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Tree regeneration in a subtropical humid forest: effect of cultural disturbance on seed production, dispersal and germination

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Summary

1. The subtropical humid forest of Meghalaya, India, has been exposed to various kinds of cultural disturbance of varying magnitude during recent years. In order to analyse the effect of disturbance on natural regeneration of a few dominant and commercially important tree species, viz. *Schima khasiana* and the oaks *Lithocarpus dealbatus* and *Quercus griffithii*, a study on seed production, dispersal and germination was carried out in three stands, differing in degree of disturbance, during the years 1988–91.

2. Seed production in *L. dealbatus* and *S. khasiana* varied significantly between the three stands and increased with increasing disturbance. It increased with increase in d.b.h. of the trees in all three species. Heavy seeding occurred in different years in different species.

3. *Lithocarpus* and *Quercus* spp. produced heavier seeds in the disturbed stands than in the undisturbed stand.

4. The number of seeds dispersed from the trees decreased with distance from the parent tree. The dispersal distance for *Lithocarpus* and *Quercus* was greater in the disturbed stands than in the undisturbed stand. However, the dispersal distance in the forest was very low irrespective of degree of disturbance.

5. Seed predation decreased and germination increased with distance from the parent tree in all three stands, suggesting that distance-related seed predation was not influenced by disturbance.

6. In an experiment with four treatments the greatest germination of seeds was observed on the moss layer, irrespective of species and forest stand. The presence of litter inhibited germination of seeds to a great extent in all the species. Germination of *Lithocarpus* and *Quercus* was better in the undisturbed stand than in the disturbed stands, while that of *Schima khasiana* was better in the disturbed stands.

7. An analysis of the fate of seed populations of the oak species revealed that loss of seeds caused through consumption by rodents and insects and transportation by various agents accounted for more than 98% of the seeds, while fewer than 1% of them germinated.

8. The findings of the study are discussed in relation to their potential application in management of the disturbed subtropical forests.

Key-words: *Lithocarpus dealbatus*, microsite, *Quercus griffithii*, *Schima khasiana*, seed disappearance.

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Introduction

The success of tree regeneration in a forest is determined by successful completion of several events in the tree life cycle, such as seed production and dispersal to safe sites, germination and seedling emergence, establishment and onward growth. Seed production of trees may be limited by various extrinsic factors such as resource availability, pollination failure, predation on flowers, fruits and leaves, and by climatic conditions, as well as by intrinsic factors such as age and size of the plant and its genetic constitution (Winn & Werner

1987). The patterns of seed production differ among populations of the same species that are adapted to different microhabitats; and individual trees within a population also vary enormously in the size of their fruit crop (Howe 1982). Seed production among populations also varies because of differences in both the number of fruiting individuals and the number of seeds produced per reproductive individual (Schupp 1990).

The interplay between seed predation and dispersal is an important determinant of seedling establishment. It has been argued that seed predation decreases with distance from the parent tree and the 'escape hypothesis' seems to hold good in many plant communities (Janzen 1971; Howe 1982).

Small-scale heterogeneity of biotic and abiotic factors divides a habitat into a mosaic of microsites, some of which favour the germination of a particular group of species depending on their germination requirements. Numerous studies have documented the optimal requirements for seed germination in tree species from this region in controlled environments (cf. references given by Ramakrishnan 1992), but information concerning the influence of microsite characteristics on germination and establishment of tree seedlings on the forest floor is limited in the humid subtropical forest of north-east India (Khan, Rai & Tripathi 1986; Khan & Tripathi 1987; Tripathi & Khan 1990).

This paper analyses the effect of cultural (man-induced) disturbance on the above-mentioned events in the oaks *Lithocarpus dealbatus* and *Quercus griffithii*, and in *Schima khasiana* in three stands of the subtropical humid forest located in the state of Meghalaya (north-east India), where the felling of trees by the local people for timber and fuelwood purposes has, of late, become a common feature. It is hoped that the findings of this study will help in understanding the influence of disturbance on natural regeneration of the dominant tree species of the subtropical forests of the region. In addition, such a study may help in prescribing appropriate silvicultural practice for regeneration of the disturbed subtropical forest ecosystem.

Methods

STUDY AREAS

The study was conducted in three stands of the northern subtropical wet hill forest of India (Champion & Seth 1968) located in the greater Shillong area (25°34′N, 91°56′E). The three forest stands were classified on the basis of a disturbance index (the basal area of the cut trees measured at ground level expressed as a fraction of the 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. All three locations are situated within a circle of radius of 15 km on the eastern aspect of gently sloping hills receiving similar annual rainfall.

The forest stand at Mawphlang, protected by the local tribes as a sacred grove, represents the relict vegetation occurring between 1500 m and 2000 m a.s.l. in the N.E. region of India (Khan *et al.* 1986). The forest was dense and semi-evergreen with the plant species distributed into four distinct strata: canopy layer, subcanopy layer, shrub layer and ground vegetation. The species composition and community characteristics of the forest stands at Mawphlang and those at Shillong and Upper Shillong have been described by Rao *et al.* (1990). In general, *Lithocarpus dealbatus* (Miquel) Rehder (= *Quercus dealbata*), *Rhododendron arboreum* Sm. and *Schima khasiana* Dyer represented the dominant trees in all the three stands. *Quercus griffithii* Miquel was a codominant species in the undisturbed and highly disturbed stands. *Pinus kesiya* Royle ex Gordon, a subtropical pine which tends to become dominant following disturbance in the broad-leaved forest community, was an important species in the highly disturbed stand at Upper Shillong. All the species considered in the present study are found in the subtropical forests occurring between 1500 m and 2000 m a.s.l. in north-east India (Kaul & Haridasan 1987; Haridasan, Chauhan & Beniwal 1993).

