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Tree seed germination and seedling establishment in treefall gaps and understorey in a subtropical forest of northeast India

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Abstract Seed germination, and survival and growth of seedlings of four dominant tree species, *Quercus dealbata, Quercus griffithii, Quercus glauca* and *Schima khasiana* were studied in the treefall gaps and forest understorey of an undisturbed mature-phase humid subtropical broadleaved forest in northeast India. Three important microenvironmental factors namely photosynthetically active radiation (PAR), soil moisture and litter depth, were also measured in the forest understorey and gaps and correlated with seedling mortality. Seed germination of *S. khasiana* was significantly higher in the treefall gaps than in the understorey; among the tree species studied, it had the highest germination. *Quercus* seedlings were abundant in the understorey and small gaps, while *S. khasiana* seedlings were more numerous in the large gaps. The survivorship curves for the seedling populations revealed that the three *Quercus* species survived better in the understorey, while *S. khasiana* did so in the gaps. PAR and soil moisture were positively correlated with tree seedling mortality, which occurred mainly during the winter months. The *Quercus* seedlings grew better in the forest understorey and small gaps and *S. khasiana* seedlings in the large gaps. The differential performance of the tree seedlings to the conditions prevailing in the understorey and gaps of two sizes indicates that different species were adapted to different light environments depending upon their optimum requirements. This could be an effective mechanism for promoting species coexistence in the forest community.

Key words: Microenvironment, *Quercus dealbata, Quercus glauca, Quercus griffithii, Schima khasiana.*

INTRODUCTION

Treefall gaps in closed canopied forests play an important role in successful regeneration of tree species by influencing survival and mortality of their seedlings (Whitmore 1978; Brokaw 1985a; Clark & Clark 1987; Welden *et al.* 1991). The behaviour of tree seedlings in treefall gaps and understorey also depends on species' niche specializations (Parrish & Bazzaz 1982) and differences in their ability to utilize the available resources in the gaps (Denslow 1980). Accordingly, species having different regeneration strategies colonize different microsites in the forest understorey and gaps; the small gaps are occupied primarily by shade-tolerant, mature-phase species (Whitmore 1978) while the large gaps are colonized by light-demanding pioneer species (Brokaw 1985b).

Colonization and establishment pattern of tree seedlings in treefall gaps and understorey are poorly understood in the humid subtropical forests of northeast India. Nonetheless, earlier findings (Khan *et al.* 1986; Barik *et al.* 1992) in the undisturbed and disturbed stands of subtropical forests reveal that seedlings of *Quercus* species (*Quercus dealbata, Quercus glauca, Quercus griffithii*) recruited mainly in the small gaps and forest understorey, and those of *Schima khasiana* were abundant in the larger gaps and disturbed stands. We therefore hypothesize that the response of these dominant species to canopy gaps differs in terms of their seed germination and seedling establishment. In order to test this hypothesis and to ascertain their regeneration strategy, a two-year study was carried out on seed germination, seedling recruitment, survival and growth in treefall gaps and understorey of an undisturbed humid subtropical forest in northeast India. The results are discussed in relation to the range of microenvironmental conditions represented by canopy gaps and forest understorey.

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Study area and species

The study was conducted in relict climax vegetation representing an undisturbed humid subtropical broad-leaved forest located at Mawphlang, 28 km southwest of Shillong (altitude 1900 m, 25°34'N, 91°56'E) in Meghalaya, northeast India. *Q. dealbata* L., *Q. glauca* Thunb., *Q. griffithii* H. and *S. khasiana* Dyer. are the dominant overstorey tree species in the forest. Life-history characteristics of these species are given in Table 1. The understorey is occupied by shrubs including *Daphne shillong* Banerjee and *Baliospermum micrantha* Muell. Arg. The forest is characterized by abundant growth of epiphytic mosses, ferns and orchids.

The climate of the area is monsoonal with a long wet summer season (mid May–mid October) and a short dry winter (December–February). The mean annual rainfall during the study period (1988–90) was

Table 1. Life history characteristics of dominant tree species in the subtropical forest at the study site

Attributes	*Quercus dealbata*	*Quercus glauca*	*Quercus griffithii*	*Schima khasiana*
Family	Fagaceae	Fagaceae	Fagaceae	Theaceae
Tree height (m)	15–20	20–22	12–14	25–30
Leaf characters	Simple, lanceolate, margin entire	Simple, lanceolate, serrated margin	Simple, lanceolate, upper part of lamina serrated, base entire	Simple, lanceolate, margin wavy
Leaf fall pattern	Evergreen	Evergreen	Deciduous	Semi-evergreen
Fruit type	Acorns	Acorns	Acorns	Capsule
Mode of seed dispersal	By rodents	By rodents	By rodents	By wind
Average seed weight (mg ± SE, $n = 500$)	490 ± 14.1	540 ± 9.2	685 ± 10.2	95 ± 6.1
Germination	Hypogeal	Hypogeal	Hypogeal	Hypogeal
Phenology				
Leaf initiation	Jun–Aug	Apr–May	Feb–Apr	Mar–May
Leaf fall	Feb–Apr	Feb–Apr	Dec–Feb	Jan–Mar
Flowering	Jan–Mar	Sep–Nov	Aug–Sep	Oct–Dec
Seeding	Oct–Nov	Nov–Dec	Sep–Oct	Feb–Mar
Seed germination	Dec–Jan	Dec–Jan	Dec–Jan	Apr–May

