Effects of forest disturbance on fruit set, seed dispersal and predation of Rudraksh (*Elaeocarpus ganitrus* Roxb.) in northeast India

M. L. Khan[1,*], Putul Bhuyan[1] and R. S. Tripathi[2]

[1]Department of Forestry, North-Eastern Regional Institute of Science and Technology, Nirjuli 791 109 India
[2]Department of Botany, North-Eastern Hill University, Shillong 793 022, India

Tropical wet evergreen forests of Arunachal Pradesh, in northeast India are being modified and degraded due to increased anthropogenic pressure. Natural populations of *Elaeocarpus ganitrus* Roxb. (Elaeocarpaceae) are threatened due to household and industrial uses. Natural regeneration is scarce, partly due to extensive harvesting of the tubercled nuts for use in jewellery. Effects of disturbance on natural regeneration are poorly understood. We studied the impact of disturbance on *E. ganitrus* demography by monitoring flowering, fruiting and seed dispersal during three consecutive years and at four sites that varied in the degree of disturbance. Pollination rate in reproductive individuals varied significantly between years, but increased with tree diameter. Fruit production differed significantly among sites, and was highest in the moderately disturbed forest and lowest in the undisturbed forest. Mean fruit weight decreased significantly with increasing disturbance. About 40–70% of the total fruits produced by *E. ganitrus* was removed during the fruit-fall period, mainly by arboreal frugivores and seed-hoarding rodents. After the fruit-fall period, most (55–99%) of the remaining fruits also disappeared, while rates increased with disturbance index. No seeds were found to be germinated. In general, about 80% of the fruits produced by *E. ganitrus* disappeared from the forest floor or was damaged severely by insects, especially ants and termites. The proportion of fruits disappearing decreased significantly with increasing distance from the parent tree. Ripe fruits with intact exocarp were removed more frequently than both unripe fruits with exocarp, and nuts. The nut bank on the soil surface decreased with increasing disturbance index. More than 85% of the nuts of the nut bank was predated. The findings on fruit set and dispersal of *E. ganitrus* may have great implications for regeneration of the species.

POLLINATION, seed production and seed dispersal have been recognized as crucial processes for long-term conservation of biodiversity[1]. Physical alterations to the habitat such as logging and silvicultural measures are likely to affect these processes, which may in turn change the spatial pattern of plant regeneration and possibly alter plant diversity. While environmental conditions and habitat types often influence pre-dispersal predation levels[2], moderate disturbances can favour certain dispersers, while negatively impacting others[3–5]. Habitat alterations may also affect animal-mediated seed dispersal and predation indirectly by changing fruit and seed characteristics (e.g. ripeness, size and nutritional content) that determine their attractiveness as food for animals. Both seed dispersers and seed predators have been shown to be highly selective in the various fruits/seeds they eat[6,7]. Tropical wet evergreen forests in India represent a habitat that is increasingly affected by physical alterations. Although their total geographical area is modest (*c.* 15,010 km^2, or 9% of the total forest cover of India), these forests are rich in biological diversity[8]. Several species are endangered, both by natural as well as anthropogenic threats. The Assam Valley northern tropical wet evergreen forests of northeast India represent climatic climax vegetation of the locality. Forest fellings in this area started in 1952, mostly for road-building, while commercial extraction of timber was started in the late sixties. Since then, heavy pressure has been built up on these forests, and therefore the forests have been degraded.

One of the threatened tree species in the tropical wet evergreen forests of northeast India is Rudraksh (*Elaeocarpus ganitrus*)[9], which produces fleshy fruits with stony endocarp. *E. ganitrus* was originally common in Assam Valley[10], but during recent years the population is dropping at an alarming rate, and presently the species is common nowhere[11]. The decrease is directly or indirectly related to sudden and often far-reaching disturbances in forest ecosystems[12]. Moreover, nut collection for religious jewellery in the form of beads reduces the volume of soil seed bank, which has adversely affected regeneration of the species (1 sapling and 125 seedlings/ha)[12]. Rudraksh depends on animals for seed dispersal. Fruit ingestion by frugivorous animals and nut scatter–hoarding by granivorous animals may help seeds escape high mortality near the parent tree, reduce sibling competition by scattering seeds, decrease genetic-relatedness of patches, and enable the species to colonize new areas. However, most consumers, including rodents, hornbills, bats, flying squirrels, monkeys, deer, wild pigs, buffaloes, mithuns, and elephants (pers. obs.) are also decreas-

*For correspondence. (e-mail: khanml@yahoo.com)

ing in numbers due to deforestation, habitat alteration and poaching.

