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Microenvironmental variability and species diversity in treefall gaps in a sub-tropical broadleaved forest

S. K. Barik, H. N. Pandey, R. S. Tripathi & P. Rao
Department of Botany, School of Life Sciences, North-Eastern Hill University, Shillong 793 014, India;
Address for correspondence: R. S. Tripathi, Department of Botany, School of Life Sciences, North-Eastern Hill University, Shillong 793 014, India

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Abstract

Microenvironmental variability and species diversity in gaps and forest understorey were studied to assess the role of treefall gaps in maintaining composition and patchy distribution in a broad-leaved sub-tropical climax forest, Mawphlang, Meghalaya, India. Photon flux density was higher in gaps than in the surrounding understorey. Relative humidity was low and the litter layer was relatively thin in gaps throughout the year. Soil moisture and photon flux density in the gaps significantly varied between seasons and gaps of different sizes. Relative humidity significantly varied between seasons but difference among gaps was insignificant. Among-gap and among-season variations in soil and air temperature were insignificant.

The number of tree species in the gaps was positively correlated with gap area, and tree species abundance showed higher equitability in larger than in smaller gaps. In gaps, α-diversity was highest for herbs and lowest for shrubs. β-diversity was highest for shrubs and lowest for tree seedlings. α-diversity of tree seedlings was higher in the gaps than in the forest understorey. Conversely, β-diversity was higher in the understorey than in the gaps. Low species similarity for tree seedlings among the gaps could be an effect of patchy distribution of parent tree species in the forest. Thus a significant change in light and moisture regimes along the gap size gradient played an important role in influencing the composition and abundance of shade tolerant and intolerant tree species in gaps on one hand, and affected the overall species diversity of the forest, on the other.

Introduction

An understanding of canopy tree replacement processes in treefall gaps provides an insight into the much debated question of whether or not a forest community tends to maintain an equilibrium in its species composition (Hubbell 1984). Tree regeneration in gaps depends on species biology, availability of propagules, and history of the forest community (Hubbell & Foster 1986). Treefall gaps offer specialized regeneration conditions due to prevailing spatial and microenvironmental heterogeneity. Even within a gap, differences in light, moisture and temperature regimes and spatial heterogeneity caused by root, bole and crown zones, create a number of potential regeneration niches. Such heterogeneities have been considered by many workers to be of fundamental importance in the maintenance and promotion of high tree diversity in tropical forest communities (Connell 1978; Denslow 1980). Brokaw (1982a, 1985a, b), Denslow (1980), Hartshorn (1978, 1980) and Whitmore (1974) have independently argued that gap size is a critical variable for the recruitment and establishment of different tree species. Brokaw (1985b) also reported that gap size is positively correlated with colonization of pioneer or shade intolerant tree species in the neo-tropical forest at Barro Colorado Island (BCI), Panama.

The role of gaps in the maintenance of species diversity and regeneration of tree species in climax sub-tropical forests is poorly understood. It is also not clear whether gap disturbance regimes and tree replacement processes in these forests are similar to those in the tropical and temperate forests or to what extent the tree species in the sub-tropical forests depend on microsite variability for their niche differentiation. The present study carried out in a sub-tropical broadleaved forest at Mawphlang, Meghalaya, India, seeks to answer these and other related questions. We studied microenvironmental conditions, composition, diversity and dominance of tree seedlings, shrubs and herbs in the gaps and forest understorey to understand the factors influencing tree regeneration in the forest.

Study area

The study was conducted in an old growth sub-tropical wet hill forest located at Mawphlang, 30 km south east of Shillong (altitude 1500 m, 25° 34′ N, 91° 56′ E) in Meghalaya, India. The climate of the area is monsoonic with an average annual rainfall of 2500 mm, distributed over seven months of the year. In the winter (December to February) the mean minimum temperature is 3 °C, and mean maximum is 16 °C. This season is also characterised by occasional rain with gusty winds. The period from March to mid-May is usually dry and warm with mean annual maximum and minimum temperatures of 22 °C and 16 °C, respectively.