Table 2. Results of Repeated-Measures MANOVA to test the effect of canopy opening on three microenvironmental variables

A. Multivariate test of significance (Wilks Lambda)

Environmental variable	Value	d.f.	Error d.f.	*F*	*P*
PAR	0.18	2	22	50.15	0.00
Soil moisture	0.47	2	22	12.47	0.00
Litter depth	0.23	2	22	36.84	0.00

B. Univariate *F*-test with 1,2 degrees of freedom.

Source of variation	Hypothetical MS	Error MS	*F*	*P*
PAR				
SG/LG *vs* US	915 774.08	94 361.04	97.05	0.00
SG *vs* LG	219 804.60	11 419.77	19.25	0.00
Huynh-Feldt Epsilon = 0.632				
Soil moisture				
SG/LG *vs* US	3.43	0.48	7.09	0.01
SG *vs* LG	2.07	0.35	5.89	0.02
Huynh-Feldt Epsilon = 0.834				
Litter depth				
SG/LG *vs* US	15.89	0.21	76.42	0.00
SG *vs* LG	0.28	0.39	7.37	0.01
Huynh-Feldt Epsilon = 0.693				

US, understorey; SG, small gaps; and LG, large gaps.

3730 mm, 80% of which occurred during summer. During winter and summer, mean minimum and maximum temperatures were 3°C and 16°C, and 16°C and 25°C, respectively. The periods between mid-March and mid-May, and mid-October to the end of November represent spring and autumn, respectively.

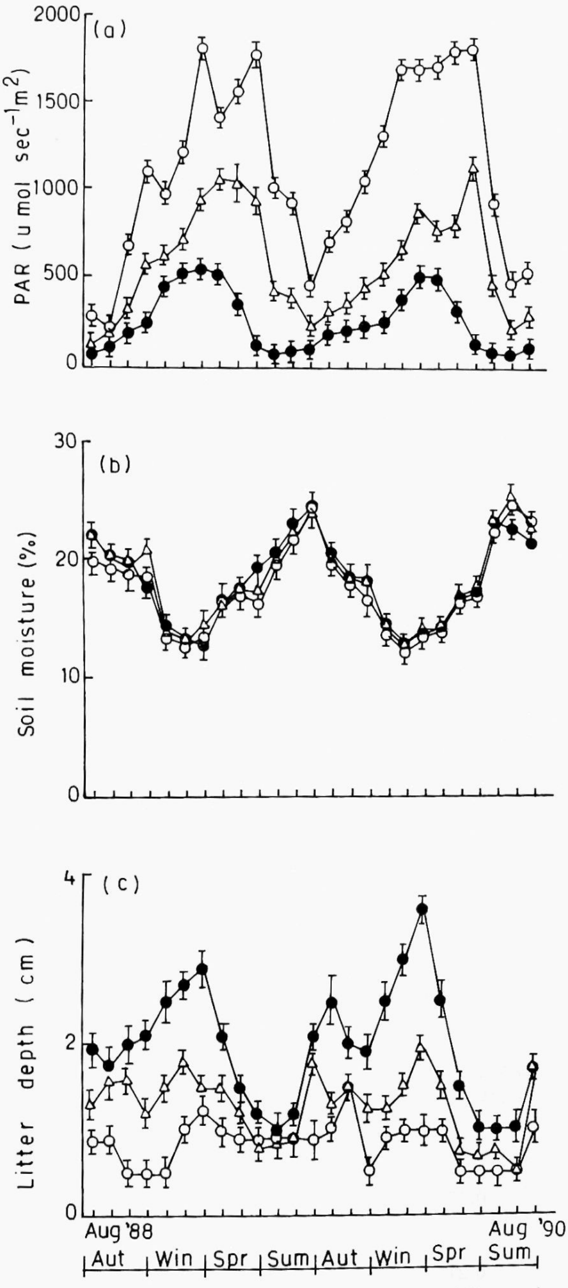

Fig. 1. Monthly variation in microenvironmental factors in the forest understorey (–●–) and small (–△–) and large (–○–) gaps. (a) PAR; (b) soil moisture; (c) litter depth. Vertical bars represent ±SE, $n = 24$.