We studied flower and fruit production, distance-related removal of fruits during fruit-fall and post-fall periods and dynamics of the nut population on the forest floor over a three-year period in four stands that differed in degree of disturbance to answer the following questions: (i) is the fruit set influenced by disturbance intensity; (ii) is the fruit dispersal affected by disturbance; and (iii) is the dispersal determined by stage of ripening of exocarp and presence or absence of fruit pulp?

Materials and methods

Study area

The study was conducted in four stands of the tropical wet evergreen Dipterocarpus forests located in the Deomali area (27°03′ and 27°13′N; 95°22′ and 95°37′E; altitude 200 m amsl) of Arunachal Pradesh[13], which correspond to Champion and Seth's IB/CI Assam Valley tropical evergreen forests[14]. The stands differed in disturbance index, calculated as the basal area of the cut trees measured at ground level expressed as a proportion of the total basal area of all trees, including felled ones[15]. Stands were classified as highly disturbed (disturbance index 70%), moderately disturbed (disturbance index 40%), mildly disturbed (disturbance index 20%) and undisturbed (disturbance index 0%). All stands are situated within a radius of 5km at about the same elevation and have little relief. The vegetation is dominated by *Dipterocarpus macrocarpus* Veque and *Shorea assamica* Dyer along with *Terminalia myriocarpa* Muell. and *Altingia excelsa* Linn. The forests exhibit a multi-tiered stratification and *E. ganitrus* occupies the sub-canopy layer.

The study area experiences tropical highly seasonal climate with well-pronounced winter (December to February) and summer (May to September) seasons. Winter months are comparatively cool and dry, and the temperature during winter may drop down to 6°C. About 85% of the anual rainfall is received during May to September. No month in the year is completely dry. The hottest months are July and August (max temperature 36°C). The mean annual values of climatic variables are more or less equal for all the four stands (rainfall 2500 mm; max and min temperatures 27 and 19°C; relative humidity 83%).

All the four stands studied occur on old alluvial soil. The texture of the soil at different parts varies from sandy loam to clay, with stones occupying 1–5% of the soil volume. The soil pH ranges from 5.5 to 7.5.

Species' study

E. ganitrus Roxb. (Elaeocarpaceae) is commonly known as 'Rudraksh' in India. It is a deciduous tree measuring up to 1.5 m girth and grows to about 25 m, with more or less a round canopy. Mature trees show buttresses. It occurs in tropical forests throughout Southeast Asia. In India, the species is sparsely distributed in the eastern Himalayas in Arunachal Pradesh and other northeastern States and in the Konkan Ghats.

E. ganitrus occupies an important place in Hindu religion. The nuts with a stony endocarp, are worn extensively by Hindu mystics and fakirs. Freaky nuts with fewer or more than five cells are believed to possess special merits attached to each number and therefore fetch much higher prices. The nuts are also economically exploited and used as beads, rosaries, etc. The population of Rudraksh in north-eastern India is shrinking at an alarming rate. Poor germination coupled with prolonged dormancy owing to the hard nature of the nuts might have also contributed to the population decline.

Rudraksh flowers during May to June and fruits ripen during November to December. Fruit weight with and without exocarp ranges from 2.5 to 5.9 g and 1.5 to 3.6 g respectively. The diameter of Rudraksh fruit along with fleshy green mesocarp is approximately 25 mm and the endocarp is about 17 mm in diameter. The ovary of Rudraksh is five-celled. Thus, an ovary may produce 1, 2, 3, 4 or 5 seeds depending upon the abortion of ovules during development into seeds (Figure 1 *a*, *b*). The ripe fruits are blue, succulent; stone normally five-celled, strongly tubercled and marked with as many longitudinal furrows as there are cells in the stone. Fruits are consumed whole by arboreal frugivores that disperse nuts by passing them whole through their digestive tract. Sometimes small birds partly strip the fleshy exocarp. The exocarp is rich in carbohydrates and proteins and provides nutritious reward to consumers[16].