The soils of Meghalaya are derived from the underlying gneisses, schists and granites and may be grouped under the latosol (oxisol) type (Pascoe 1950). The top soil (0–10 cm) in the Mawphlang forest is a sandy loam and shows acidic reaction (pH) 5.3). The mean values of organic matter and nitrogen contents are 5.6 and 0.28%, respectively (Rao *et al.* 1990).

The forest stand covers an area of about 150 ha. It is a sacred grove which has been left undisturbed due to religious belief of the local people and represents the climax vegetation of the area. The forest shows floristic affinity with those occupying lower elevations of the eastern Himalaya (Champion & Seth 1968). The tree component of the forest is dominated by *Quercus griffithii* Hk. f., *Q. dealbata* L., *Q. glauca* Thunb. Bl. and *Schima khasiana* Dyer., while *Symplocos chinensis* (Lour.) Druce and *Daphne shillong* Banerjee are the main shrub components. There is a heavy growth of a large number of species of epiphytic orchids, mosses, ferns and lianas in the forest.

Methods

An experimental area of about 50 ha was surveyed to locate treefall gaps in the forest. A gap was considered as an 'opening in the forest extending down through all foliage levels to an average height of 2 m above ground' (Brokaw 1982b). All gaps larger than 20 m^2, originating either from single or multiple treefalls or branchfalls, were identified and the area of each gap was measured. On the basis of enquiry from the local people and from remnants of fallen trees and successional stage of vegetation in the gaps, all gaps were grouped into age classes of 3–4, 5–10, and > 10 years old. Slope angle and orientation of each gap were measured with a clinometer. Microsite characteristics such as root mats, pits and

Table 1. Physical features and microsite heterogeneity of the treefall gaps in the subtropical broadleaved forset at Mawphlang, India.

Gap number	Area (m^2)	No. of tree falls	Probable cause	Topography	Microsite heterogeneity
1.*	34.3	Single	Branch fall	Level surface	Branch fall debris
2.†	36.3	Single	Tree fall	Level surface	Root mats
3.†	61.0	Single	Natural death	Level surface	Dead tree trunk
4.†	79.5	Single	Tree fall	Level surface	Pits
5.†	107.1	Double	Wind	Level surface	Broken stump and stony surface
6.†	131.5	Single	Tree fall	36° South	Pits
7.†	157.5	Single	Wind	Level surface	Broken stump
8.†	210.0	Single	Tree fall	26° South	Root mats and mounds
9.†	215.0	Double	Tree fall	30° South West	Soil mounds
10.*	335.0	Single	Fire	Level surface	Burnt tree remnants
11.**	723.5	Multiple	Natural, wind, rain	Level surface	Decaying log
12.**	950.0	Multiple	Unknown	60° West	No tree remnants

Note: Estimated age of gap: * 3–4 yrs; † 5–10 yrs; ** > 10 yrs.

mounds (*Sensu* Beatty & Stone 1986) and tree debris at different decompositional stages were also recorded in each gap (Table 1).

The microenvironment of gaps and the surrounding forest understorey were measured at monthly intervals. The climatic and edaphic variables were measured in the centre of the gaps and at five points in the surrounding forest understorey, 5 m away from the gap-edge at 1200 h. The Photon flux density was measured at ground level using an infra-red CO_2 gas analyser (ADC, London) with PAR sensor as an accessory. The relative humidity and air temperature were measured at ground level using a hygrometer and a thermometer, respectively. Soil temperature and soil moisture content were measured down to 10 cm depth using a soil thermometer and a digital moisture meter (OSK-2800, Tokyo), respectively. The

Table 2. Principal components of microenvironmental factors, tree seedling density and total species diversity in twelve treefall gaps in the subtropical broadleaved forest at Mawphlang, India.

