	100	7052	42.1	100	4123	24.2	100
Number of species		76	(61)		88	(75)		87	(79)		71	(56)
Simpon's diversity		0.04	(0.05)		0.04	(0.04)		0.02	(0.03)		0.05	(0.04)
Shannon's diversity		3.37	(3.18)		3.63	(3.50)		3.77	(3.70)		3.45	(3.41)
Hill's N1 diversity		29.11	(24.59)		37.58	(33.06)		43.47	(40.35)		31.40	(30.35)

to the second eigenvalues (0.20 and 0.32 respectively). The scattering of the quadrats along DCA axis 1 is exactly similar to that of the CA, therefore, only DCA ordination is considered here. Along DCA axis 1, the sample quadrats extend in a somewhat linear sequence from the most exposed windward slopes to the protected creek bottoms. For clarity, the DCA ordination has been delimited sequentially into four quadrat clusters. The DCA clustering of quadrats, when plotted on the topographic map of the plot, revealed the predominant relationship between forest composition and directional exposure to wind. (Figure 2C). The four quadrat groups, thus identified, were labeled as windward, transition, leeward, and creek forest types. Table 1 presents vegetation characteristics and species diversity for each forest type.

Windward forest

This type comprises 28 quadrats on the northeast- and east-facing slopes. A total of 76 woody species were found in the forest. The trees are densely stocked, usually reach 3–5 m in height. The canopy is apparently windclipped and rather broken. The number of stems is 19993 stems ha^{-1}. The average stem diameter is small (4.7 cm). The basal area of all stems attains 41.0 m^2 ha^{-1}. The most important tree species, as measured by IV, are *Illicium arborescens*, *Castanopsis carlesii*, *Eurya hayatai*, *Cyclobalanopsis championii*, *Syzygium buxifolium*, *Raphiolepis indica* var. *hiiranensis*, *Osmanthus marginatus*, *Ilex matsudai*, *Daphniphyllum glaucescens* subsp. *oldhamii*, *Microtropis japonica*, and *Ilex triflora* var. *kanehirai*. The first eight dominant species account for 49.6% of the stems and 62.2% of the total basal area. *Illicium arborescens* is the most abundant species at all levels of the forest.

Transition forest

The transition forest occupies the areas (26 quadrats) between windward and leeward forests on broad ridges and the lower positions of east-facing slopes. Trees in these areas are not directly exposed to strong winds, but do suffer some degree of wind damage. A total of 88 species and 9358 individuals were recorded in this habitat. The height of canopy trees is between 5 and 8 m, and there is minimal stratification in the forest. The average stem diameter is 6.6 cm. The basal area of all stems attains 39.9 m^2 ha^{-1}. Values for the three diversity indices are generally intermediate between the windward and leeward forests. Windward forest species retaining their prominence include *Castanopsis carlesii*, *Illicium arborescens*, *Daphniphyllum glaucescens* subsp. *oldhamii* and *Osmanthus marginatus*. Some of the dominant species in the leeward forest are also important components here. Examples are *Ilex cochinchinensis*, *Psychotria rubra*, *Cyclobalanopsis longinux* and *Ilex uraiensis*. The first eight dominant species account for 44.8% of the stems and 56.8% of the total basal area.

Leeward forest

This type is composed of 33 quadrats on the southwest- and west-facing slopes. All of these slopes are well protected by mountain ridges. The forest contains 87 woody species and has the highest values of diversity. The height of the canopy trees ranges from 10 to 15 m. The forest has more complicated stratification, although the layers are not very distinct. The trees are upright with intact crowns and few dead or broken branches. Compared to the windward forest, the tree density is much lower, about 7052 stems ha^{-1}. The mean dbh is 7.97 cm. However, the total basal area (42.1 m^2 ha^{-1}) is comparable to that of the windward forest. The principal species are, in order of IV, *Ilex cochinchinensis*, *Castanopsis carlesii*, *Schefflera octophylla*, *Psychotria rubra*, *Cyclobalanopsis longinux*, *Daphniphyllum glaucescens* subsp. *oldhamii*, *Litsea acutivena* and *Ilex uraiensis*. These eight spe-

Table 2. Summary of redundancy analysis of soil data for the first two axes. Correlation coefficients measure the strength of the relation between soil properties and external (topographic and vegetation) variables.