CLIMATE AND SOIL

The climate is typically monsoonal with distinct wet (May to mid-October) and cool (mid-November to February) seasons. The periods mid-October to mid-November and March to mid-May represent autumn and spring seasons, respectively. About 85% of the annual rainfall is received during the wet season. During winter, the temperature may fall to 3 °C and there is occasional frost during the night. The mean annual values of climatic variables, which are more or less equal for all the three sites and were obtained from the meteorological station at Upper Shillong, are: rainfall, 2500 mm; maximum and minimum temperatures, 16 °C and 3 °C; and relative humidity 85% (Rao *et al.* 1990).

The soil is lateritic and derived from gneisses, schists and granites of Archean age (Gansser 1964). The texture of the top soil (0–10 cm) in the undisturbed, mildly disturbed and highly disturbed stands was loamy silt, sandy loam and loam, respectively. In the top soil organic matter content ranged from 3·2 to 6·4%, total nitrogen from 0·17 to 0·28% and pH from 5·0 to 5·7. These were determined according to methods outlined by Allen *et al.* (1974).

ESTIMATION OF SEED PRODUCTION

Ten fruiting trees of *L. dealbatus* and *Q. griffithii* and five fruiting trees of *S. khasiana*, in each of the three d.b.h. classes 10–20 cm, 20–30 cm and 30–40 cm, were marked in each stand during August–October 1988. The numbers of seeds produced by these marked trees were estimated for three consecutive years during 1988–91. Appearance of brown colour on the seed coat was taken as an indication of maturity. The aborted seeds were not included in determining seed production. Seeds were counted just before maturation in mid-October for *L. dealbatus*, mid-August for *Q. griffithii* and mid-January for *S. khasiana*. Since predation of seeds starts during their maturation on the tree itself, seed production estimates made on the tree in the initial stage of maturation represented the total seed production including those lost to predation during the maturation phase.

The seed production for each tree was estimated as follows:

Total seed production = Total number of branches × mean number of sub-branches per main branch × mean number of inflorescences per sub-branch × mean number of acorns/fruits per inflorescence × mean number of seeds per fruit (for *S. khasiana*).

For each tree, mean number of inflorescences per branch was calculated from a sample of 10 branches and mean number of acorns per inflorescence was calculated from a sample of 50 inflorescences. Average number of seeds per fruit was determined from 100 random samples to estimate the seed production in *S. khasiana*. The data were pooled for each d.b.h. class, each stand and each year, and three-way ANOVA (fixed effect–restricted randomization) was performed to test the effect of each of these factors. However, in view of the unreplicated stand, the inferential statistics for disturbance (i.e. stand factor) was not used for interpreting results and drawing conclusions. To avoid the effect of pseudoreplication, seed production data have been presented in a tabular form giving standard deviations (see Hurlbert 1984).

Average seed weight for each tree species was determined from a composite sample of 500 fresh seeds collected from each of the marked trees. Seeds of *Lithocarpus* and *Quercus* were classified into four classes, 300–500 mg, 500–700 mg, 700–900 mg and 900–1100 mg, and the percentage of seeds in each size class was determined.

DISPERSAL OF SEEDS

Although no seed-eating animal was seen during the daytime, a large number of damaged or partly damaged *Lithocarpus* and *Quercus* seeds around the parent trees provided strong evidence of the presence of acorn-eating birds and other animals in the forests. The bird population was quite low and wild animals other than a few rodents, viz. *Rattus rattus rufescens* (Gray), *R. rattus brunneusculus* (Hodgson), *Micromys minutus erythrotis* (Blyth), were rare in these forests. Therefore, rodents seemed to be the main consumers, dispersers and hoarders of acorns. They also acted as the dispersal agents for the oak seeds. Insect larvae also fed on the acorns, damaging a considerable portion of the total seed population.

We marked five sample fruiting trees of *Lithocarpus dealbatus* and *Quercus griffithii* in each of the three forest stands for seed dispersal and predation studies. The trees marked for this study were growing at least 100 m apart and no other trees of the same species were present within this distance range. Seed dispersal was studied in concentric circles around each fruiting tree spaced at 2·5 m radial increments beyond the crown radius. The seeds falling under the tree crown were not taken into account in the seed dispersal study. The first of the concentric circles had a radius of 5 m and the maximum radius considered was 40 m. The circles were visited at 3-day intervals over a period of 2 weeks during the peak period of seedfall of the respective species. During each visit, acorns in all circles were collected and counted separately. The dispersal was expressed as the number of seeds per 100 m^2. Suitable regression models were proposed to establish the relationship between dispersal distance and number of seeds dispersed.