Gap area (m^2)	Principal component – 1	Principal component – 2	Tree seedling density (ha^{-1})	Total species diversity (e)
34.3	– 7.173	– 1.260	2621	1.10
36.3	– 7.841	– 0.528	1651	0.98
61.0	– 3.261	– 0.008	1967	1.02
79.5	– 3.083	1.099	1761	1.40
107.1	– 1.415	0.953	747	1.36
131.5	0.570	0.685	836	0.80
157.5	0.025	0.381	380	0.82
210.0	– 0.397	0.153	475	0.90
215.0	3.245	– 0.546	140	0.80
335.0	4.962	0.190	538	0.70
723.5	7.283	– 0.299	995	0.86
950.0	7.084	– 0.819	211	0.80

* Eigen value = 4.778; accounts for ca. 80% of total variation.
** Eigen value = 0.690; accounts for ca. 12% of total variation.

litter depth was determined by line intercept method (Mueller-Dombois & Ellenberg 1974). Monthly and seasonal variation in microenvironmental variables in gaps and understorey was analysed using two-way ANOVA. The first two Principal Components obtained from the Principal Component Analysis of Photon flux density, relative humidity, air temperature, soil temperature, soil moisture and litter depth were used to analyse the variability among gaps with respect to total species diversity and density of tree seedlings (Table 2).

Species composition in the gaps and forest understorey was studied during August–September 1988, when majority of plants are at peak vegetative growth, and the total number and basal area of tree seedlings (height ≤ 20 cm) and shrubby plants in each gap were determined. Density and basal area of herbs were determined by laying 2–10 quadrats of 1 m × 1 m size depending on the size of the gap. In the understorey region surrounding each gap, density and basal area of tree seedlings, shrubs and herbs were also determined. For this purpose, twelve quadrats, 10 m × 10 m size for tree seedlings and shrubs and 1 m × 1 m size for herbs, were laid 5 m away from the gap-edge.

Similarity for gaps and the understorey was measured using presence/absence data of herbs, shrubs and tree seedlings according to Sørensen's similarity index (Sørensen 1948).

Species diversity in the gaps and understorey was determined by using Pielou's evenness index (Pielou 1966), taking relative density and basal cover values together as an index of abundance.

Species diversity of gaps and understorey has been discussed on the basis of α-and β-diversity (Brokaw & Scheiner 1989; Whittaker 1972). Here, α-diversity refers to the mean number of species per gap and β-diversity is the mean similarity among gaps. These indices were also computed for understorey vegetation adjacent to each gap. α- and β-diversities of tree seedlings and shrubs were calculated on the basis of the sampling plot whose area (100 m^2) was close to the minimum gap area (157 m^2) which contained 87% of the total species content of all the gaps. For the computation of β-diversity, gap similarity matrices for herbs, shrubs and tree seedlings were separately prepared using Spatz's similarity index (Spatz 1970).

In the similarity matrices,

$$\alpha_{ij} = R \times \frac{M_c}{M_i + M_j + M_c} \times 100$$

where R is the sum of the fractions obtained by the division of smaller abundance values of species common to both i and j gaps by that of the greater and finally dividing the resulting fraction by the total number of species in the two (i and j) gaps, M_i is the total abundance of all species occurring only in i gap, M_j is the total abundance of all species occurring in j gap and M_c is the total abundance of all species common to both i and j gaps. In order to examine the relationship between gaps and their respective species composition, Principal Component Analysis was used. Total number of individuals of shade tolerant and

