

# Dynamics of tree seedling populations in a humid subtropical forest of northeast India as related to disturbance

S.K. Barik, P. Rao, R.S. Tripathi, and H.N. Pandey

**Abstract:** Recruitment and survival of four important broad-leaved tree species, viz *Quercus dealbata* L., *Quercus griffithii* Hk., *Rhododendron arboreum* Sm., and *Schima khasiana* Dyer., were studied over 2 years in the undisturbed, mildly disturbed and highly disturbed forest stands of a subtropical humid forest of Meghalaya, northeast India. Recruitment of *S. khasiana* seedlings was maximum in the highly disturbed stand, while *Q. dealbata* seedlings were abundant in the undisturbed and mildly disturbed stands. Seedlings of *Q. dealbata*, *Q. griffithii*, and *R. arboreum* were equally successful in all the stands, while *S. khasiana* seedlings showed better survival in the highly disturbed stand than in the mildly disturbed and undisturbed stands. Six microenvironmental factors, viz photosynthetically active radiation, relative humidity, air temperature, soil temperature, soil moisture, and thickness of litter on the forest floor, were correlated with the age-specific mortality rate of seedlings. In *Q. dealbata*, *Q. griffithii*, and *S. khasiana*, mortality rate was significantly affected by microenvironmental factors, while in *R. arboreum* mortality was not correlated with any of the microenvironmental factors. On the basis of seedling recruitment and survival pattern, it was concluded that *Q. dealbata*, *Q. griffithii*, and *R. arboreum* were successful in both disturbed and undisturbed forest stands, while *S. khasiana* seedlings showed better survival and establishment in the disturbed stands.

**Résumé :** Le recrutement et la survie de quatre feuillus importants, à savoir, *Quercus dealbata* L., *Quercus griffithii* Hk., *Rhododendron arboreum* Sm. et *Schima khasiana* Dyer, ont été étudiées pendant 2 ans dans des peuplements forestiers non perturbé, faiblement perturbé et fortement perturbé d'une forêt humide subtropicale de Meghalaya, dans le Nord-Est de l'Inde. Le recrutement des semis de *S. khasiana* était à son maximum dans le peuplement fortement perturbé, alors que les semis de *Q. dealbata* étaient abondants dans les peuplements non perturbé et faiblement perturbé. Les semis de *Q. dealbata*, de *Q. griffithii* et de *R. arboreum* ont connu un succès égal dans tous les peuplements, alors que les semis de *S. khasiana* survivaient mieux dans le peuplement fortement perturbé que dans les deux autres peuplements. Six facteurs micro-environnementaux, à savoir, la radiation photosynthétiquement active, l'humidité relative, la température de l'air, la température du sol, l'humidité du sol et l'épaisseur de la litière du parterre forestier ont été corrélés avec le taux de mortalité spécifique à l'âge des semis. Chez *Q. dealbata*, *Q. griffithii* et *S. khasiana*, le taux de mortalité était influencé de façon significative par les facteurs micro-environnementaux, contrairement à celui de *R. arboreum*, qui n'était corrélé à aucun de ces facteurs. Sur la base du recrutement des semis et du patron de survie, il a été conclu que *Q. dealbata*, *Q. griffithii* et *R. arboreum* ont réussi à survivre et à s'établir à la fois dans les peuplements forestiers perturbé et non perturbé, alors que les semis de *S. khasiana* ont mieux réussi, à ce titre, dans les peuplements perturbés.  
[Traduit par la Rédaction]

## Introduction

Studies on population behaviour of tree seedlings in different forests show that their recruitment, growth, and survival are influenced by a variety of microclimatic and edaphic factors (Augspurger 1984a, 1984b, 1984c; Streng et al. 1989; Welden et al. 1991) and activity of pathogens (Rhoades 1985), herbivores (Coley and Aide 1991), and predators (Sork 1987; Schupp 1988; Howe 1990). Grubb (1977) and Brokaw (1987) suggested that most of the observed patterns in tree seedling population behaviour in

forests are caused by temporal and spatial variations in environmental factors that are influenced both by endogenous and exogenous disturbances.