The soil is derived from the underlying gneisses, schists and granites and may be classified as a latosol (Pascoe 1950). Surface soil has a sandy loam texture, a pH of 5.3, about 6% organic matter and 0.28% nitrogen content (Rao *et al.* 1990).

METHODS

An experimental area of 50 ha was demarcated in the forest during August 1988 and all gaps larger than 20 m^2 originating from either single or multiple treefalls or branchfalls were identified. An opening in the forest extending down through all foliage levels to an average height of 2 m above the ground was considered as a treefall gap (Brokaw 1982). In the present study the area of the gap on the ground was considered equal to the size of the canopy opening. The area of each gap was calculated following Simpson's rule:

$$\text{Area} = 1/3h\ [(y_0 + y_n) + 4(y_1 + y_3 \ldots + y_{n-1}) + 2\ (y_2 + y_4 \ldots + y_{n-2})]$$

where y is the length of the chord, h is the distance between the chords and n is the number of chords. A chord represents the length between two points lying opposite to each other on the canopy edge in a gap. In the present study, an even number of parallel chords were laid at a predetermined distance (0.5 m) in each gap and their length was measured to determine the gap area. Twelve gaps identified in the experimental area were arbitrarily grouped into two size classes, small gaps (20–250 m^2) and large gaps (250–950 m^2). There were ten gaps in the small size group and two in the large size category (Barik *et al.* 1992).

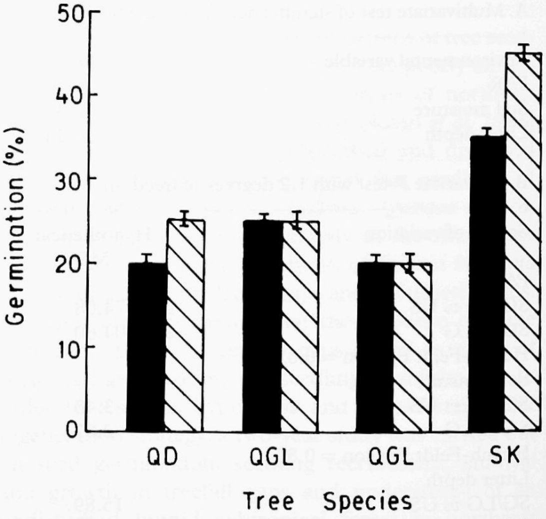

Fig. 2. Seed germination of *Q. dealbata* (QD), *Q. griffithii* (QG), *Q. glauca* (QGL) and *S. khasiana* (SK) in the forest understorey (■) and gaps (▨). Vertical bars represent ± SE, $n = 3$.

The microenvironmental conditions in the forest understorey and treefall gaps were studied by measuring photosynthetically active radiation (PAR), soil moisture content and litter depth. PAR and soil moisture were measured at two random points in each gap and in the permanent quadrat laid in the understorey adjacent to each gap at two-hourly intervals from 0800 to 1600 h on three random days of a month. PAR was measured at ground level using an infra-red CO_2 gas analyser (ADC ASUM-2, London) with PAR sensor as an accessory. Soil moisture was determined down to 10 cm depth using a digital moisture meter (OSK-2800, Tokyo). The litter depth was measured at 5–20 points with a scale along two line-transects in each gap and adjacent understorey.

For the germination study, seeds of *Q. dealbata*,

Table 3. Mean population density (± SE) and per cent mortality of seedlings of study species

Species	Canopy opening	Seedling density (Plants ha^{-1})		Seedling mortality
		Aug 1988	Aug 1990	Aug 1988–1990
Quercus dealbata	FU	725 ± 95	322 ± 64	55.6
	SG	526 ± 84	195 ± 36	62.9
	LG	143 ± 14	23 ± 10	83.9
Quercus glauca	FU	391 ± 50	156 ± 49	60.1
	SG	124 ± 33	32 ± 19	74.1
	LG	64 ± 32	12 ± 6	81.3
Quercus griffithii	FU	250 ± 40	142 ± 44	56.8
	SG	139 ± 56	46 ± 17	66.7
	LG	68 ± 27	18 ± 8	73.5
Schima khasiana	FU	125 ± 33	0	100.0
	SG	192 ± 25	24 ± 13	87.5
	LG	248 ± 26	188 ± 42	24.2

FU, forest understorey (*n* = 12); SG, small gaps (*n* = 12); and LG, large gaps (*n* = 2).