ASSESSMENT OF THE FATE OF SEED POPULATIONS

Experimental differentiation between the fraction of seed population lost to predation and transport is very difficult (van Tooren 1988). Therefore, the term 'disappearance' used in this paper includes the seed loss due to predation as well as to transport and dispersal by animals, run-off and wind. Five wooden seed traps, 100 × 100 cm and 30 cm deep, were laid at random under the tree crown of each of the five marked trees at the beginning of seedfall and were visited until the completion of seed shedding. All the seeds in each trap were counted. The undamaged seeds were separated from seeds damaged by insects and rodents. The difference between total seed production and the undamaged seeds that fell beneath the tree crown represented the fraction of seed populations disappearing during the seedfall period.

The fate of undamaged seeds after seedfall was studied by sowing 25 seeds in each of the five 1 × 1-m plots under each sample tree. The plots were visited at 15-day intervals up to 3 months. On each observation date, the number of seeds that had germinated, disappeared or rotted was noted. The percentage of seeds in each category was determined and the means ($n = 5$ trees) for each stand were calculated. The experiment was repeated during 1990 to study the year-wise variation in pattern of seed loss. Finally, the fractions of seed populations that had disappeared, rotted or germinated, were expressed as percentages of total seed production for both years of study.

EFFECT OF DISTANCE FROM PARENT TREES ON SEED DISAPPEARANCE AND GERMINATION

In order to study seed predation at different distances from the parent tree, three 1 × 1-m plots were randomly demarcated on each of the concentric circles with radii of 5, 15, 25 and 35 m from the base of the fruiting tree. Twenty acorns were marked with waterproof paint and placed in each plot. This procedure simulated the conditions experienced by seeds dropped by rodents or birds while being carried away for hoarding or consumption during seedfall and/or post-seedfall periods. The fate of seeds was monitored at weekly intervals over a period of 3 months for determining losses due to damage, disappearance and germination. At the end of 3 months, the numbers of seeds that had germinated or disappeared (having been consumed or transported by herbivores or other agencies) were recorded. This study was conducted during 1989 and 1990. The data for the 2 years were pooled and analysis of variance was performed to test whether the seed predation and germination were influenced by distance from the parent tree.

EFFECT OF MICROSITES ON SEED GERMINATION

To study the effect of forest floor microsites on germination of *Lithocarpus dealbatus*, *Quercus griffithii* and *Schima khasiana*, 144 plots of 1 × 1 m for each species of oak and 36 plots for *S. khasiana* were demarcated across the three forest stands. In each stand seeds were sown on the moss layer, the litter layer, below the litter layer and on the cleared forest floor.

Seeds of *L. dealbatus* and *Q. griffithii* were grouped into four classes according to their weight: 300–500 mg, 500–700 mg, 700–900 mg and 900–1100 mg. Such grouping was not possible in the case of *S. khasiana* seeds because of their light weight and morphological characteristics. Thus, for the oaks the experimental design consisted of 3 forest stands × 4 microsites × 4 seed weight classes × 3 replicates and for *S. khasiana* it comprised 3 forest stands × 4 microsites × 3 replicates. Twenty seeds each of *L. dealbatus* and *Q. griffithii* were sown in each plot during October–November 1989 and the same number of seeds of *S. khasiana* was sown in each plot during February 1990. The dates of seed sowing coincided with the natural seed fall period. Germination in each plot was monitored at 15-day intervals up to a period of 3 months, after which no viable seed was found in the plot. The seeds of these species did not germinate after 3 months even under ideal laboratory conditions (unpublished data). The germination data were subjected to three-way ANOVA (restricted randomization) to determine the effects of disturbance, microsite and seed weight on germination after arcsine transformation of the percentage values.

Results

SEED PRODUCTION

Seed production significantly increased ($P < 0{\cdot}01$) with increase in d.b.h. of fruiting trees in all the three species studied and year-wise variation in seed production also varied significantly ($P < 0{\cdot}001$: Table 1). In *L. dealbatus*, the seed production was maximum during 1989 and 1990 in the highly disturbed stand.

Table 1. Year-wise variation in mean (±SD) seed production by trees of different d.b.h. classes in the disturbed and undisturbed stands. Tabulated values are actual values $\times 10^{-3}$