Primary dispersal is by large frugivorous birds and arboreal mammals. Hornbill (*Anthracoceros malagricus* Gmelin), flying squirrel (*Belomys pearsoni* Gray, *Petaurista magnificus* Hodgson), bat (*Rousettus* sp., *Scotophilus* sp.) and monkey (*Presbytis entellus* Dufresne, *P. pileatus* Blyth) eat the ripe fruits of Rudraksh[17]. Secondary dispersal is by frugivorous as well as granivorous mammals. Deer (*Cervus unicolor* Kerr., *Axis axis* Erxleben, *Muntiacus muntjak* Zim.) eat the ripe fruits that had fallen on the forest floor[17] and may in turn disperse the nuts. Viable nuts were also found in the dung balls of elephant (*Elephas maximus* Linnaeus)[17]. A few other wild animals, e.g. buffalo (*Bubalus bubalis* Linnaeus), mithun (*Bos frontalis* Linnaeus) and wild pig (*Sus scrofa* Blyth) were also sighted near Rudraksh trees during the fruiting period[17]. Moreover, nuts are removed and stored by rodents (*Vandeleuria deracea* Bennet, *Rhizomus pruinosus* Blyth, *Mus musculus* Linnaeus, *Rattus rattus rufescens* Linnaeus, *R. rattus brunneusculus* Hodgson, *Micromys minutus erythrotis* Blyth; Figure 1 *c*, *d*), sometimes through scatter–hoarding[17], which serves as secondary dispersal mode. The species mainly reproduces through seeds. In nature, the seeds appear to germinate mostly on sites that supply adequate moisture and light.

Figure 1. Rudraksh (*Elaeocarpus ganitrus*) fruits/nuts (***a***) showing locules and seeds (***b***) within them. ***c***, Nuts larder hoarded by rodents and stored in rotten log. ***d***, Nuts found washed away by water run-off, especially in disturbed stands, and trapped in fallen branches or exposed roots of plants.

Fruit set

Five fruiting trees of *E. ganitrus* in each of the three classes of circumference at breast height (CBH), viz., 60–90 cm (11 ± 1.5 m height, 60 ± 2 m^2 canopy cover), 90–120 cm (18.5 ± 1.8 m height, 85 ± 2 m^2 canopy cover) and 120–150 cm (25 ± 1.8 m height, 120 ± 3.5 m^2 canopy cover) were marked in each stand during May 1997. The number of flowers and fruits produced by these marked trees was estimated for three consecutive years (1997–99). Flower bud count was the criterion to estimate flower production. For this, branches were randomly selected from different layers of the canopy of a tree. A portable steel ladder was used to reach the tree canopy. Appearance of a shiny bluish colour of the fruit coat indicated maturity. Fruits were counted just before maturation in mid-November. Since dispersal of fruits starts as colour changes begin, fruit production estimates made on the tree in the initial stage of maturation represented the total fruit production, including those dispersed during the maturation phase.

Flower and fruit production for each tree was estimated as follows:

Total flower or fruit production = Total number of branches × mean number of sub-branches per main branch × mean number of inflorescences per sub-branch × mean number of flower buds or fruits per inflorescence[18].

For each tree, mean number of inflorescences per branch was calculated from a sample of ten sub-branches and mean number of flower buds or fruits per inflorescence was calculated from a sample of 50 inflorescences. The data were pooled for each CBH 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 the absence of replication of stands, the inferential statistics for disturbance (i.e. the stand factor) was not used for interpreting results and drawing conclusions. To avoid the effect of pseudoreplication, flower and fruit production and flower abortion data have been presented in a tabular form giving standard deviations[19]. Pollination success was calculated by following the per cent flowers setting fruits.

From each of the five marked trees in each stand, 100 fresh fruits were collected and average fruit weight was determined for each stand from the composite sample of 500 fruits. After fermenting the fruit exocarp of the same sample in a soil pit for one week, nuts were cleaned in running tap water and their fresh weight was determined. The procedure to determine the fruit and nut weight was repeated for three consecutive years (1997–99) and means were calculated.

Primary seed dispersal

Five sample fruiting trees of *E. ganitrus* were marked in each of the four forest stands for fruit dispersal and predation studies. The trees marked for this study were growing at least 100 m apart and no other conspecific adults were present between any two marked trees. The primary seed shadow was measured by counting dispersed nuts (often still with remains of fruit pulp) in 2.5 m-wide concentric circles around each fruiting tree, starting at the crown edge, up to 45 m distance. The circles were visited every two days over a period of 20 days during the peak period of fruit-fall. The dispersal was expressed as the number of fruits per 100 m^2.