Table 4. Results of Repeated-Measures MANOVA to test the effect of canopy opening on seedling density and study species

A. Multivariate test of significance (Wilks Lambda)

Study species	Value	d.f.	Error d.f.	*F*	*P*
Quercus dealbata	0.007	2	7	491.87	0.000
Quercus glauca	0.089	2	7	36.04	0.000
Quercus griffithii	0.037	2	7	89.44	0.000
Schima khasiana	0.011	2	7	312.821	0.000

B. Univariate *F*-test with 1,2 degrees of freedom

Source of variation	Hypothetical MS	Error MS	*F*	*P*
Quercus dealbata				
SG/LG *vs* US	1 168 410.89	3861.76	302.56	0.000
SG *vs* LG	25 523.63	134.75	189.41	0.000
Huynh-Feldt Epsilon = 0.533				
Quercus glauca				
SG/LG *vs* US	178 005.56	2343.06	75.97	0.000
SG *vs* LG	22 407.41	428.24	52.33	0.000
Huynh-Feldt Epsilon = 0.525				
Quercus griffithii				
SG/LG *vs* US	76 570.89	510.89	149.88	0.000
SG *vs* LG	4 160.67	150.67	27.62	0.001
Huynh-Feldt Epsilon = 0.901				
Schima khasiana				
SG/LG *vs* US	114 401.39	163.89	698.04	0.000
SG *vs* LG	16 537.50	402.08	41.13	0.000
Huynh-Feldt Epsilon = 0.917				

US, understorey; SG, small gaps; and LG, large gaps.

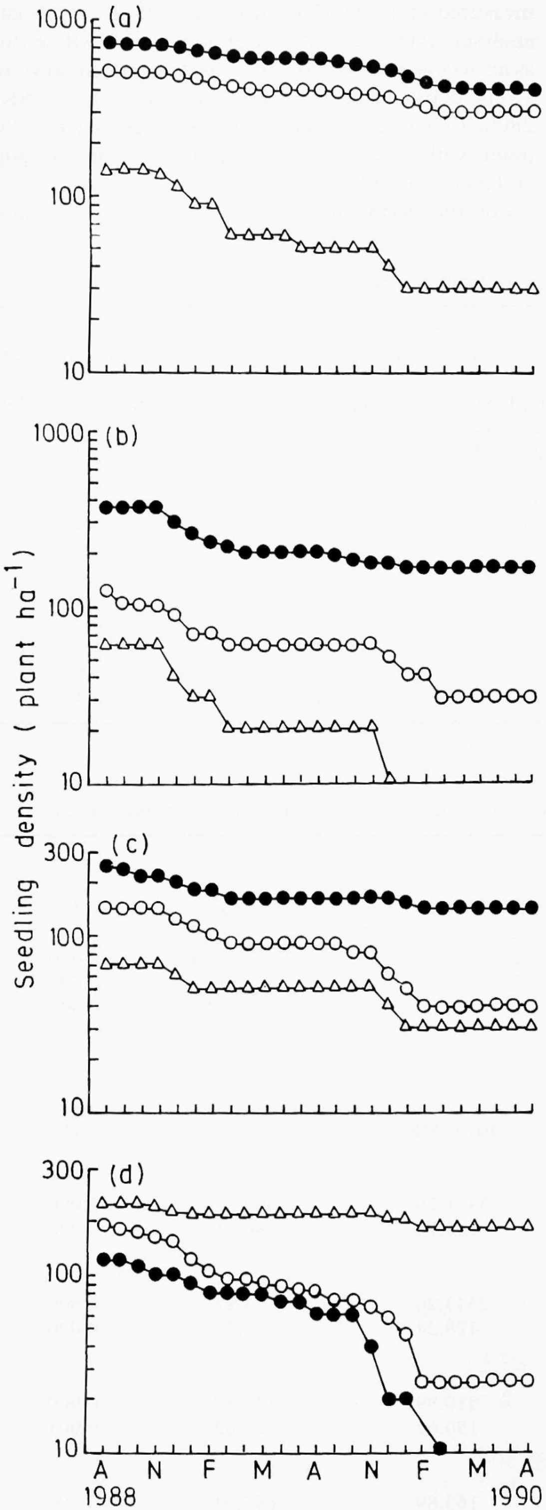

Fig. 3. Survivorship curves of tree seedlings of four species in the forest understorey (–●–), small gaps (–△–) and large gaps (–○–). (a) *Q. dealbata*; (b) *Q. glauca*; (c) *Q. griffithii*; (c) *S. khasiana*.

Q. glauca, *Q. griffithii* and *S. khasiana* were sown in 24, 1 × 1 m plots, of which 12 were in the gaps and 12 in the understorey. For each species six plots, three in gaps and three in the adjacent understorey, were randomly selected and 25 freshly collected seeds of each species were sown on mineral soil during October 1989 to February 1990, depending on the period of their seed dispersal. Germination was monitored in all the plots at 15-day intervals until its completion.