The role of disturbance in forest community dynamics has also been emphasized by Denslow (1980, 1985), Whitmore (1984, 1991), Pickett and White (1985), and Collins (1989). The recruitment and survival patterns of tree seedlings in relation to gap disturbance and other natural disturbances in forest communities have been studied by Canham and Marks (1985), Clark and Clark (1985), and Streng et al. (1989). A brief review on the subject is given in Denslow (1987). Keeping in mind that disturbance causes a series of environmental variations in forests, an experiment was designed to study the effect of man-induced disturbances on the forest microenvironment and tree seedling population dynamics in a humid subtropical forest of northeast India. We hypothesize that microclimatic and

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edaphic conditions play a key role in recruitment and survival pattern of tree seedling populations in this forest, since there was not enough evidence of the damage to seedling populations due to leaf predation, grazing, and pathogen attack (Barik 1992). This hypothesis has been tested by collecting monthly data on seedling recruitment and mortality patterns of *Quercus dealbata* L., *Quercus griffithii* Hk., *Rhododendron arboreum* Sm., and *Shima khasiana* Dyer. and concomitantly measuring of photosynthetically active radiation (PAR), relative humidity, air temperature, soil moisture, soil temperature, and litter thickness in undisturbed and disturbed forest stands for 2 years.

## Materials and methods

### Study area

The study was conducted in three stands of the northern subtropical wet-hill forest of India (Champion and Seth 1968) located in the greater Shillong area (25°34'N, 91°56'E). The three forest stands were classified on the basis of disturbance index (ratio between the basal area of the cut trees and total basal area of all trees, including felled ones (Rao et al. 1990)), into highly disturbed (location, Upper Shillong; altitude, 1800 m; disturbance index, 60%), mildly disturbed (location, Shillong; altitude, 1720 m; disturbance index, 10%), and undisturbed (location, Mawphlang; altitude, 1700 m; disturbance index, 0%) stands. Harvesting of the overstorey in the two disturbed stands was done through selective tree felling by the local people during 1986–1987.

The forest stand at Mawphlang, protected by the local tribes as a sacred grove, represents the relic climax vegetation occurring between 1500 and 2000 m in the northeastern hill region of India. It has no recorded history of major human disturbance during the past century. The forest is dense, semi-evergreen, and plant species are distributed into four distinct strata: canopy layer, subcanopy layer, shrub layer, and ground vegetation. The species composition and community characters of the forest stands at Mawphlang and those at Shillong and Upper Shillong have been dealt with in detail by Rao et al. (1990). In general, *Quercus dealbata*, *R. arboreum*, and *S. khasiana* represent the dominant tree component in all the three stands. *Quercus griffithii*, a codominant species in the undisturbed and highly disturbed stands, was absent in the mildly disturbed stand. *Pinus kesiya* Royle ex Gordon, a tropical pine that quickly colonizes disturbed broad-leaved forests, was an important species in the highly disturbed stand at Upper Shillong.

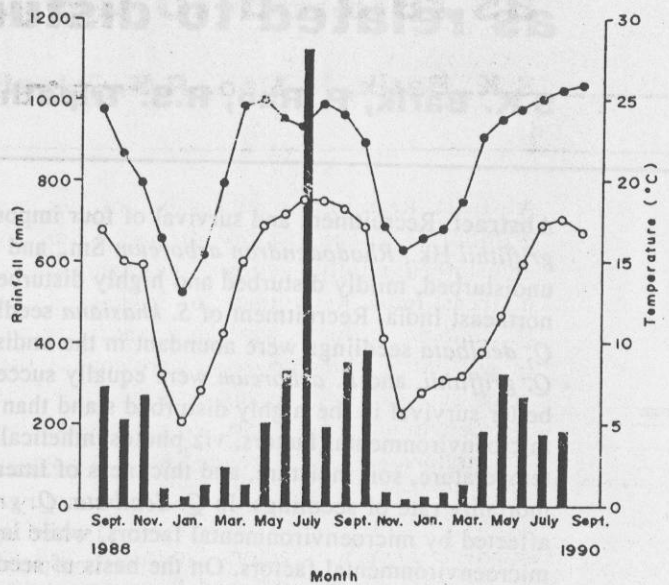
### Climate

The climate is monsoonic with an average annual rainfall of 2500 mm, distributed over 7 months of the year. Around 85% of the total annual rainfall occurs during mid-May to September (rainy season). October and November represent the autumn, which is a transitional period between rainy and winter seasons. The autumn gives way to winter (December to February), which is characterized by low temperatures (mean minimum 3°C and mean maximum 16°C) and occasional rain. During the study period, March–mid-May (spring season) was warmer than the preceding winter months and received little rainfall. The mean annual maximum and minimum temperatures were 22°C and 16°C, respectively (Fig. 1).