Rates of fruit removal were estimated using fruit traps. Five wooden fruit 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 fruit-fall and were visited until the completion of fruit shedding. All the fruits in each trap were counted. The difference between total fruit production and the number of fruits that fell beneath the tree crown was used as a measure for the proportion of primary dispersal, assuming that all missing fruits had been taken by arboreal frugivores.

Secondary seed dispersal

The fate of undamaged fruits after fruit fall was studied by surface-sowing of 30 fruits with exocarp in each of the five 1×1 m plots beneath each sample tree. The plots were visited at 7-day intervals up to 3 months. On each observation date, the number of fruits remaining and those that had disappeared were noted. The percentage of fruits was determined and the means ($n = 5$ trees) for each stand were calculated. The study was repeated during 1998 and 1999 to study the annual variation in pattern of fruit removal. The fractions of fruit cohorts that had disappeared and those that remained were presented as percentages of total fruit production for the three years of study.

To study the fate of dispersed fruits, we simulated dispersal at different distances from the parent tree, by randomly placing three 1×1 m quadrats in each of the concentric circles with radii of 5, 10, 15, 20, 25, 30, 35, 40, 45 m from the base of the fruiting tree. Each quadrat had 30 fruits of *E. ganitrus*, marked with a small spot of waterproof blue-paint matching. Fruit removal was monitored at 3-day intervals for one month and then at weekly intervals over a period of 2 months. This was done during all three years. Analysis of variance was performed to test the effect of distance from the parent tree on removal.

Effect of fruit stage on removal

Nuts may fall on the ground embedded in ripe exocarp, unripe exocarp or just the endocarp. All may contain viable seeds[17]. To study whether unripe fruits would still be removed, we randomly placed five 1×1 m quadrats under the crown of the marked fruiting trees in each forest stand. Each quadrat had ten ripe fruits (exocarp shiny bluish), ten unripe fruits (exocarp shiny greenish), and ten nuts (obtained by removing ripe exocarp), all marked with a small spot of waterproof paint. Fruit and nut removal was monitored at 3-day intervals for forty-five days. At the end of the observation period, the number of fruits that disappeared (consumed or transported by herbivores or other agencies) was recorded. This was done during all three years. The data for the three years were pooled and analysis of variance was performed to test whether removal was influenced by the ripeness of fruit exocarp.

Seed predation

To assess the fate of non-dispersed seeds, we counted the seeds that were still present beneath the five marked trees in each stand just before the next fruit rain in October 1997, 1998 and 1999. Since stony nuts are persistent and remain viable for 2–3 years, old nuts were removed from the forest floor after counting to avoid the inclusion of nut/seed banks of previous years. To study predation of seeds after primary dispersal, we randomly established five 1×1 m quadrats on each of nine concentric circles with radii of 5, 10, 15, 20, 25, 30, 35, 40, 45 m from the base of the fruiting tree. The nuts were collected from each quadrat and the total bank was computed for each marked tree. The fractions of predated and undamaged nuts were calculated. The study was carried out during 1997, 1998 and 1999. Analysis of variance was performed to test the year-to-year differences in addition to the nut/seed bank and the predation of nuts.

Results

About 89% of flowers aborted and only 11% matured into fruits in all the forest stands irrespective of disturbance intensity. More than 70% of fruits disappeared within three months of their fall (Figure 2). Removal was maximum in the highly disturbed stand. Furthermore, about 45% of the removal of the remaining fruits on the soil surface occurred during the nine months before the next fruit rain. This removal was maximum (79.6%) in the highly disturbed stand and minimum in the mildly disturbed and undisturbed stands. Of the remaining cohort of fruits on the soil surface, about 87% was predated and only about 13% was alive (Figure 2).

Fruit set

Fruit set, defined as the proportion of flowers that developed into fruits, increased significantly with CBH of fruiting trees (Table 1; $F = 150.15$, df $= 2$, $P < 0.001$; three-way ANOVA), and varied significantly among years ($F = 2906.76$, df $= 2$, $P < 0.002$), being greater in 1997 and 1999 than in 1998. Stands (disturbance levels) did not differ in fruit set, yet they did differ significantly in the absolute number of fruits produced ($F = 61.3$, $df = 3$, $P < 0.001$). Fruit production was highest in 1999 in the moderately disturbed forest and lowest in 1998 in the undisturbed forest. In contrast, the mean fresh weight of fruits and nuts decreased significantly with increasing disturbance index (Table 2; $F = 7872.4$ and 3545.2 respectively; df = 3; $P < 0.001$; one way ANOVA).