In August 1988 all naturally occurring new seedlings of *Q. dealbata*, *Q. glauca*, *Q. griffithii* (height 7 cm, leaf no. 3–5) and *S. khasiana* (height < 3 cm, leaf no. 2–3) in each gap were tagged using wax-coated weatherproof labels. Simultaneously, one permanent quadrat of 10 × 10 m size was also laid out in the understorey region near each gap and all seedlings of the four tree species were located and tagged in a similar fashion. Survival and growth (shoot length and leaf area) of tagged seedlings were monitored at monthly intervals until August 1990. Age specific mortality rate (qx) for seedling populations of different species were calculated using the following formula:

$$qx = dx/lx$$

where lx is the initial number of individuals in the population and dx is the number of individuals dying during each of the one month census periods.

Leaf area was measured using a portable leaf area meter (LICOR-300, USA). The relative shoot growth rate for each three-month interval was calculated according to Coombs *et al.* (1985).

The relative shoot growth rate equalled $\ln X_2 - \ln X_1 / t_2 - t_1$ where X_1 was the initial height of the seedling at time t_1 (beginning of the first month), and X_2 was the height of the seedling at time t_2 (end of the third month).

The mean monthly values of each microenvironmental variable were calculated for forest understorey (FU), small gaps (SG) and large gaps (LG). The effects of canopy opening that is the understorey, small and large gaps on microenvironmental variables and density, mortality rate, relative shoot growth rate and leaf area increment rate of seedlings of the study species were analysed using Repeated Measures MANOVA. The variables were transformed to form orthonormalized difference contrasts. All multivariate test statistics namely Pillai's trace, Wilks lambda, and Hotelling–Lawley trace showed similar levels of significance for all the variables tested. Therefore, statistics for Wilks Lambda only have been presented in the MANOVA tables. The relative importance of various microenvironmental factors on seedling mortality rate was determined through partial correlation analysis, for which a computer program written in BASIC language was developed on the basis of the steps given in Zar (1974). The sequence of microenvironmental variables entered into partial correlation analysis was PAR, soil moisture and litter depth. For each species, the mean monthly values for the microenvironmental variables were correlated with the corresponding seedling mortality rate.

RESULTS

Microenvironment in gaps and understorey

PAR was significantly influenced by canopy opening in the forest as well as between the gaps and the understorey (Table 2). It markedly increased from the understorey to the large gaps in all seasons. Both gaps and understorey received maximum radiation during the dry winter months and minimum during the wet summer season (Fig. 1). Soil moisture content was similar in gaps and understorey. Peak values were obtained during the wet summer season and then dropped to the lowest level during the winter months. Litter accumulation registered a significant decline from the understorey to the large gaps (Table 2). It also exhibited a marked seasonal trend by recording highest values during the winter and lowest during the wet summer season (Fig. 1).

Table 5. Results of Repeated-Measures MANOVA to test the effect of canopy opening on seedling mortality rate (Qx) of study species

A. Multivariate test of significance (Wilks Lambda)

Study species	Value	d.f.	Error d.f.	*F*	*P*
Quercus dealbata	0.021	2	6	2.784	0.14
Quercus glauca	0.842	2	6	0.565	0.59
Quercus griffithii	0.201	2	6	0.604	0.58
Schima khasiana	0.314	2	6	0.556	0.03

B. Univariate *F*-test with 1,2 degrees of freedom.

Source of variation	Hypothetical MS	Error MS	*F*	*P*
Quercus dealbata				
SG/LG *vs* US	0.021	0.004	6.01	0.04
SG *vs* LG	0.042	0.021	2.02	0.198
Huynh-Feldt Epsilon = 0.589				
Quercus glauca				
SG/LG *vs* US	0.011	0.017	0.66	0.442
SG *vs* LG	0.004	0.011	0.42	0.540
Huynh-Feldt Epsilon = 1.00				
Quercus griffithii				
SG/LG *vs* US	0.011	0.008	1.37	0.280
SG *vs* LG	0.002	0.013	1.40	0.720
Huynh-Feldt Epsilon = 1.00				
Schima khasiana				
SG/LG *vs* US	0.260	0.057	4.57	0.03
SG *vs* LG	0.145	0.029	2.08	0.07
Huynh-Feldt Epsilon = 0.625				

US, understorey; SG, small gaps; and LG, large gaps.

Table 6. Partial correlation coefficients (r) between age-specific mortality rate (qx) and microenvironmental factors

Species	PAR (μM sec^{-1} m^2)			Soil moisture (%)			Litter depth (cm)			
	FU	SG	LG	FU	SG	LG	FU	SG	LG	*n*
Quercus dealbata	−0.442*	−0.467*	NS	NS	−0.695**	−0.635**	0.596**	NS	NS	24
Quercus. glauca	−0.321*	NS	−0.346*	NS	−0.369*	−0.416**	0.405**	NS	0.431*	24
Quercus griffithii	NS	NS	NS	NS	−0.596**	−0.650**	0.436**	NS	NS	24
Schima khasiana	−0.490*	−0.477*	NS	−0.398*	−0.444*	−0.688**	NS	NS	NS	21

*significant at $P < 0.05$
**significant at $P < 0.01$
NS not significant.
FU, forest understorey; SG, small gaps; and LG, large gaps.