	Undisturbed stand d.b.h. class (cm)			Mildly disturbed stand d.b.h. class (cm)			Highly disturbed stand d.b.h. class (cm)		
Year	10–20	20–30	30–40	10–20	20–30	30–40	10–20	20–30	30–40
Lithocarpus dealbatus									
(*n* = 10)									
Nov 1988	0·3 ± 0·1	0·8 ± 0·3	2·0 ± 0·9	0·8 ± 0·3	1·4 ± 0·3	2·1 ± 0·6	1·1 ± 0·3	1·8 ± 0·6	2·2 ± 0·6
Nov 1989	0·6 ± 0·3	1·9 ± 0·3	3·3 ± 0·6	1·1 ± 0·3	3·0 ± 0·6	4·3 ± 0·6	2·6 ± 1·6	4·1 ± 1·2	7·2 ± 1·6
Nov 1990	0·7 ± 0·3	2·4 ± 0·9	4·0 ± 1·6	0·5 ± 0·3	2·1 ± 0·6	3·2 ± 0·9	2·5 ± 1·6	3·5 ± 1·2	6·0 ± 1·9
Quercus griffithii									
(*n* = 10)									
Dec 1988	9·1 ± 2·8	19·9 ± 8·2	43·0 ± 8·2	–	–	–	12·9 ± 8·2	18·7 ± 5·1	46·7 ± 7·6
Dec 1989	3·5 ± 1·6	9·5 ± 3·8	22·7 ± 10·4	–	–	–	4·7 ± 3·5	9·5 ± 3·8	22·8 ± 8·5
Dec 1990	7·5 ± 4·1	14·3 ± 6·3	37·7 ± 12·3	–	–	–	7·1 ± 5·6	15·0 ± 5·7	30·9 ± 12·1
Schima khasiana									
(*n* = 5)									
Jan 1989	6·6 ± 1·7	10·7 ± 1·7	17·5 ± 6·3	6·6 ± 1·6	13·1 ± 5·1	21·8 ± 5·8	14·2 ± 8·2	18·7 ± 2·9	34·3 ± 6·5
Jan 1990	6·4 ± 3·4	14·8 ± 4·2	20·5 ± 7·6	5·4 ± 2·5	15·5 ± 5·4	24·1 ± 5·8	14·2 ± 6·9	18·4 ± 3·1	39·7 ± 8·9
Feb 1991	5·3 ± 2·2	8·4 ± 4·2	13·2 ± 8·7	7·0 ± 2·9	8·8 ± 1·1	11·8 ± 2·5	8·1 ± 0·4	10·7 ± 1·1	28·7 ± 8·9

– Absence of trees.

Table 2. Mean seed weight (mg ± SE) of *Lithocarpus dealbatus* and *Quercus griffithii* in undisturbed and disturbed forest stands

Species	Year	Undisturbed	Mildly disturbed	Highly disturbed
Lithocarpus dealbatus	1988	499·4 ± 11·0	566·9 ± 6·2	698·5 ± 11·8
	1989	483·9 ± 12·7	564·6 ± 8·0	708·9 ± 6·7
Quercus griffithii	1988	679·2 ± 10·0	–	835·0 ± 15·6
	1989	712·0 ± 9·7	–	852·0 ± 23·3

– Absence of trees.

Seed production in *Q. griffithii* was maximum during 1988 and in *S. khasiana* during 1990. In *L. dealbatus* and *S. khasiana*, the seed production significantly increased ($P < 0{\cdot}01$) with increasing disturbance.

The mean seed weight of *L. dealbatus* and *Q. griffithii* varied significantly ($P < 0{\cdot}05$) among the stands: it increased with increasing disturbance in both species (Table 2). Year-wise variation in mean seed weight was insignificant. In the undisturbed stand, 57–65% seeds of *L. dealbatus* were small in size (300–500 mg). In the mildly disturbed stand, 53–58% of seeds were in the medium weight class (500–700 mg) and 52–62% in the highly disturbed stand belonged to the heavier category (700–900 mg). The fraction of seed population in the heaviest class (900–1100 mg) was lowest (2–5%) in all the three stands. In *Q. griffithii*, which was present only in the undisturbed and highly disturbed stands, seeds were comparatively larger than in *L. dealbatus*. In the undisturbed stand around 51% of the total seed production during 1988 and 62% during 1989 was in the 700–900 mg class. In the highly disturbed stand, 52% during 1988 and 64% during 1989 were in the heaviest class (900–1100 mg). The lowest fraction of seed population in the undisturbed stand was in the 900–1100-mg class, while in the highly disturbed stand it was in the 500–700-mg class (Fig. 1).

SEED DISPERSAL

The number of seeds per unit area of the forest floor decreased significantly ($P < 0{\cdot}05$) with increase in distance from the parent tree crown (Fig. 2). Such a seed dispersal pattern was observed in both species of oak in all the three stands. The highest number of seeds (120–220 seeds per 100 m^2) was observed within 5 m of the tree. Regression models showing the relationship between number of seeds and dispersal distance in the disturbed and undisturbed stands are given in Table 3.

FATE OF SEED POPULATIONS

During the seed fall period, 52–60% of the total seeds produced by *Lithocarpus dealbatus* disappeared and the corresponding value for *Quercus griffithii* ranged from 84 to 91%. Disappearance of seeds, largely attributable to seed consumption, was maximal in the highly disturbed stand (*c.* 60%) and minimal in the mildly disturbed stand (*c.* 52%) in *L. dealbatus*. In *Q. griffithii*, the fraction of seed damaged by insects and rodents was more in the undisturbed (*c.* 91%) than in the disturbed stand (84·0%: Table 4). During the good seed year, the fraction of damaged seeds was lower than that during the lean year. The fraction of the seed population damaged by insects was quite low (2·3–10·3%) but was generally larger in the disturbed than in the undisturbed stand.

During the post-seedfall period, more than 95% of the remaining seeds disappeared. There was no difference in the pattern of seed disappearance in the three stands during the post-seedfall period.