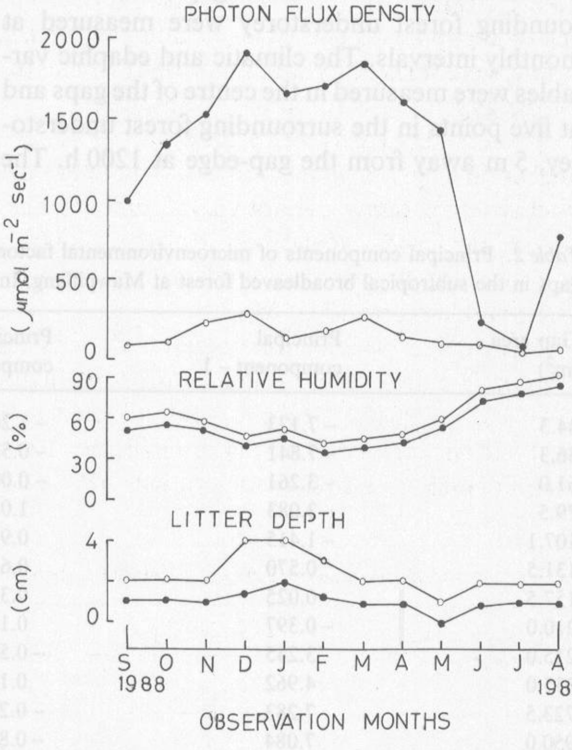

Fig. 1. Monthly variation in microenvironmental factors in gaps and forest understorey. The values for gaps are means of 5 medium sized gaps. Symbols: (●) gap; (○) understorey.

Table 3. Species diversity and total stem density (plants ha^{-1}) in treefall gaps and forset understorey and index of species similarity (%) between the two habitats in the Mawphlang forest.

Vegetation components	Gaps		Understorey		Similarity index (%)
	Species diversity	Density	Species diversity	Density	
Herbs*	0.9	1649 ± 0.5	1.0	17.1 ± 0.3	53.8
Shrubs	0.9	151 ± 4.1	1.0	560 ± 7.9	53.3
Tree seedlings	0.8	1056 ± 21.7	0.86	2160 ± 346.1	93.3

* Density values are $\times 10^3$; ± S.E.

shade intolerant tree species was taken as two variables and the combined species coordinates in each gaps were used to ordinate the gaps (Poole 1974).

Results

Creation and microenvironment of gaps

Heavy rain and wind created most gaps in this forest. Majority of them were caused by uprooting or snapping off of the bole of a single tree and a few were formed by multiple treefall. The area of the gaps ranged from 34 to 950 sq.m.

Photon flux density was significantly ($P < 0.01$) higher in gaps. Soil moisture, soil temperature and air temperature did not vary significantly between gaps and understorey. Relative humidity and litter depth were significantly higher ($P < 0.01$) in the understorey (Fig. 1).

Seasonal as well as among-gap variations for photon flux density and soil moisture were highly ($P < 0.01$) significant (Fig. 2). But difference in soil and air temperature was insignificant. Relative humidity significantly varied ($P < 0.01$) among the seasons, but difference among gaps was insignificant (Fig. 2). Photon flux density increased with increase in gap size in all the four seasons; the increase was less prominent during rainy season. The soil moisture content showed almost a reverse trend. Relative humidity in the gaps was influenced more by the season than by the gap size. Thickness of litter layer in the gaps was affected by gap size, surrounding vegetation and topography. Small gaps with level topography had a litter layer as thick as 3 cm, while the largest gap, located on 60° slope, did not contain any litter at all. Gap size (A) and the first principal component (Y) of microenvironmental variables were positively correlated (Fig. 3) and they showed the following relationship:

$$Y = 0.014A - 3.68 (r^2 = 0.69)$$

Species diversity in gaps and understorey

Diversity of trees, shrubs and herbs was high in the understorey (Table 3). Tree species composition showed 93% similarity between gaps and understorey, while shrub and herb components

Table 4. α and β diversities of different vegetation components in the gaps and adjacent forest understorey.

Vegetation components	α-diversity		β-diversity	
	Gaps	Understorey	Gaps	Understorey
Herbs	11.5	1.6	16.7	2.5
Shrubs	1.6	3.2	17.8	3.8
Tree seedlings	2.9	1.8	10.2	12.5

were less similar between the two habitats in the forest (Table 3).

In the gaps, α-diversity was highest for the herbs and lowest for the shrubs (Table 4). Shrubs having highest β-diversity value, showed greater similarity among the gaps than the other two components. Tree seedlings showed the least similarity among the gaps (Table 4).