Primary dispersal

About 40–70% of the total fruits produced by *E. ganitrus* was removed from the tree crowns. Fruit removal was mainly by frugivorous birds and other animals that eat the fleshy exocarp, and then drop the remains away from the parent tree. Removal was maximum in the undisturbed stand (*c.* 65%) and minimum in the moderately disturbed forest (*c.* 45%: Table 3). The fraction of damaged seeds was lower in good seed years than that in the lean year. Though the fraction of the fruit population damaged by the insects was quite low (3.38–17.2%), it was generally

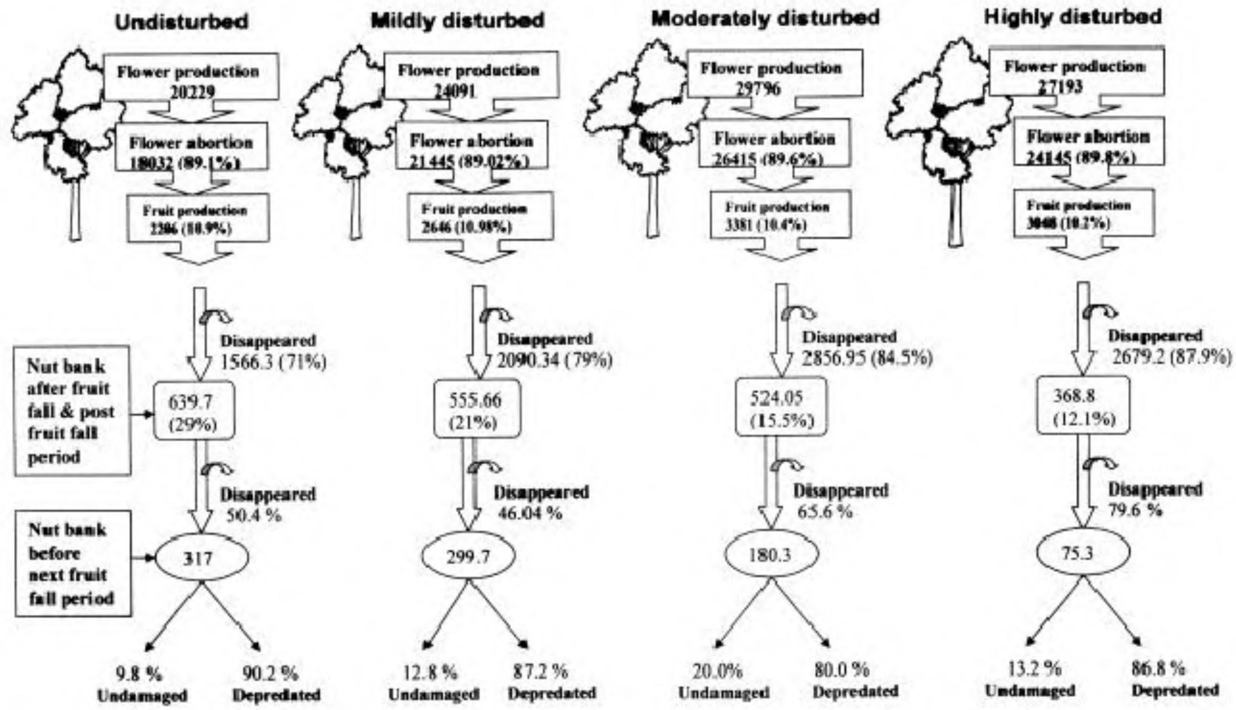

Figure 2. Schematic diagram of general trend of different events in *E. ganitrus*. Values are average of different events.