Soil and Ellenberg 1974). The mean monthly values for

The soils are derived from the underlying gneisses, schists, and granites. They have been grouped under the Latosol type

Fig. 1. Climogram of the study sites during the study period, showing total monthly rainfall (bars), mean monthly maximum temperature (●), and mean monthly minimum temperature (○).



(Pascoe 1950). The topsoil (0–10 cm) of the mildly disturbed and highly disturbed forest stands has lower organic matter (3.2–4.1%) and pH (5.0–5.2) than the soil of the undisturbed forest stand (organic matter content 6.4% and pH 5.7). The nitrogen content of the soils in the three stands ranges from 0.17 to 0.28%. The mineral soil in the undisturbed stand is covered with a thick detrital layer, composed of duff and litter intermingled with fine roots of trees and ground vegetation.

### Methods

An experimental area of 50 ha was demarcated in each stand, and 10 permanent quadrats, each 10 × 10 m, were randomly laid during July 1988. The newly recruited seedlings of *Q. dealbata*, *Q. griffithii*, *R. arboreum*, and *S. khasiana* in each quadrat were tagged with weather-proof labels in the last week of July 1988 and their survival was monitored at monthly intervals until August 1990. The age-specific mortality rate ( $q_x$ ) of the seedling populations was calculated on a monthly basis using the following expression (Poole 1974):

$$Q_x = \frac{d_x}{l_x}$$

where  $l_x$  is the number of individuals at the beginning of the month and  $d_x$  is the number of individuals that died during the 1-month period.

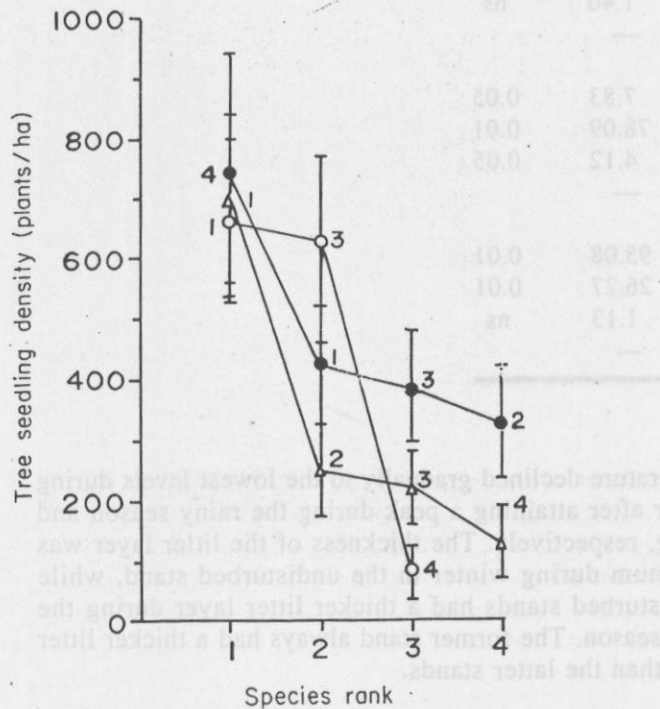
The measurements of microenvironmental variables, viz. PAR, relative humidity, air temperature, soil moisture, and soil temperature, were taken at two random points in each permanent plot at 2-h intervals from 08:00 to 16:00 on 3 randomly chosen days of a month. PAR was measured at ground level using the PAR sensor accessory of an infrared CO<sub>2</sub> gas analyser (ADC, London). The relative humidity and air temperature were measured at ground level using a hygrometer and thermometer, respectively. Soil temperature and soil moisture were determined down to 10 cm depth using a soil thermometer and a digital moisture meter (OSK -2800, Tokyo), respectively. The thickness of litter was measured by the line-intercept method (Mueller-Dombois and Ellenberg 1974). The mean monthly values for each microenvironmental variable were calculated and statistically analysed using three-way ANOVA (fixed effects model)

**Table 1.** Seedling recruitment (plants/ha) and mortality (%) of seedling populations of tree species in disturbed and undisturbed forest stands during 2 years of study.

	Undisturbed		Mildly disturbed		Highly disturbed	
	Recruitment	Mortality	Recruitment	Mortality	Recruitment	Mortality
<i>Quercus dealbata</i>	700±138	14.3	660±123	24.2	420±92	4.8
<i>Quercus griffithii</i>	250±76	28.0	—	—	320±87	56.3
<i>Rhododendron arboreum</i>	220±55	9.1	620±146	6.5	380±89	26.3
<i>Schima khasiana</i>	130±55	100.0	80±36	75.0	740±189	55.4

Note: Recruitment values are shown as the mean ± SE. —, species absence.