Axis	Layer 1		Layer 2		Layer 3	
	1	2	1	2	1	2
Eigen value	0.18	0.12	0.14	0.11	0.10	0.07
Cumulative% variance	18.20	29.70	13.90	24.80	10.40	17.40
Correlation coefficients	0.72	0.72	0.77	0.66	0.74	0.57
P-value	0.01	0.01	0.01	0.02	0.16	0.51

cies accounts for 37.4% of all stems and 42.4% of the total basal area.

Creek forest
This type is composed of 13 quadrats along the main creek. The trees are generally upright (about 15 m tall), showing no sign of wind-pruning. The creek forest differs from those so far considered in its smallest number (71) of species, and much lower density (4123 stems ha^{-1}) and total basal area (24.2 m^2 ha^{-1}). The average dbh is 8.6 cm, and is the largest among the three forest types. Floristically the forest is quite distinct from those on slopes and ridges. *Schefflera octophylla* forms the major component of the tree stratum, achieving more than 15% of the IV. Other species with IV $\geq$ 3.7% include *Alniphyllum pterospermum*, *Wendlandia formosana*, *Astronia ferruginea*, *Pithecellobium lucidum*, *Helicia formosana*, *Evodia merrillii* and *Castanopsis stellato-spina*. These eight leading species account for 34.9% of all individuals and 72.8% of the total basal area.

Soil-landscape relationships

In Figure 3 the RDA biplots show the positions of 40 soil samples with respect to the first two ordination axes in the upper two layers. Both soil and topographic variables are indicated by arrows. The Monte Carlo permutation test shows that the first two axes are significant ($P < 0.05$) in layers 1 and 2 (Table 2). The results of the partial RDA show that only the topographic variables are more significant than the vegetation types in explaining the soil data. For layer 1 soil, the topography variables alone are sufficient to explain the soil variation. For layer 2, the vegetation types have to be considered as well. The two variables best correlated with the first two axes in layer 1 are elevation and aspect (Table 3). For layer 2, aspect is retained,

Table 3. Correlation coefficients of external variables with the first two axes of redundancy analysis (** significant at the 0.01 level, * significant at the 0.05 level).

Axis	Layer 1		Layer 2	
	1	2	1	2
Topography:				
Elevation	-0.56^{**}	-0.35^{*}	-0.08	-0.50^{**}
Aspect	0.44^{**}	-0.55^{**}	-0.55^{**}	0.11
Slope	-0.02	0.43^{**}	-0.54^{**}	0.17
Vegetation:				
Windward type	0.54^{**}	-0.15	0.21	0.45^{**}
Transition type	-0.18	-0.45^{**}	0.45^{**}	-0.38^{*}
Leeward type	-0.36^{*}	0.27	-0.63^{**}	-0.11
Creek type	0.08	0.35^{*}	0.05	0.08

but slope becomes more important than elevation in defining the first axis.

The RDA biplot for layer 1 is shown in Figure 3A. The ANOVA results (Table 4) indicate that soil properties differing significantly ($P < 0.05$) among landforms are pH, available N, exchangeable K, Ca, Mg, Al and CEC. These variables are represented by longer arrows in Figure 3A, and the angles between arrows are inverse measure of their correlations. Average concentrations of available N and exchangeable K in leeward samples are distinctly higher than in windward samples. CEC is somewhat similar to the trend for available N. The level of exchangeable Al is consistently higher on the leeward slopes, where there does appear to be a trend of increasing exchangeable Al with increasing elevation. Exchangeable Ca and pH values increase monotonically downslope in both windward and leeward soils. Exchangeable Mg also increases downslope, and is related to exchangeable Ca ($r = 0.79$, $P < 0.0001$). Exchangeable K and CEC are the only soil properties that are clearly related to slope differences, perhaps due to greater leaching on the more gentle slopes. The results of correlation