In the understorey, α-diversity was highest for the shrubs and lowest for the herbs. Here tree seedlings showed highest β-diversity followed by herbs and shrubs (Table 4). Total species diversity (Y) in gaps yielded the following relationship with gap area (A) and the Principal Component$_{1 \text{ and } 2}$ of six microenvironmental factors which together accounted for about 92% variation.

$$Y = 0.8138 + 0.0006A - 0.053PC_1 + 0.1986PC_2 (r^2 = 0.60)$$

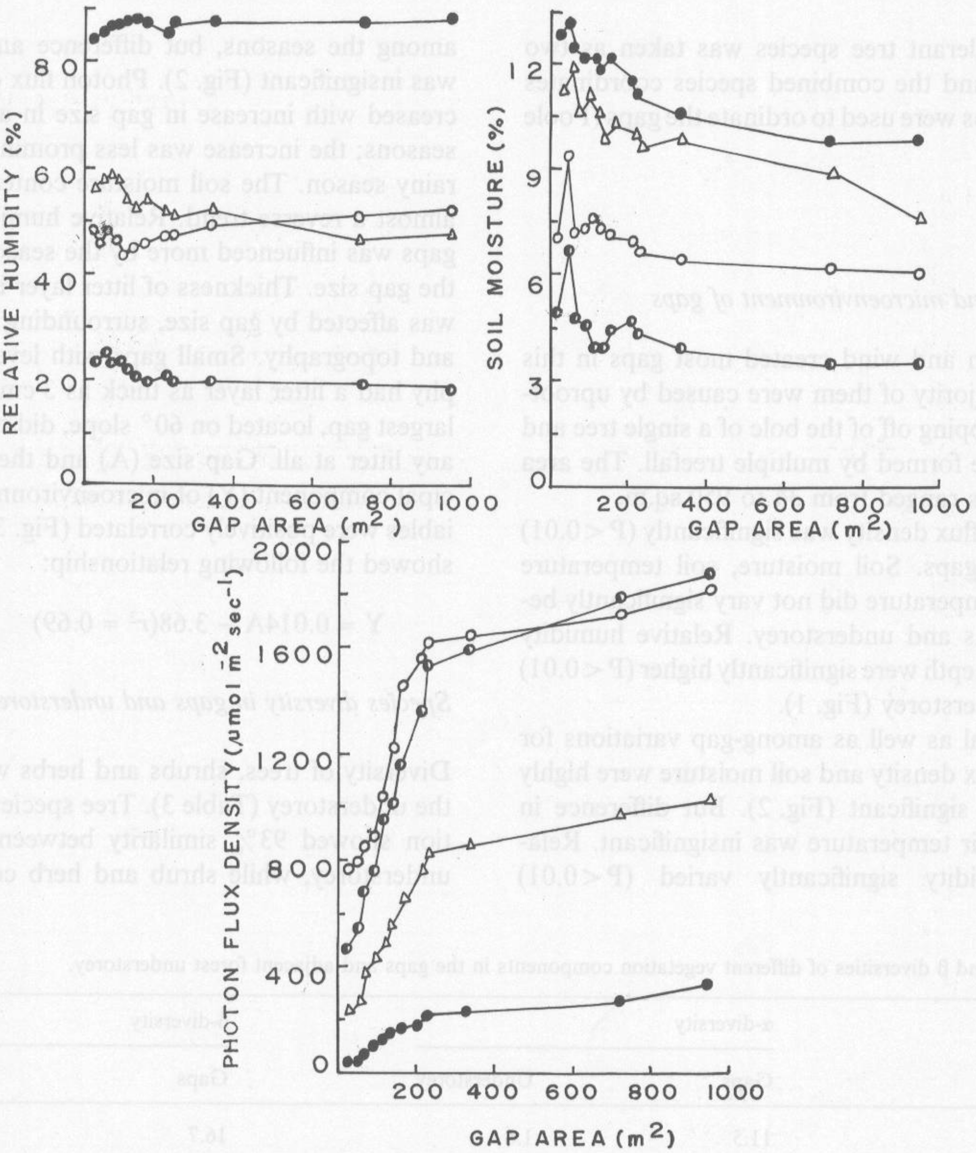

Fig. 2. Seasonal variation in photon flux density, relative humidity and soil moisture content in gaps as a function of gap size. Symbols: (●) rainy (June–Aug.); (△) autumn (Sept–Nov.); (○) winter (Dec–Feb); (○) spring (March–May).