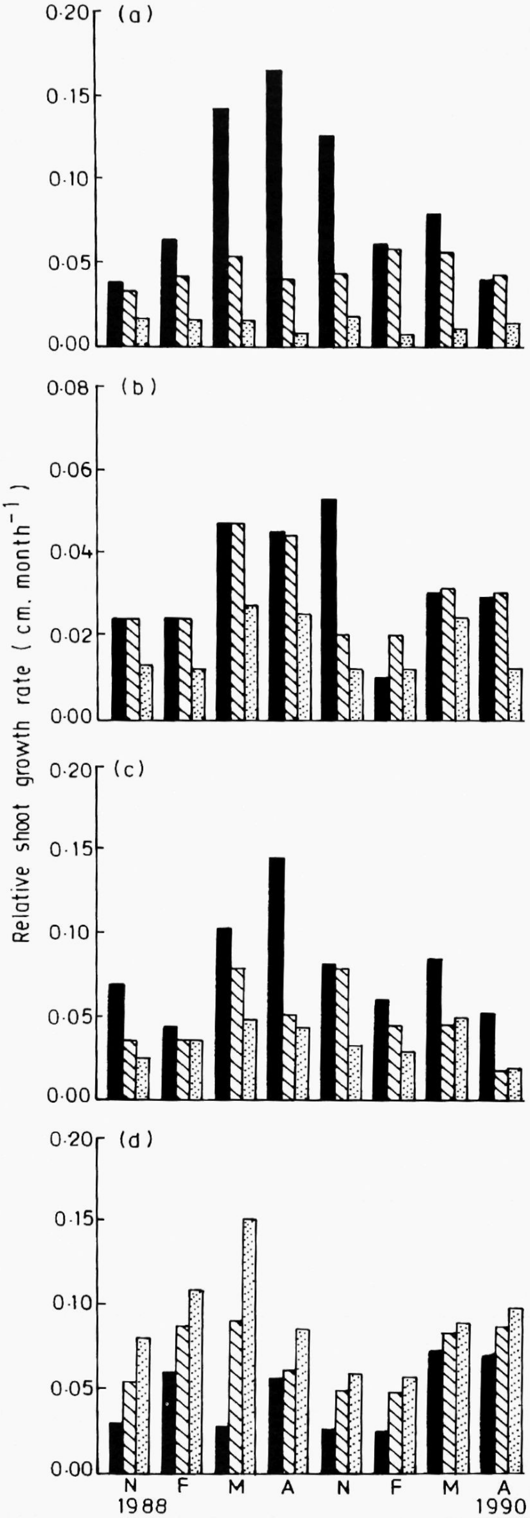

Fig. 4. Relative shoot growth rate of tree seedlings of the study species in the understorey (■), small gaps (▧) and large gaps (░). (a) *Q. dealbata*; (b) *Q. glauca*; (c) *Q. griffithii*; (d) *S. khasiana*.