**Fig. 2.** Ranking of tree species on the basis of their seedling density in undisturbed ( $\Delta$ ), mildly disturbed ( $\circ$ ), and highly disturbed ( $\bullet$ ) forest stands. Key to species number: 1. *Q. dealbata*, 2. *Q. griffithii*, 3. *R. arboreum*, and 4. *S. khasiana*.



in order to test the variation due to forest stands, seasons, and months. Tukey's multiple comparison test was employed following ANOVA to compare the variation between the forest stands.

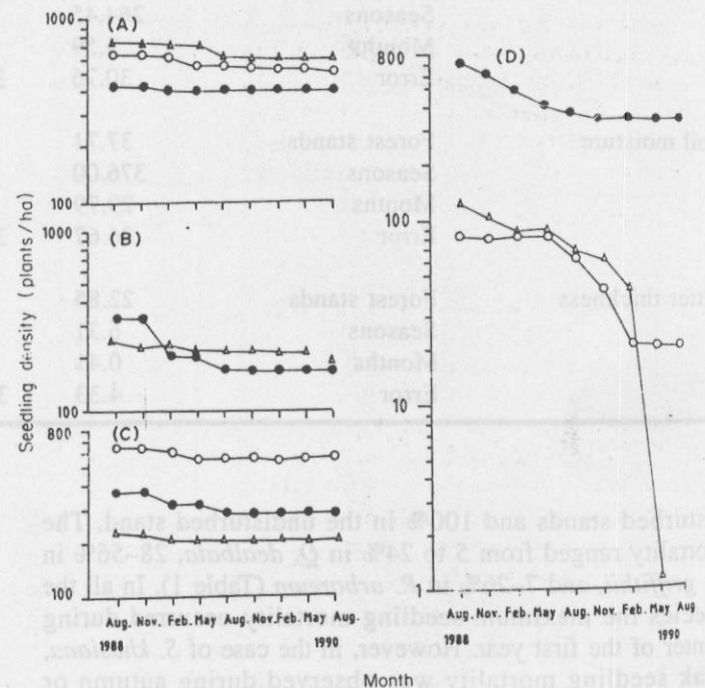
Relationship between age-specific mortality rate ( $Q_x$ ) of seedling populations and microenvironmental factors was analysed using a computer programme for partial correlation analysis developed as per the steps given by Zar (1974).

## Results

### Recruitment and mortality of tree seedlings

Recruitment of *S. khasiana* seedlings was maximum in the highly disturbed stand, while that of *Q. dealbata* seedlings was maximum in the undisturbed and mildly disturbed

**Fig. 3.** Survivorship curves of seedlings of *Q. dealbata* (A), *Q. griffithii* (B), *R. arboreum* (C), and *S. khasiana* (D) in the undisturbed ( $\Delta$ ), mildly disturbed ( $\circ$ ), and highly disturbed ( $\bullet$ ) forest stands.



stands (Table 1). *Quercus griffithii*, which was absent in the mildly disturbed stand, had a slightly lower density in the undisturbed stand than in the highly disturbed stand. The density of *R. arboreum* was higher in the disturbed stands than in the undisturbed stand. The rank-density curves for the tree seedlings showed that the forest floor vegetation in both undisturbed and highly disturbed stands was mainly composed of *Q. dealbata* and *S. khasiana* seedlings, respectively (Fig. 2). In the mildly disturbed stand, *R. arboreum* along with *Q. dealbata* dominated the seedling community.

The survivorship curves for *Q. dealbata*, *Q. griffithii*, and *R. arboreum* in all the stands were characterized by either very low or no mortality over the 2-year period. But *S. khasiana* seedling mortality occurred throughout the study period (Fig. 3), the values being 55–75% in the

**Table 2** Results of analysis of variance performed on the data for six microenvironmental variables to test the variation due to forest stands, seasons, and months.