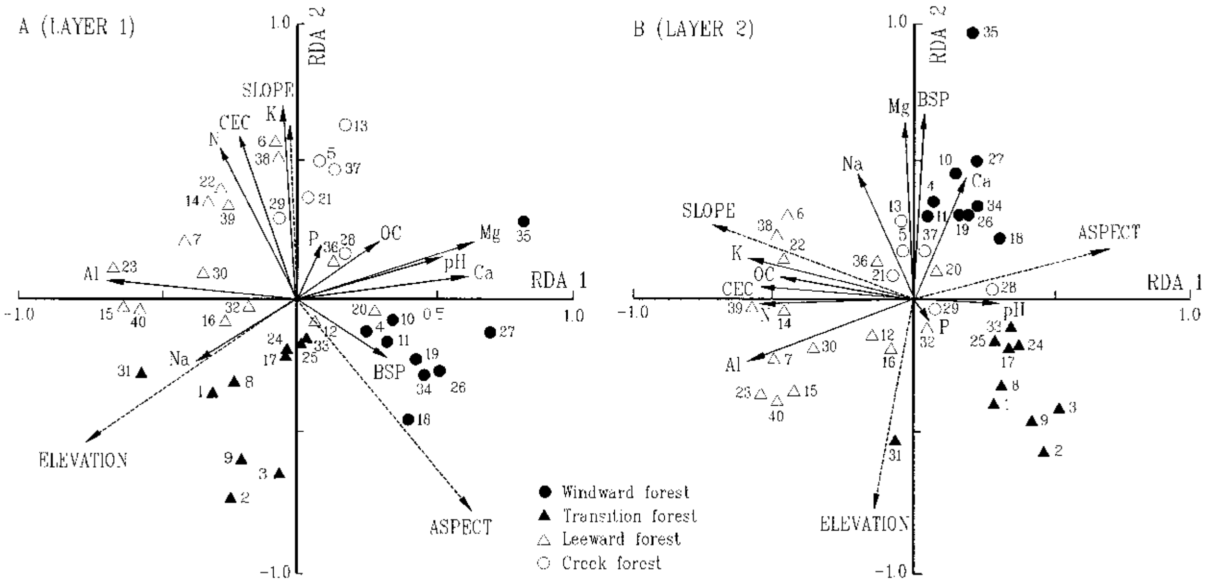

Figure 3. Biplots based on redundancy analysis (RDA) of soil data in the 0–20 cm (layer 1) and 20–40 cm (layer 2) depths. Arrows represent the directions of maximum variation of soil and topographic variables. Soil samples are designated by symbols representing the four vegetation types. N = available N; P = available P; K, Ca, Na, Mg, Al = exchangeable K, Ca, Na, Mg, Al, respectively; BSP = base saturation; OC = organic C; CEC = cation exchange capacity.

tests relating soil properties to topographic variables (Table 5) are generally in close agreement with those of the RDA method.

In a RDA of layer 2, the correlation coefficient is low for elevation (Table 3). Aspect is the major determinant of axis 1 with slope also significantly correlated. The relative higher concentrations of available N, exchangeable Al and K, and CEC are the primary sources of difference between soils on steep slopes and those on the gentle parts of the slopes (Figure 3B; Table 4). On the other hand, the analysis of variance shows higher concentrations of available N and exchangeable K in the leeward soils than in the windward soils (Table 4). On the second axis, elevation is the most important factor. Both exchangeable Ca and Mg increase in a downslope direction, and these trends are somewhat similar to those observed in layer 1.

In layer 3 significant differences among landforms are limited to exchangeable Al content and CEC (Table 4), both of which are somewhat higher in the leeward soils. However, the RDA (not shown) cannot show a clear separation between soils of each landform along the first axis.

Soil-vegetation relationships

When the vegetation types from the DCA are superimposed on the soil RDA diagram, it is clear that both axes 1 and 2 are needed to produce a clear separation of the four vegetation types for layer 1 soils (Figure 3A). As mentioned before, the patterns of exchangeable Ca and Mg, pH, and, to some extent, exchangeable Al seem to be related to a gradient of elevation. The soil samples from both southwest- and northeast-facing slopes run roughly parallel to the elevation arrow (Figure 3A) with the transition and windward forest soils in the lower right region separated from the upper left region of the leeward and creek forest soils. These soils extend in a somewhat linear sequence from ridges to the creek bottoms. This also indicates a generality of soil response to topographic position for a given catena. Consequently, it is difficult to separate topographic and vegetation effects on the soil properties.