In general, more than 98% of the total seeds produced by the oaks disappeared from the forest floor; this included the seeds damaged by rodents and

Table 3. Relationship between seed density per 100 m^2, y, and dispersal distance (m), x, in *Lithocarpus dealbatus* and *Quercus griffithii*

Species Stand	Regression model	r^2	n	Range of values for x
Lithocarpus dealbatus				
Undisturbed	$\log y = 156{\cdot}8 - 4{\cdot}9x$	0·70	16	2·5–40
Mildly disturbed	$\log y = 102{\cdot}9 - 3{\cdot}1x$	0·76	16	2·5–35
Highly disturbed	$\log y = 140{\cdot}5 - 4{\cdot}0x$	0·77	16	2·5–40
Quercus griffithii				
Undisturbed	$\log y = 244{\cdot}3 - 7{\cdot}7x$	0·63	16	2·5–35
Highly disturbed	$\log y = 252{\cdot}8 - 7{\cdot}6x$	0·70	16	2·5–35

** $P < 0{\cdot}01$.

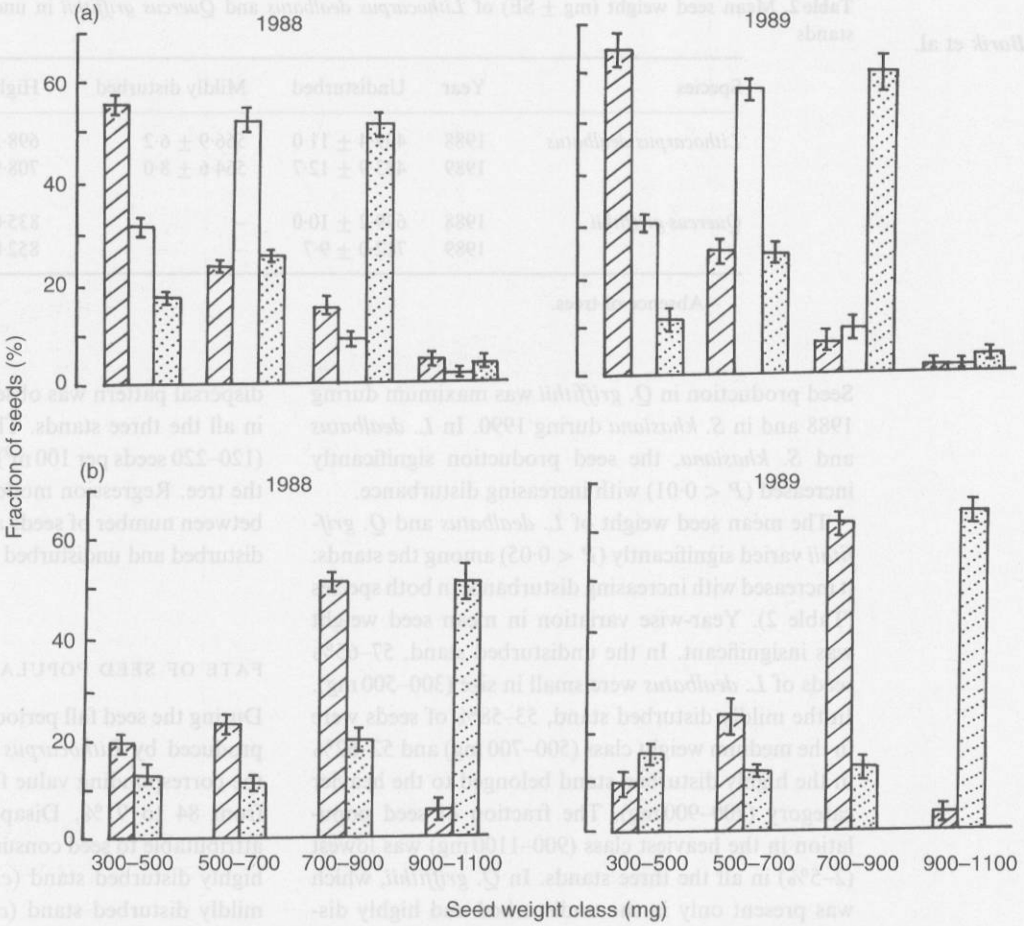

Fig. 1. Fraction(%) of seeds of (a) *Lithocarpus dealbatus* and (b) *Quercus griffithii* in different seed weight classes in undisturbed (▨) mildly disturbed (☐) and highly disturbed (▦) forest stands. Vertical bars indicate ±SE.

insects. 0·1–0·5% were rotten and less than 1% (0·1–0·8%) could germinate (Table 5).

SEED DISAPPEARANCE AND GERMINATION IN RELATION TO DISTANCE FROM PARENT TREE

Seed predation decreased with increase in distance from the tree and it was maximum in the highly disturbed stand and minimum in the mildly disturbed stand (Fig. 3). More than 75% of the sown seeds of the oaks were consumed within a 5-m circle around the tree, while about 25% of seeds were consumed in the concentric circle at a distance of 35 m from the tree. In *Schima khasiana* the predation was quite low (20–45%) as compared with the oaks and it varied significantly ($P < 0{\cdot}05$) among the stands. Germination increased with distance in all three species (Fig. 3). In the oaks germination was *c.* 5–10% in the 5-m circle and 15–30% at a distance of 35 m from the parent tree; the corresponding germination percentages for *S. khasiana* were 20% and 40%, respectively. The germination of sown seeds varied significantly ($P < 0{\cdot}05$) among the three stands. In the oaks it was greater in the undisturbed stand, while in *S. khasiana* it was greater in the highly disturbed stand.