Density and importance value of tree seedlings along the gap size gradient

The cumulative number of species increased upto the gap size of 335 m^2 and then remained constant (Fig. 3b). Tree species richness in the large gaps (Gap Nos. 10 and 11) with level topography was higher than the small gaps as well as the largest gap e.g., Gap No. 12 situated on the slope. Density of tree seedlings (Y) in gaps was negatively correlated with the first principal component of microenvironmental factors (Fig. 3a,c) which exhibited a positive correlation with gap area. Dominance was more equitably distributed among the tree species in the larger gaps than in the smaller ones where 70–80% dominance was concentrated in one species (Fig. 4).

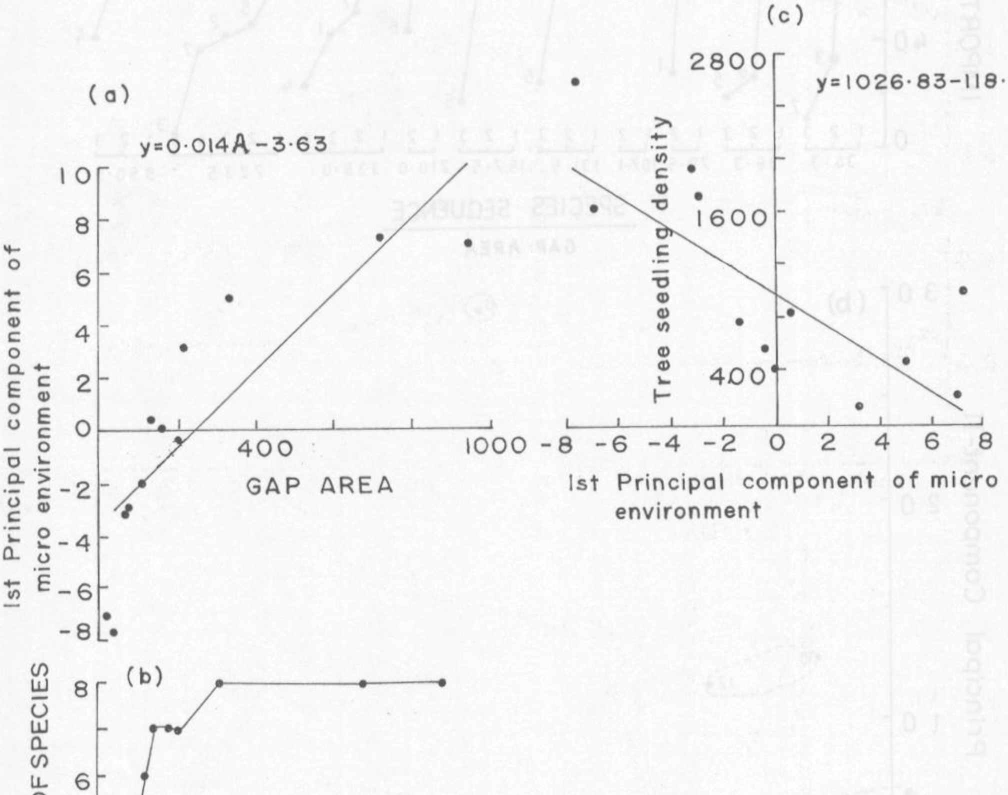

Fig. 3. Relationship between (a) gap area and Principal Component – 1 of microenvironmental factors, (b) gap area and cumulative number of species, and (c) density of tree seedlings and Principal Component – 1 of microenvironmental factors.