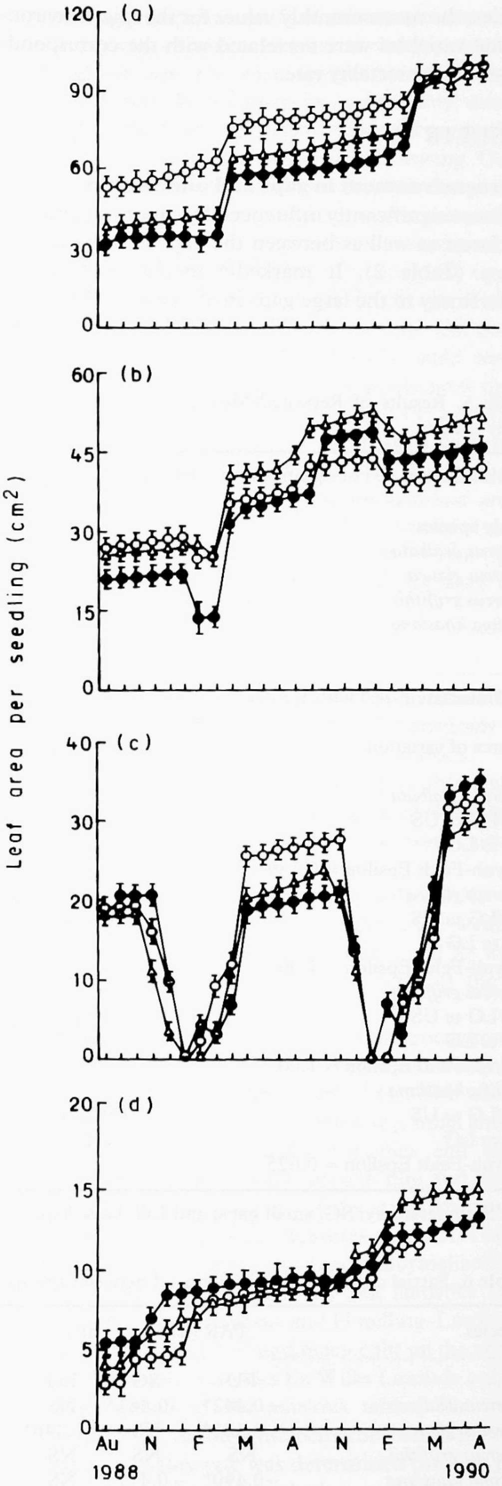

Fig. 5. Growth in leaf area of tree seedlings of the study species in the understorey (–●–), small gaps (–△–) and large gaps (–○–). (a) *Q. dealbata*; (b) *Q. glauca*; (c) *Q. griffithii*; (d) *S. khasiana*. Vertical bars represent ± SE, $n = 24$.

Seed germination and seedling recruitment

Seed germination ranged between 20–30% in *Quercus* species and between 40–50% in *S. khasiana*. Canopy opening significantly ($F = 4.23$, $P < 0.05$) increased germination percentage in *S. khasiana*, but had no effect on *Q. dealbata*, *Q. glauca* and *Q. griffithii* (Fig. 2).

Seedling population density of the four tree species varied significantly between the small and large gaps as well as between gaps and understorey (Table 3, 4). Seedlings of the three *Quercus* species were more abundant in the understorey and small gaps while those of *S. khasiana* were more abundant in the large gaps (Table 4).

Seedling survival

Survivorship curves show a marked difference in the mortality pattern of seedlings in the gaps and understorey (Fig. 3). All three *Quercus* species suffered greater mortality in the gaps than in the understorey, although this difference was not highly significant. Seedlings of *S. khasiana* showed significantly higher mortality in the gaps than in the understorey region (Table 5). However, in all four species mortality occurred mainly during October–March both in gaps and understorey as indicated by a sharp drop in seedling density during this period (Fig. 3).

In the understorey, PAR showed significant negative correlations with age-specific seedling mortality for all species except *Q. griffithii* (Table 6). In the small and large gaps, soil moisture yielded significant negative correlations with seedling mortality rate in all species. In the understorey, however, only *S. khasiana* showed this relationship. Relationships with litter depth were significantly positive for *Quercus* species in the understorey (Table 6). However, it should be noted that the relative importance of a given microenvironmental factor in influencing seedling mortality varied from species to species and between gaps and understorey.

Seedling growth

The duration of active shoot growth in all the four species varied between March and November; the peaks of different species, however, occurred in different months and under different environment regimes (Fig. 4). The shoot growth rate varied significantly with canopy opening. In the three *Quercus* species it was significantly higher in the understorey than the gaps, but in case of *S. khasiana* the reverse was true (Table 7).

Table 7. Results of Repeated-Measures MANOVA to test the effect of canopy opening on relative shoot growth rate of seedlings of study species

A. Multivariate test of significance (Wilks Lambda)

Study species	Value	d.f.	Error d.f.	*F*	*P*
Quercus dealbata	0.084	2	6	32.89	0.001
Quercus glauca	0.231	2	6	29.96	0.012
Quercus griffithii	0.121	2	6	21.82	0.002
Schima khasiana	0.317	2	6	6.48	0.032

B. Univariate *F*-test with 1,2 degrees of freedom

Source of variation	Hypothetical MS	Error MS	*F*	*P*
Quercus dealbata				
SG/LG *vs* US	0.020	0.001	19.04	0.003
SG *vs* LG	0.002	0.001	0.38	0.559
Huynh-Feldt Epsilon = 0.559				
Quercus glauca				
SG/LG *vs* US	0.001	0.0001	12.19	0.010
SG *vs* LG	0.0001	0.0004	3.72	0.090
Huynh-Feldt Epsilon = 0.716				
Quercus griffithii				
SG/LG *vs* US	0.008	0.001	21.92	0.002
SG *vs* LG	0.001	0.0002	1.84	0.217
Huynh-Feldt Epsilon = 5.000				
Schima khasiana				
SG/LG *vs* US	0.008	0.001	14.44	0.007
SG *vs* LG	0.0001	0.0002	7.49	0.052
Huynh-Feldt Epsilon = 0.552				

US, understorey; SG, small gaps; and LG, large gaps.

Leaf area increment in the four tree species varied significantly between the understorey and gaps of different sizes. Leaf area was significantly greater in the gaps than in the understorey in all the four species (Table 8). All four species were characterized by a marked seasonality in foliage dynamics. The decline in leaf area was quite marked in *Q. griffithii* and corresponded with the period of leaf fall while a rise in leaf area coincided with the period of leaf initiation (Fig. 5).