EFFECT OF MICROSITES ON GERMINATION

Germination on the moss layer was much higher than in the other microsites in all three species (Table 6). The lowest germination was observed on the litter layer. Both the oaks showed best germination in the undisturbed stand followed by mildly and highly disturbed stands. In *Schima khasiana*, germination was significantly higher ($P < 0{\cdot}05$) in the mildly and highly disturbed stands than in the undisturbed stand. In both the oak species, larger seeds showed better germination than smaller ones. Analysis of variance revealed a significant variation ($P < 0{\cdot}01$) in germination of the oaks due to the microsites, seed weight and disturbance regimes. In *S. khasiana*, too, the variation in germination percentage due to microsites and disturbance regimes was significant ($P < 0{\cdot}01$). However, interpretation of the effect of disturbance on seed germination has limitations because of pseudoreplication within sites.

Discussion

The year-wise variation in seed production by the three species is in conformity with the findings of Grubb (1977), Clark & Clark (1987) and many other

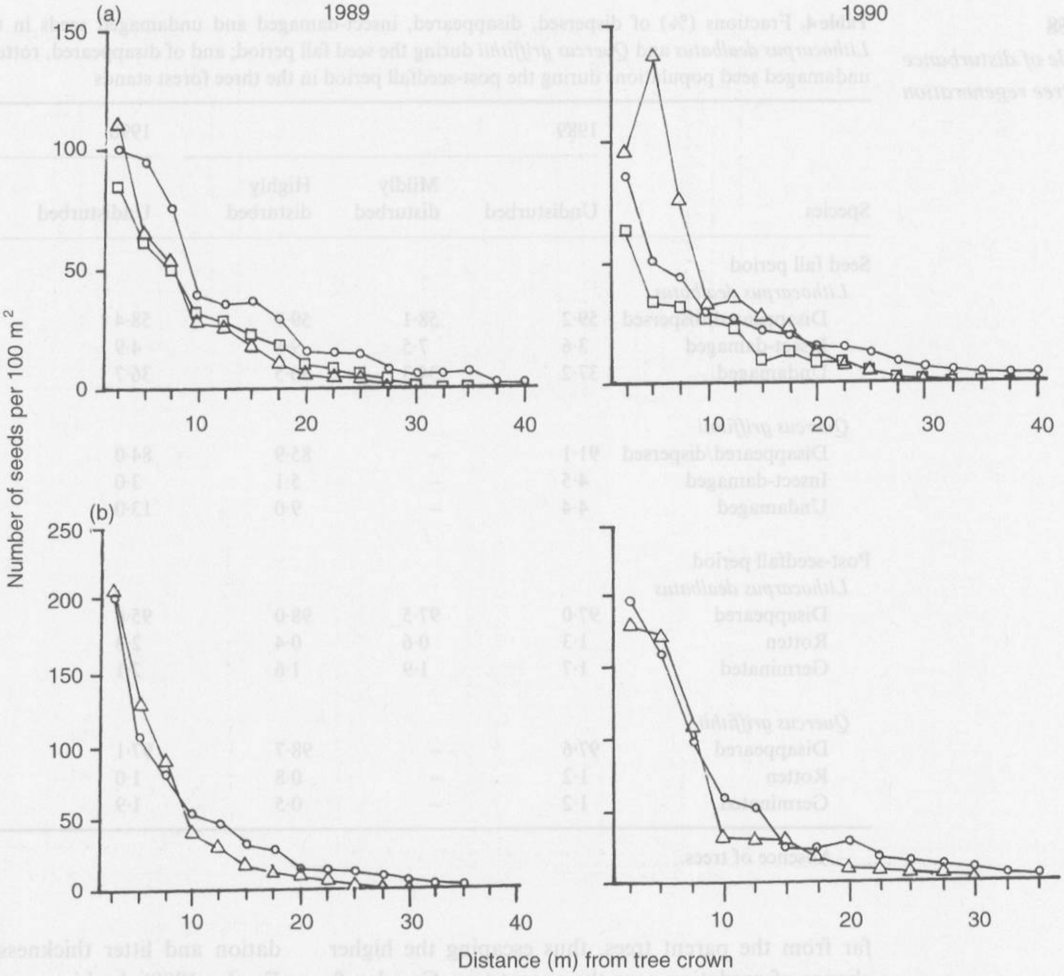

Fig. 2. Dispersal curves of (a) *Lithocarpus dealbatus* and (b) *Quercus griffithii* in the undisturbed (△), mildly disturbed (□) and highly disturbed (○) forest stands.

workers as cited by Schupp (1990) for shade-tolerant species and Milton *et al.* (1982) for light-demanding pioneer species. The ultimate cause of a cycle of alternate bearing is not known in detail, but most hypotheses suggest that resource limitation is the main cause of this in trees (Monselise & Goldschmidt 1982; Fenner 1991). Howe (1982) and Janzen (1971) have argued that year-wise variation in heavy fruiting events ensures the recruitment of a particular species despite heavy seed and seedling predation by herbivores. Heavy fruiting may occur because of prolonged depression of minimum night temperature, increasing length of dry season and a dry sunny year following a wet year (Anonymous 1978). Significant increase in seed production in *Lithocarpus dealbatus* and *Schima khasiana* with increasing disturbance indicates that disturbance may also influence the seeding event in these species.

Differences in seed weight of the two oaks among the three stands (Table 2) could be due to differential environmental influences in the three stands as well as to genetic differences among the parent trees. The wide seed size variation among different individuals within a population of *Virola surinamensis* was attributed to similar factors by Howe & Richter (1982).