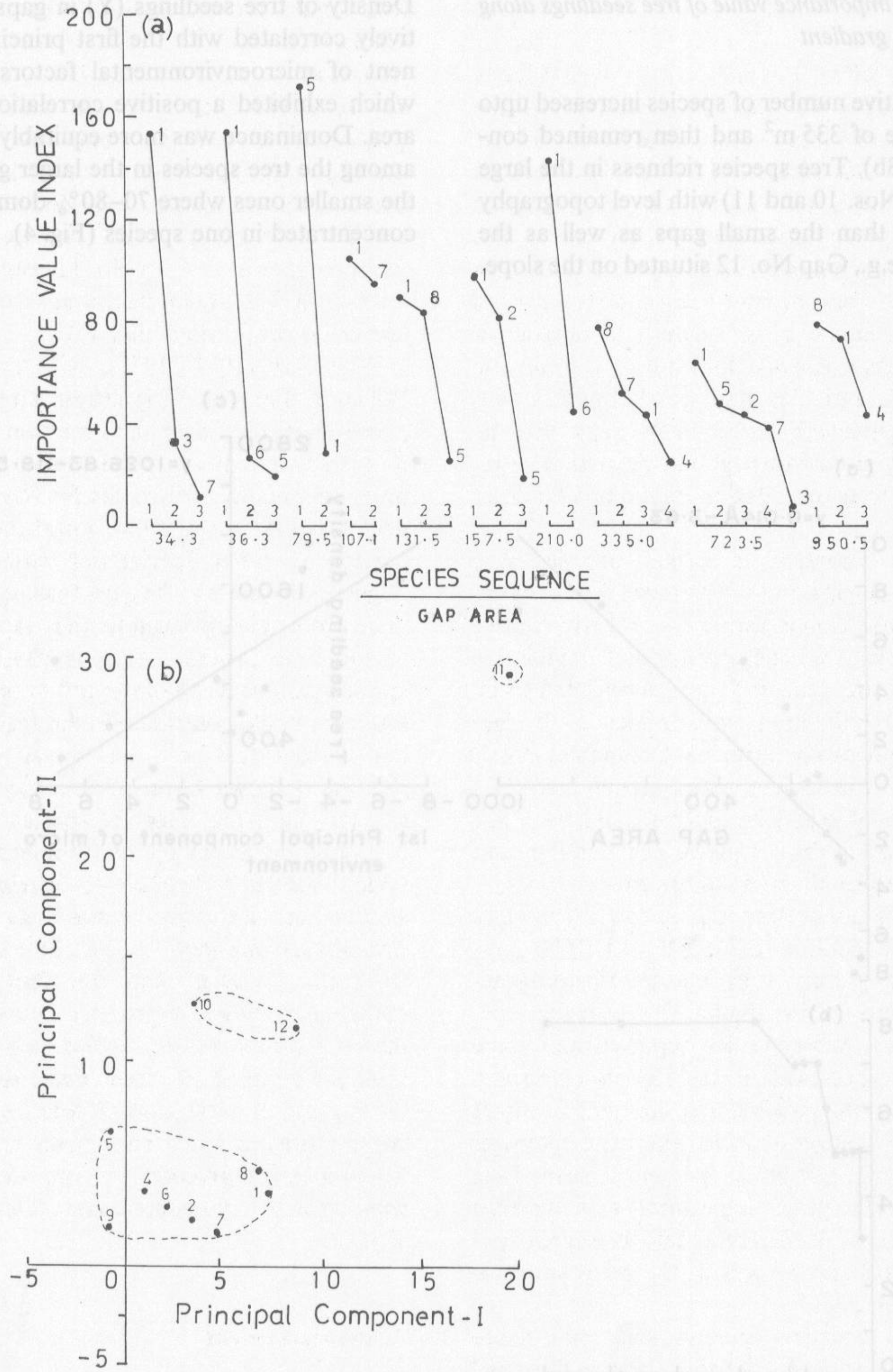

Fig. 4. (a) Rank-abundance curves showing the relative abundance of tree species in the gaps. Species are ranked from most abundant on the left, to least abundant on the right. Gaps with only one species have not been drawn. Key to species number: 1. *Q. dealbata*, 2. *Q. griffithii*, 3. *R. arboreum*, 4. *Q. glauca*, 5. *T. baccata*, 6. *T. tomentosa*, 7. *S. khasiana*, 8. *M. esculenta*; (b) Distribution of gaps within the component space derived by Principal Component Analysis of shade tolerant and shade intolerant species.

Discussion

Heavy rain often associated with high velocity wind during the wet season is an important factor that creates treefall gaps in different forests (Oldeman 1972; Falinski 1978; Brokaw 1982a). Our observation at the Mawphlang forest reveals that heavy precipitation during rainy season and high wind speed during February and March are the major factors, besides natural death of aged trees which create gaps. Analysis of microenvironmental data showed that out of six climatic and edaphic variables studied, photon flux density was significantly higher in the gaps than the understorey almost throughout the year. The reverse was true for relative humidity and litter depth.

Seasonal variation in these variables was marked in all gaps, but it was more prominent in the large gaps. Soil moisture content and relative humidity in gaps was negatively related to the size of opening and solar radiation received therein, whereas litter thickness was influenced by gap size and topography. Principal Component Analysis shows that microenvironmental variables were affected due to differences in gap area which in turn regulated the density of tree seedlings and the total species diversity in the gaps.

Several authors (Harper *et al.* 1961; Struick & Curtis 1962; Bratton 1976; Falinski 1978) have emphasized that fine scale microsite heterogeneity affects species distribution and enhances species richness. Beatty (1984) reported that some understorey species are exclusively present in pits, mounds or in undisturbed soil sites and Beatty & Sholes (1988) suggested that microsite heterogeneity helps in maintaining species richness of the forest through spatial segregation of competing species. Our results indicate that none of the species was exclusive to any of the microsites observed in the gaps.