Microenvironmental variable	Source of variation	Sum of squares	df	F	P
PAR	Forest stands	9 382 848.00	2	131.85	0.01
	Seasons	2 892 132.00	2	40.64	0.01
	Months	9 760.00	3	0.09	ns
	Error	1 280 912.00	36	—	
Relative humidity	Forest stands	554.88	2	4.89	0.05
	Seasons	17 797.03	2	156.97	0.01
	Months	1 060.28	3	6.23	0.01
	Error	2 040.84	36	—	
Air temperature	Forest stands	43.62	2	24.31	0.01
	Seasons	982.30	2	491.20	0.01
	Months	4.18	3	1.39	ns
	Error	36.00	36	—	
Soil temperature	Forest stands	12.14	2	7.10	0.01
	Seasons	264.45	2	154.73	0.01
	Months	3.59	3	1.40	ns
	Error	30.76	36	—	
Soil moisture	Forest stands	37.71	2	7.83	0.05
	Seasons	376.00	2	78.09	0.01
	Months	29.79	3	4.12	0.05
	Error	86.67	36	—	
Litter thickness	Forest stands	22.85	2	95.08	0.01
	Seasons	6.31	2	26.27	0.01
	Months	0.41	3	1.13	ns
	Error	4.33	36	—	

disturbed stands and 100% in the undisturbed stand. The mortality ranged from 5 to 24% in *Q. dealbata*, 28–56% in *Q. griffithii*, and 7–26% in *R. arboreum* (Table 1). In all the species the maximum seedling mortality occurred during winter of the first year. However, in the case of *S. khasiana*, peak seedling mortality was observed during autumn or spring. Seedling mortality was minimum during the rainy season in all the species (Fig. 3).

#### Forest microenvironment

Relative humidity, air temperature, and PAR near the forest floor showed a marked seasonal variation in all stands (Table 2). Relative humidity and air temperature were minimum during winter and maximum during the rainy season; PAR was highest during winter and lowest during the rainy season (Fig. 4). PAR and air temperature were significantly higher (Tukey's multiple comparison test  $P < 0.01$ ) in the highly disturbed stand than in the mildly and undisturbed stands, while relative humidity was significantly higher (Tukey's multiple comparison test  $P < 0.01$ ) in the undisturbed stand than in the disturbed stands.

Soil moisture, soil temperature, and litter layer also exhibited a distinct seasonal pattern. Soil moisture and

temperature declined gradually to the lowest levels during winter after attaining a peak during the rainy season and spring, respectively. The thickness of the litter layer was maximum during winter in the undisturbed stand, while the disturbed stands had a thicker litter layer during the rainy season. The former stand always had a thicker litter layer than the latter stands.

#### Effect of microenvironmental factors on seedling mortality

The partial correlation coefficients between age-specific mortality rate of seedlings and various microenvironmental variables yielded significant results only in the case of *Q. dealbata*, *Q. griffithii*, and *S. khasiana*. However, the relative importance of a given factor varied from stand to stand and from species to species (Table 3). None of the microenvironmental factors were significantly correlated with the mortality rate of *R. arboreum* seedlings, while soil moisture was negatively correlated with seedling mortality in *Q. dealbata*, *Q. griffithii*, and *S. khasiana* in the undisturbed and mildly disturbed stands. Mortality in *S. khasiana* seedlings was negatively correlated with PAR in the undisturbed and mildly disturbed stands.

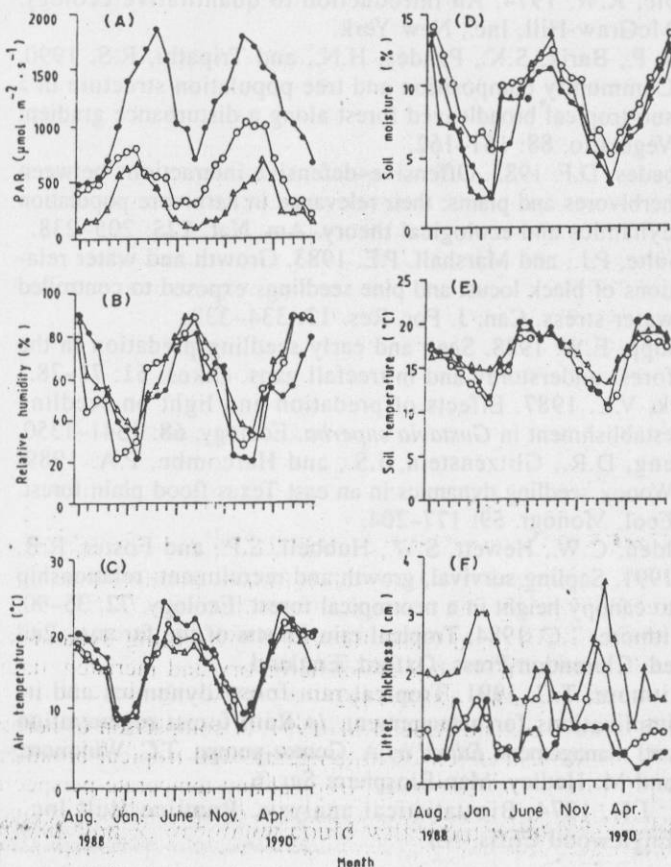
**Table 3.** Partial correlation coefficients ( $r$ ) between age-specific mortality rate ( $q_x$ ) of tree seedlings and six microenvironmental variables in the undisturbed (UD), mildly disturbed (MD) and highly disturbed (HD) forest stands.