Production of greater numbers of heavier seeds in the disturbed stands than in the undisturbed stand does not conform to the generally held view that the number of seeds and their size are negatively correlated. Increase in both seed size and seed output in disturbed stands could be attributed to enhanced availability of resources (Waring 1991), since disturbance increases light availability and nutrient percolation through the soil and facilitates nutrient uptake by the plant (Bazzaz 1984).

Rapid disappearance of seed from the forest floor has been ascribed to transportation by mice, voles and other rodents (Jensen 1985; Kikizawa 1988) which consume and/or scatter and hoard seeds beneath the deep litter layer or below ground. This could be the reason for poor recruitment of oak seedlings in the forest despite large seed production. In the absence of any strong defence against herbivory except a thickened seed coat and rounded form, the acorns are highly prone to herbivory by rodents in the forest owing to their high food content. Predation and germination patterns in relation to distance from the parent tree (Figs 2, 3) support the 'escape hypothesis' of Chesson & Warner (1981), which suggests that the probability of germination increases if the seeds are transported

Table 4. Fractions (%) of dispersed, disappeared, insect-damaged and undamaged seeds in the total seed population of *Lithocarpus dealbatus* and *Quercus griffithii* during the seed fall period; and of disappeared, rotten and germinated seed in the undamaged seed populations during the post-seedfall period in the three forest stands

	1989			1990		
Species	Undisturbed	Mildly disturbed	Highly disturbed	Undisturbed	Mildly disturbed	Highly disturbed
Seed fall period						
Lithocarpus dealbatus						
Disappeared/dispersed	59·2	58·1	59·9	58·4	51·7	58·8
Insect-damaged	3·6	7·5	9·6	4·9	8·2	10·3
Undamaged	37·2	34·3	30·5	36·7	40·1	30·9
Quercus griffithii						
Disappeared/dispersed	91·1	–	85·9	84·0	–	86·0
Insect-damaged	4·5	–	5·1	3·0	–	2·3
Undamaged	4·4	–	9·0	13·0	–	11·7
Post-seedfall period						
Lithocarpus dealbatus						
Disappeared	97·0	97·5	98·0	95·6	97·6	98·7
Rotten	1·3	0·6	0·4	2·3	1·4	0·4
Germinated	1·7	1·9	1·6	2·1	1·0	0·9
Quercus griffithii						
Disappeared	97·6	–	98·7	97·1	–	98·7
Rotten	1·2	–	0·8	1·0	–	0·5
Germinated	1·2	–	0·5	1·9	–	0·8

– Absence of trees.

far from the parent trees, thus escaping the higher chance of predation near the parent tree. Crawley & Long (1995) reported that, in the case of *Quercus robur*, seed density, microsites and predators affected the recruitment in south-east England, but to differing degrees in different places.

Numerous variables limit the abundance and performance of individuals within a population through regulating seed germination and seedling establishment. In particular, these include factors operating at small scales, such as specific germination requirements, microsite characteristics (Harper 1977), predation and litter thickness (Collins & Good 1987; Fowler 1988), herbivore and carnivore density, and structure and successional status of vegetation (Crawley & Long 1995). The moss layer, having a relatively high moisture retention capacity, provided most favourable conditions for germination among the different microsites studied, irrespective of the stands. Germination and emergence of a number of species of chalk grassland have been reported to be better on the moss layer (Keizer, van Tooren & During 1985) than on the top soil layer (van Tooren 1988). Several workers studying the seed ecology of *Quercus* species

Table 5. Dispersed, disappeared, rotten and germinated seeds expressed as fractions (%) of the total number produced by *Lithocarpus dealbatus* and *Quercus griffithii* in undisturbed and disturbed forest stands

	1989			1990		
Species	Undisturbed	Mildly disturbed	Highly disturbed	Undisturbed	Mildly disturbed	Highly disturbed
Lithocarpus dealbatus						
Disappeared/dispersed	98·9	99·1	99·4	98·4	99·0	99·6
Rotten	0·5	0·2	0·1	0·8	0·6	0·1
Germinated	0·6	0·7	0·5	0·8	0·4	0·3
Quercus griffithii						
Dispersed	2·2	–	2·8	4·4	–	5·1
Disappeared	97·6	–	97·1	95·2	–	94·8
Rotten	0·1	–	0·1	0·1	–	0·1
Germinated	0·1	–	0·1	0·3	–	0·1

– Absence of trees.

Table 6. Effect of microsites on the moss layer (ML), on the litter layer (OL), below the litter layer (BL), cleared forest·line floor (CF) and seed mass on mean percentage germination (±SE) of *Lithocarpus dealbatus*, *Quercus griffithii* and *Schima khasiana* in the undisturbed and disturbed forest stands