DISCUSSION

The better germination of *S. khasiana* seeds in treefall gaps than in the adjacent understorey, and recruitment of a large number of its seedlings in the large gaps indicates that the microenvironment in the large gaps favours that species' recruitment. Based on these observations and in the light of the reports by Vazquez-Yanes & Smith (1982) and Raich & Khoon (1990) that gaps in the canopy favour seed germination of pioneer species on the forest floor, *S. khasiana* could be classified as a pioneer species. The results also reveal that the seed germination and survival pattern and growth response of the seedlings of the study species differed in the gaps and understorey (Table 9). High survivorship and high growth rates of *S. khasiana* seedlings in large gaps relative to other species is

Table 8. Results of Repeated-Measures MANOVA to test the effect of canopy opening on relative shoot growth rate of seedlings of study species

A. Multivariate test of significance (Wilks Lambda)

Study species	Value	d.f.	Error d.f.	*F*	*P*
Quercus dealbata	0.118	2	6	22.46	0.002
Quercus glauca	0.153	2	6	16.57	0.004
Quercus griffithii	0.426	2	6	4.05	0.077
Schima khasiana	0.359	2	6	4.462	0.077

B. Univariate *F*-test with 1,2 degrees of freedom

Source of variation	Hypothetical MS	Error MS	*F*	*P*
Quercus dealbata				
SG/LG *vs* US	1346.34	32.74	41.12	0.000
SG *vs* LG	53.36	1.24	42.91	0.000
Huynh-Feldt Epsilon = 0.535				
Quercus glauca				
SG/LG *vs* US	153.51	4.64	33.10	0.001
SG *vs* LG	9.73	17.94	0.54	0.485
Huynh-Feldt Epsilon = 0.815				
Quercus griffithii				
SG/LG *vs* US	38.28	14.17	9.18	0.019
SG *vs* LG	0.02	18.39	0.001	0.977
Huynh-Feldt Epsilon = 0.835				
Schima khasiana				
SG/LG *vs* US	4.48	0.48	9.40	0.022
SG *vs* LG	10.41	0.42	1.27	0.064
Huynh-Feldt Epsilon = 1.00				

US, understorey; SG, small gaps; and LG, large gaps.

Table 9. Favoured niche of the study species as indicated by seedling response attributes

Species	Germination	Survivorship	Relative shoot elongation rate	Leaf area
Understorey-small gap species:				
Quercus dealbata	Gaps	Understorey	Understorey	No preference
Quercus glauca	No preference	Understorey	Small gaps Understorey	Large gaps
Quercus griffithii	No preference	Understorey	Understorey	Small gaps Understorey
Large gap species:				
Schima khasiana	Gaps	Gaps	Large gaps	Large gaps

indicative of the regeneration niche preferred by this species. The regeneration of the three *Quercus* species was favoured in the understorey and small gaps. This clearly suggests that the resource needs of the *Quercus* species were different from those of *S. khasiana* at least during the juvenile phase. Brokaw (1985a) also reported greater height growth in the gaps for pioneer species than for primary species. Thus, based on their performances in the gaps and understorey, the species studied could be categorized into two main response groups:

(1) Large gap species: *S. khasiana*.

(2) Undercanopy–small gap species: *Q. dealbata*, *Q. glauca* and *Q. griffithii*.

Survival and growth of these two groups of species both in gaps and understorey were correlated with PAR, soil moisture and litter depth. The favourable effect of distinct diurnal fluctuations in PAR and temperature conditions on *S. khasiana* is clearly evident from better survival and growth of its seedlings in the large gaps compared to the understorey and small gaps where the PAR was significantly lower. The greater seedling mortality observed during winter, when soil moisture content was at a minimum both in gaps and understorey, depicts the importance of soil moisture in regeneration of the study species. Earlier studies by McLeod & Murphy (1977), Mueller-Dombois *et al.* (1980) and Khan *et al.* (1986) have also revealed a detrimental effect of soil moisture stress on survival and growth of tree seedlings. Collins & Good (1987) have emphasised the role of litter depth in regulating tree seedling survival in the tropical forests.

As discussed, the recruitment and mortality patterns of the two groups of species are quite distinct. In general, the undercanopy–small gap species represented by *Quercus* species were characterized by high recruitment and better juvenile survivorship under closed canopy and small gaps (Table 8), while the large gap species *S. khasiana* exhibited low recruitment and high seedling mortality in these environments. Thus, the differential response of the study species in terms of their seed germination and seedling survival and growth to gap and understorey environment strengthens the argument that treefall gaps help natural regeneration of species differing in their life-history characteristics (Table 1), for example in degree of deciduousness in the present case, and help promote coexistence of species in the community.

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