Rank abundance curves indicate that shade tolerant species *Q. dealbata* dominant in the small gaps (Fig. 4a), was also present in the larger ones. The shade intolerant pioneers *S. khasiana* and *M. esculenta* were, however, important in the larger gaps. Ordination of gaps on the basis of their similarities and dissimilarities with respect to species composition resulted into clustering of smaller gaps (Gap Nos. 1 to 9) having higher density of shade tolerant species viz. *Q. dealbata*, *Q. glauca* and *Q. griffithii* into one group, while the larger gaps (Gap Nos. 10 & 12) having comparatively higher number of shade intolerant species like *S. khasiana* and *M. esculenta* constituted the second cluster. Gap No. 11 contained shade tolerant and shade intolerant species in more or less equal proportion (Fig. 4b).

Whittaker (1972, 1977), MacArthur (1965), Wilson & Shmida (1984) and Brokaw & Scheiner (1989) have discussed the importance of α- and β-diversity in explaining the species richness of a plant community. α-diversity for the tree component was low in this sub-tropical forest in comparison to other species-rich tropical forests. Higher α-diversity in the gaps than in the adjacent understorey clearly suggests that gaps favour the regeneration process of some shade intolerant species such as *S. khasiana* and *M. esculenta* and thus they could contribute to the species richness and mosaicness of the forest community. β-diversity shows the mean similarity among gaps and measures the extent of species replacement or biotic change along environmental gradients (Whittaker 1972; Brokaw & Scheiner 1989). It also reflects the extent of similarity and habitat diversity among gaps. In this forest, β-diversity for trees is lower than the shrub and herb components of the vegetation as well as that in the BCI forest studied by Brokaw & Scheiner (1989). Clumping of parent trees, seed dispersal mechanism and creation of small sized gaps in those places in the forest which had abundant shade-tolerant juveniles in the under canopy region might have contributed to lower β-diversity.

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