Species Seed weight (mg)	Undisturbed				Mildly disturbed				Highly disturbed			
	ML	OL	BL	CF	ML	OL	BL	CF	ML	OL	BL	CF
Lithocarpus dealbatus												
300–500	20 ± 2·9	5 ± 1·7	10 ± 4·4	10 ± 1·7	10 ± 1·7	5 ± 2·4	5 ± 1·7	10 ± 4·4	10 ± 2·9	0	5 ± 0	20 ± 2·9
500–700	25 ± 1·7	5 ± 2·9	10 ± 1·7	10 ± 1·7	15 ± 2·9	5 ± 1·7	10 ± 1·7	15 ± 4·4	10 ± 1·7	0	5 ± 0	10 ± 1·7
700–900	30 ± 4·4	10 ± 1·7	15 ± 2·4	15 ± 1·7	15 ± 2·9	5 ± 1·7	10 ± 2·4	15 ± 2·4	15 ± 2·4	5 ± 0	5 ± 1·7	15 ± 2·4
900–1100	30 ± 2·9	10 ± 1·7	15 ± 2·4	20 ± 4·4	20 ± 1·7	5 ± 2·9	10 ± 2·9	20 ± 4·4	15 ± 2·4	5 ± 1·2	10 ± 1·2	15 ± 2·9
Quercus griffithii												
300–500	35 ± 1·7	10 ± 1·7	20 ± 4·4	15 ± 2·4	25 ± 2·9	10 ± 1·7	20 ± 2·4	15 ± 1·7	20 ± 2·9	5 ± 1·7	10 ± 0	10 ± 1·7
500–700	40 ± 2·4	15 ± 1·7	25 ± 2·9	20 ± 2·9	35 ± 2·7	10 ± 1·7	25 ± 1·7	20 ± 2·9	30 ± 1·7	5 ± 1·7	10 ± 1·7	10 ± 2·9
700–900	50 ± 2·9	20 ± 2·4	30 ± 2·9	25 ± 1·7	40 ± 2·9	15 ± 1·7	30 ± 1·7	20 ± 2·4	35 ± 2·9	10 ± 2·4	20 ± 2·4	15 ± 1·7
900–1100	60 ± 2·9	20 ± 1·7	30 ± 2·4	25 ± 1·7	45 ± 2·9	15 ± 1·7	30 ± 1·7	25 ± 1·7	40 ± 1·7	10 ± 2·4	20 ± 2·4	20 ± 2·9
Schima khasiana												
	50 ± 3·5	5 ± 2·2	25 ± 2·2	35 ± 1·6	65 ± 5·0	10 ± 4·0	25 ± 3·2	45 ± 3·2	65 ± 3·5	5 ± 1·6	35 ± 3·2	40 ± 2·2

(see Shaw 1968) have reported that the unconsumed scatter-hoarded fraction of the disappeared seed population often germinates, owing to favourably moist conditions below the litter, and gives rise to a sizeable population of seedlings. Poor germination of seeds of all three tree species during winter, when the forest floor is usually dry and the temperature low, indicates that low soil moisture and low temperature together might have inhibited germination.

A partial harvesting of the tree canopy might favour the production of heavier seeds in the surviving trees of the oak species, probably by improving the availability of resources. However, this could also interfere with seed germination by limiting the number of favourable microsites on the forest floor. An alteration in forest microclimate and microsite characteristics, consequent upon exposure of the forest floor to insolation, favoured both seed production and germination in the shade-intolerant *Schima khasiana*.

The data on seed ecology of the three tree species presented in this paper may be helpful in evolving strategies for reforestation of disturbed subtropical humid forests in north-east India. Natural regeneration of oak species through seedlings is rather poor in this region on account of heavy seed predation and unfavourable microsites on the forest floor. The poor seed germination observed on most of the microsites has implications for the forest management. Rela-

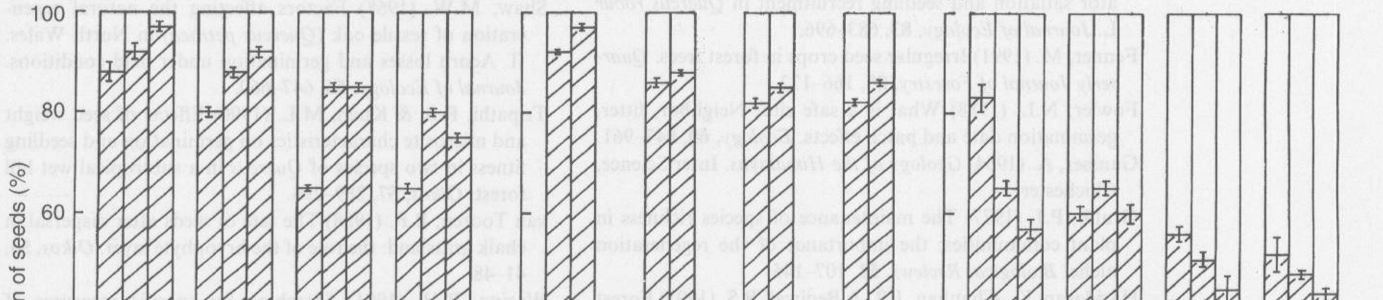

Fig. 3. Disappearance (▨) and germination (□) of seeds as influenced by distance from parent tree for (a) *Lithocarpus dealbatus* (b) *Quercus griffithii* and (c) *Schima khasiana* in undisturbed (UD), mildly disturbed (MD) and highly disturbed (HD) forest stands. Vertical bars indicate ±SE.

tively higher seed production and germination in *Lithocarpus dealbatus* in the mildly disturbed stand suggest that a moderate level of disturbance may be helpful to its regeneration. Better performance of *Schima khasiana*, a secondary successional species, in the highly disturbed stand indicates that this species could be a good choice for raising plantations on such sites.

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