When the effects of slope positions are set aside, layer 1 properties that show a striking contrast between vegetation types are evident along the aspect arrow (Figure 3A). This trend is well expressed by CCA. In the CCA ordination (Figure 4A), only the first axis is significant ($P < 0.001$). Unlike the RDA ordination, elevation is no longer correlated with the first axis. The only topographic variable that is capable of

Table 4. Mean values (± SD) of soil properties for the four landforms. Means with the same letter within a row ($\alpha = 0.05$) are not significantly different.

	Layer	Ridge	Windward slope	Creek	Leeward slope
pH	1	4.38 ± 0.13^{b}	4.48 ± 0.14^{b}	4.66 ± 0.31^{a}	4.35 ± 0.15^{b}
	2	4.36 ± 0.15	4.35 ± 0.14	4.41 ± 0.19	4.29 ± 0.11
	3	4.43 ± 0.14	4.44 ± 0.09	4.41 ± 0.16	4.30 ± 0.14
Available N	1	45.89 ± 9.36^{bc}	40.32 ± 6.17^{c}	53.40 ± 5.64^{ab}	60.69 ± 4.02^{a}
(mg/kg)	2	21.13 ± 9.64^{b}	24.45 ± 0.86^{b}	29.68 ± 9.49^{ab}	38.33 ± 1.34^{a}
	3	9.66 ± 5.39	11.91 ± 11.79	20.63 ± 16.58	20.51 ± 9.50
Available P	1	8.55 ± 2.33	8.32 ± 2.94	8.76 ± 2.86	8.11 ± 2.41
(mg/kg)	2	5.77 ± 3.17	5.78 ± 3.92	5.69 ± 2.53	5.42 ± 1.93
	3	3.29 ± 2.20	2.80 ± 0.91	4.26 ± 2.12	3.58 ± 0.78
Exchangeable K	1	0.19 ± 0.06^{b}	0.20 ± 0.03^{b}	0.32 ± 0.09^{a}	0.31 ± 0.11^{a}
(cmol(+)/kg)	2	0.14 ± 0.05^{b}	0.16 ± 0.04^{b}	0.20 ± 0.06^{a}	0.23 ± 0.06^{a}
	3	0.14 ± 0.08	0.18 ± 0.05	0.21 ± 0.07	0.18 ± 0.06
Exchangeable Ca	1	0.50 ± 0.57^{b}	1.02 ± 0.62^{a}	1.03 ± 0.52^{a}	0.29 ± 0.32^{b}
(cmol(+)/kg)	2	0.11 ± 0.08^{b}	0.17 ± 0.13^{b}	0.39 ± 0.44^{a}	0.07 ± 0.03^{b}
	3	0.38 ± 0.73	0.10 ± 0.07	0.24 ± 0.20	0.04 ± 0.03
Exchangeable Na	1	0.18 ± 0.90	0.62 ± 0.63	0.41 ± 0.51	0.91 ± 0.89
(cmol(+)/kg)	2	0.51 ± 0.23	0.81 ± 0.66	0.76 ± 0.70	0.84 ± 0.84
	3	0.26 ± 0.16	0.67 ± 0.24	0.29 ± 0.22	1.20 ± 1.22
Exchangeable Mg	1	0.66 ± 0.33^{c}	1.05 ± 0.29^{ab}	1.11 ± 0.42^{a}	0.74 ± 0.33^{bc}
(cmol(+)/kg)	2	0.34 ± 0.24^{b}	0.65 ± 0.24^{a}	0.67 ± 0.35^{a}	0.49 ± 0.19^{ab}
	3	0.49 ± 0.28	0.74 ± 0.19	0.59 ± 0.29	0.42 ± 0.21
Exchangeable Al	1	2.52 ± 0.33^{b}	2.02 ± 0.34^{bc}	1.79 ± 0.99^{c}	3.33 ± 0.86^{a}
(cmol(+)/kg)	2	2.89 ± 0.79^{bc}	3.36 ± 0.26^{b}	2.46 ± 0.63^{c}	3.96 ± 0.49^{a}
	3	3.14 ± 0.57^{b}	4.08 ± 0.56^{a}	2.76 ± 0.52^{b}	3.92 ± 0.50^{a}
Base saturation	1	40.82 ± 18.50	42.75 ± 11.31	38.78 ± 13.10	27.92 ± 14.49
(%)	2	18.46 ± 5.94^{b}	27.38 ± 15.00^{ab}	32.67 ± 14.04^{a}	21.25 ± 11.62^{b}
	3	21.17 ± 13.88	22.40 ± 2.61	20.38 ± 7.82	26.27 ± 19.19
Organic C	1	1.31 ± 0.16	1.32 ± 0.17	1.42 ± 0.42	1.32 ± 0.19
(%)	2	0.58 ± 0.21	0.65 ± 0.29	0.74 ± 0.27	0.87 ± 0.22
	3	–	–	–	–
CEC	1	6.31 ± 1.08^{c}	6.80 ± 1.04^{bc}	7.57 ± 1.00^{ab}	8.31 ± 0.89^{a}
(cmol(+)/kg)	2	5.88 ± 1.01^{b}	6.52 ± 0.75^{b}	6.21 ± 1.40^{b}	7.72 ± 0.82^{a}
	3	5.80 ± 1.74^{b}	7.57 ± 0.77^{a}	6.62 ± 1.22^{ab}	7.40 ± 0.93^{a}