	Forest stand	$n$	Partial correlation coefficients <sup>a</sup>					
			PAR	RH	AT	ST	SM	LT
<i>Quercus dealbata</i>	UD	24	-0.209	-0.174	-0.281	0.302	0.253	0.233
	MD	24	-0.295	0.506**	-0.478**	0.007	-0.395*	0.501**
	HD	24	-0.029	-0.090	-0.653**	0.573**	-0.217	0.003
<i>Quercus griffithii</i>	UD	24	-0.159	0.281	0.424*	-0.169	-0.441*	0.168
	HD	24	-0.182	-0.180	-0.004	0.039	-0.212	0.331
<i>Rhododendron arboreum</i>	UD	24	0.016	-0.023	-0.114	0.174	-0.179	0.187
	MD	24	-0.166	-0.038	0.002	-0.150	-0.109	-0.171
	HD	24	0.280	0.258	-0.339	0.155	-0.181	-0.100
<i>Schima khasiana</i>	UD	20	-0.522**	0.478*	0.479*	0.423	-0.510**	-0.395
	MD	24	-0.751**	-0.827**	0.692**	-0.192	0.236	0.102
	HD	24	0.196	0.212	0.254	-0.218	-0.129	0.114

Note: \* $P < 0.05$ ; \*\* $P < 0.01$ .

<sup>a</sup>PAR, photosynthetically active radiation; RH, relative humidity; AT, air temperature; ST, soil temperature; SM, soil moisture; LT, litter thickness.

**Fig. 4.** Monthly variation in PAR (A), relative humidity (B), air temperature (C), soil moisture (D), soil temperature (E), and litter thickness (F) in the undisturbed ( $\Delta$ ), mildly disturbed ( $\circ$ ), and highly disturbed ( $\bullet$ ) forest stands.



## Discussion

Greater seedling recruitment of *S. khasiana* in the highly disturbed stand is in conformity with the findings of Khan et al. (1987). In other species the intensity of disturbance did not alter the seedling recruitment pattern. Survival of newly recruited *S. khasiana* seedlings in the undisturbed and mildly disturbed stands was dependent on the amount of PAR received by the forest floor, as is clearly evident from a significant negative correlation between mortality rate and PAR. Therefore, it may be argued that low PAR could have adversely affected the survival of seedlings of this species in the undisturbed and mildly disturbed stands, while high PAR in the highly disturbed stand might have favoured better survival of its seedlings. Other factors such as soil moisture, relative humidity, and air temperature also affected the seedling mortality of *S. khasiana*. *Quercus dealbata*, *Q. griffithii*, and *R. arboreum*, on the other hand, showed better survival than *S. khasiana* in all the three stands, provided their seedlings survived the marked seasonal fluctuations in soil moisture and temperature during the first year of growth. Seedling mortality of these species during winter could be ascribed to the prevailing low soil moisture and low temperature conditions. The importance of soil moisture in influencing tree seedling survival and growth in forests has been reported in a number of earlier papers (McLeod and Murphy 1977; Mueller-Dombois et al. 1980; Schulte and Marshall 1983).

The seedling survival pattern in disturbed and undisturbed forest stands clearly revealed that seedlings of *Q. dealbata*, *Q. griffithii*, and *R. arboreum* could withstand wide fluctuations in PAR, relative humidity, air temperature, and

soil moisture caused by seasonal cycle as well as by human disturbances. In the case of *S. khasiana*, partial canopy harvesting was essential for seedling survival during the initial stages of establishment. This finding, however, does not fully explain the presence of *S. khasiana* in the overstorey of the undisturbed forest stand at Mawphlang, where shade-intolerant *S. khasiana* was also present with shade-tolerant species. Since this forest has been protected from human disturbances for a long time, past natural disturbance might have been responsible for the presence of *S. khasiana* as a constituent of the top canopy layer. It may be mentioned here that windstorms during the premonsoon period are the most common natural cause for the creation of tree-fall gaps in this forest (Barik et al. 1992) and, therefore, the possibility of large-scale disturbance caused by windstorms in the past may not be excluded.

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