reflecting composition variation and some of the soil properties is aspect. Along this axis, available N, CEC and exchangeable K are all higher in the soils of the southwest-facing leeward forest and creek forest (in the left half of Figure 4A, comparable to the upper left half of Figure 3A) than in those of the mid-slope northeast-facing windward forest and transition forest (in the right half of Figure 4A, comparable to the lower right half of Figure 3A). The ANOVA results (windward and leeward slopes in Table 4) agree in general with the results of the RDA and CCA ordinations. The RDA and CCA biplots for layer 2 soils with vegetation types superimposed yields a similar pattern (Figures 3B and 4B). In layer 3 differences between forest types are no more significant for all soil properties.

To explore relationships between vegetation structure and soil nutrient contents, soil properties were compared with total basal area, average basal area, density and canopy height. The results indicated that available N and exchangeable K throughout the upper 40 cm soil depths were strongly correlated with canopy height ($r = 0.44$, $P = 0.0001$ for N, and $r = 0.48$, $P = 0.0001$ for K) and average basal area ($r = 0.32$, $P = 0.004$ for N, and $r = 0.26$, $P = 0.018$ for K), and both were negatively correlated with density ($r = -0.26$, $P = 0.018$ for N, and $r = -0.28$,

Table 5. Correlation coefficients between soil and topographic variables (** significant at the 0.01 level, * significant at the 0.05 level).

	Layer 1			Layer 2		
	Elevation	Slope	Aspect	Elevation	Slope	Aspect
pH	−0.50**	0.10	0.22	−0.21	0.06	0.12
Available N	−0.02	0.18	−0.61**	−0.13	0.46**	−0.46**
Available P	−0.14	−0.12	−0.11	0.00	0.02	−0.02
Exchangeable K	−0.37*	0.49**	−0.51**	−0.17	0.52**	−0.54**
Exchangeable Ca	−0.49**	0.01	0.31*	−0.39*	0.08	0.26
Exchangeable Na	0.45**	−0.27	−0.08	−0.17	0.07	−0.10
Exchangeable Mg	−0.56**	0.17	0.25	−0.46**	0.28	0.19
Exchangeable Al	0.53**	0.06	−0.47**	0.41**	0.33*	−0.31
Base saturation	−0.10	−0.24	0.31*	−0.44**	0.09	0.06
Organic C	−0.23	−0.07	0.01	−0.06	0.34*	−0.32*
CEC	−0.08	0.40**	−0.55**	0.07	0.45**	−0.28

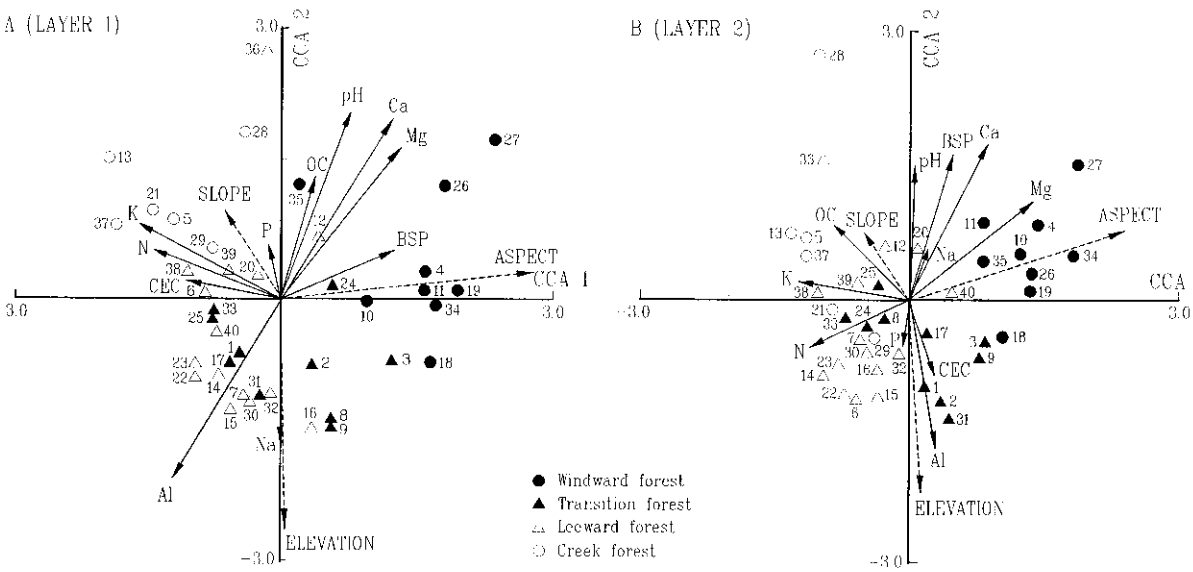

Figure 4. CCA ordination diagrams showing 40 sample quadrats, topographic variables, and properties of: (A) layer 1 soils; and (B) layer 2 soils. Quadrats are designated by symbols representing the four vegetation types. Abbreviations are given in Figure 3.

$P = 0.014$ for K). There was also significantly correlation between CEC and canopy height ($r = 0.04$, $P = 0.0002$). However, none of these soil properties were significantly correlated with the total basal area.

Discussion

The landscape pattern on the plot appears to represent the extreme contrast of climax vegetation types in close proximity, within a defined climatic region, and on soils developed from the same parent materials. The results of the direct gradient analyses and analysis of variance supported that topography position was the most important determinant for the soil properties in the subtropical rain forests of the Nanjenshan Reserve. Levels of pH, exchangeable Ca and Mg tend to increase downslope on both windward and leeward slopes (Figure 3). This pattern may reflect an underlying gradient of soil moisture. It also points to the importance of slope processes which lead to a gradual removal of dissolved materials from linear slope and the accumulation of these materials near the creek site. The greater content of exchangeable Al near the ridge may be the result of lower pH value in that area. Exchangeable Al is also the only important discriminator lower in the profile over all landscape positions, indicating that subsoil horizons act as a considerable sink for Al. The distribution of Na among slope positions was the reverse of Ca and Mg (Figure 3A). It seems that proximity of the ocean and onshore winds may have been responsible for the relative higher concentration of Na on the ridge sites.

It has been pointed out that changes induced in soil chemical properties by species composition are generally superficial (Stone 1975). From this study it seems that soil samples of the top 20 cm are sufficient to establish meaningful correlation between soil and vegetation. Further inspection of the RDA results indicate that all of the three topographic variables account for some portions of the soil variance either on the first axis or the second axis. However, the CCA ordinations show that only the aspect and associated soil properties are significantly correlated with vegetation. From these results we infer that the soil-vegetation relationship is not stronger than the soil-landscape relationship. Nevertheless, the results have shown that differences in soil properties attributed to the influence of the occupying vegetation can be detected even under the strong effects of topographic factors. Such soil differences are especially aspect dependent, as shown in the RDA and CCA biplots (Figures 3A and 3B; 4A and 4B). On the other hand, for a given catena (either northeast- or west-facing slope), differences in soil properties among forests are likely obscured with the complication of slope processes.

Due to differences among plant species in the chemical constituents of above- and below-ground litter, leachates and exudates, differences in the properties of mineral soils may be formed under specific communities growing on a uniform parent material. This reflection is most apparent over broad community gradients (Boerner 1984) or after long periods of occupancy by a specific vegetation type (Alban 1969). In Nanjenshan forests, differences in concentrations of available N, exchangeable K, and CEC between soils of the leeward and windward forests may suggest distinctive nutrient-cycling characteristics of specific communities. As in many other low-stature forests on tropical mountains, the leaves of the trees in the windward slopes of the Nanjenshan area are mostly thick and more or less coriaceous. Low foliar concentrations of N and P have been associated with sclerophyllous leaves in montane forests (Grubb 1977; Tanner 1977; Medina et al. 1990), and it has been suggested that this leaf type is selected in environments where N and especially P are deficient (Beadle 1966; Medina et al. 1990). Comparisons of the foliar (Su 1993) and litterfall nutrient concentrations (Liu 1994) between the two forests under study, however, showed that only N was markedly lower in the windward forest, and was positively correlated with soil concentration of N. This suggests that N appears to cycle less in the windward forest than in the leeward forest.

Topographic features associated with differential drainage regimes and soil properties have been found to be strongly correlated with species distribution on a local scale (Bourgeron, 1983; Johnston 1992). In Nanjenshan forests, however, the topographic-related exposure to wind should be considered as well. As a result, any attempt to correlate small-scale soil heterogeneity with floristic composition will always confounded by other factors and by the ability of plants to alter soils (Newbery & Protor 1984). Nevertheless, the interaction of wind stress and resource availability, particularly light and soil N, has been proposed to explain the physiognomic and floristic differences between the windward and leeward forests (Sun et al. 1996).

An increase in monsoon wind exposure not only affects plant composition in these forests, but also plant diversity. With the exception of the creek bottom forest, both richness and diversity were negatively correlated with exposure (Table 1). It seems that under a heavy wind stress, diversity will be low. The data in soil study also suggested a negative correlation between exposure and soil fertility related factors, including N, K and CEC (Table 4). This indicates that the forest of a relatively higher diversity is more likely to grow on fertile soils. Studies relating species diversity and nutrient availability always show contradictory results. It has been shown that both regular disturbance and lower nutrient availability promote a high diversity (Huston 1980; Wilson & Tilman 1991). Other found a positive correlation between diversity and soil fertility (Whittaker 1977; Palmer 1991). The Nanjenshan data are more likely consistent to the latter.

Although there are few positive correlations existing between soil chemistry and forest stature, a strong correlation has been reported between vegetation structure (height, basal area and density) and soil N, P and K contents in the cerrado vegetation of Brazil (Goodland & Pollard 1973). The present study indicates that the nutrient-poor soils and relatively poor growth condition on the windward slopes may be reflected in the high density of small stems. It therefore seems probable that there is a fertility gradient occurring in the rain forest, and with the mid-slope windward forest and leeward forest representing two opposite segments of the gradient.

This study has shown that within the wet subtropical rain forest in the Nanjenshan area, the topography dictates patterns of slope processes in leaching and accumulation of minerals, and thus the properties of the soils among landscape positions. On the other hand, the soil differences are, to some degree, ascribed to the physiognomic nature of the forests. Although significant differences among landforms were found for most soil properties studied, only available N, exchangeable K and CEC were possibly attributed to vegetation difference.

Acknowledgements

We greatly appreciate the staff of the Kenting National Park for their continuous support, and for permission to use the Research Station at Nanjenshan. Financial support was provided partially by the Kenting National Park and the National Science Council of the Republic of China (NSC-79-0211-B002-06) to C.-F. Hsieh.

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