Table 1. Year-wise variation in fruit set (per cent flowers setting fruit) in trees of different CBH classes of *Elaeocarpus ganitrus* in different forest stands experiencing different degrees of disturbance. ± indicates SD values (n = 5 trees)

	Undisturbed stand CBH class (cm)			Mildly disturbed stand CBH class (cm)			Moderately disturbed stand CBH class (cm)			Highly disturbed stand CBH class (cm)			
	60–90	90–120	120–150	60–90	90–120	120–150	60–90	90–120	120–150	60–90	90–120	120–150	F
Fruit set (%)													
1997	11.51	12.17	14.75	11.45	13.20	14.24	10.04	12.79	14.43	11.35	13.71	14.20	Stand = 0.15; P = 0.93
	±1.21	±0.53	±0.98	±1.11	±1.17	±0.54	±1.50	±1.02	±0.80	±0.65	±0.94	±0.98	CBH = 150.2; P = 0.001
													Year = 2906.8; P = 0.001
													Year × CBH = 240.7; P = 0.001
1998	3.17	4.12	7.21	3.16	3.38	7.65	3.00	3.62	6.46	3.28	3.47	6.39	Year × stand = 6.6; P = 0.001
	±0.73	±0.28	±0.13	±0.52	±0.09	±0.17	±0.62	±0.15	±0.19	±0.29	±0.27	±0.09	CBH × stand = 6.3; P = 0.001
													Year × CBH × stand = 2.01; P = 0.027
1999	10.99	11.23	16.34	9.53	12.33	16.16	11.18	13.40	17.05	10.71	12.84	15.50	
	±0.55	±0.23	±0.43	±1.03	±0.62	±0.27	±0.10	±0.88	±0.43	±0.66	±0.55	±0.58	

Table 2. Mean fruit weight (g ± SD, n = 500) of *E. ganitrus* in different forest stands

	Forest stand					
	Undisturbed	Mildly disturbed	Moderately disturbed	Highly disturbed	F	P
Fruit with pulp	5.89 ± 0.47	4.55 ± 0.35	3.24 ± 0.34	2.85 ± 0.39	7872.43	0.001
Nut	3.55 ± 0.34	3.00 ± 0.58	1.83 ± 0.26	1.80 ± 0.24	3545.24	0.001

Table 3. Fraction (%, ± SD, $n = 5$ trees) of dispersed/disappeared, insect-damaged and undamaged fruits in total fruit population of *E. ganitrus* during fruit-fall period; and of disappeared, dormant and germinated nuts in the undamaged nut population during post fruit-fall period in four forest stands (stands I, II, III, and IV are undisturbed, mildly disturbed, moderately disturbed and highly disturbed forest patches respectively)

	1997				1998				1999				
	Stand				Stand				Stand				
	I	II	III	IV	I	II	III	IV	I	II	III	IV	*F* value
Fruit-fall period													
Disappeared/	63.08	56.56	42.38	49.74	70.0	60.6	50.7	48.1	62.9	59.7	40.6	53.4	Stand = 249.6; P = 0. 001
dispersed	±2.47	±0.82	±1.21	±2.98	±3.8	±1.9	±1.7	±2.1	±2.9	±1.3	±0.7	±1.9	Year = 19.05; P = 0. 001
													Year × stand = 14.2; P = 0. 001
Insect-	3.94	6.02	12.1	12.58	7.14	7.42	17.2	13.0	3.38	5.3	10.8	11.6	Stand = 153.8; P = 0. 001
damaged	±0.6	±0.71	±1.43	±2.12	±0.4	±0.7	±1.1	±2.0	±0.7	±0.6	±1.1	±2.1	Year = 29.6; P = 0. 001
													Year × stand = 6.4; P = 0. 001
Undamaged	32.98	37.42	45.52	37.68	22.8	32.0	32.1	38.9	33.7	35.0	49.0	35.0	Stand = 54.4; P = 0. 001
	±2.4	±0.92	±2.18	±4.68	±4.1	±2.4	±2.4	±3.7	±2.4	±1.6	±1.2	±3.4	Year = 33.7; P = 0. 001
													Year × stand = 15.1; P = 0. 001
Post fruit-fall period													
Disappeared	60.32	76.28	91.08	98.2	67.1	82.0	97.0	99.6	54.6	73.3	89.5	97.0	Stand = 593.3; P = 0. 001
	±3.85	±3.49	±2.58	±1.83	±2.4	±1.9	±2.5	±0.7	±3.2	±2.4	±2.6	±2.3	Year = 36.5; P = 0. 001
													Year × stand = 3.2; P = 0.01
Dormant	39.68	23.72	8.92	1.8	32.9	18.0	2.98	0.42	45.4	26.7	10.5	3.0	Stand = 593.3; P = 0.001
	±3.85	±3.49	±2.58	±1.83	±2.4	±1.9	±2.5	±0.7	±3.2	±2.4	±2.6	±2.3	Year = 36.5; P = 0.001
													Year × stand = 3.2; P = 0.01
Germinated	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	

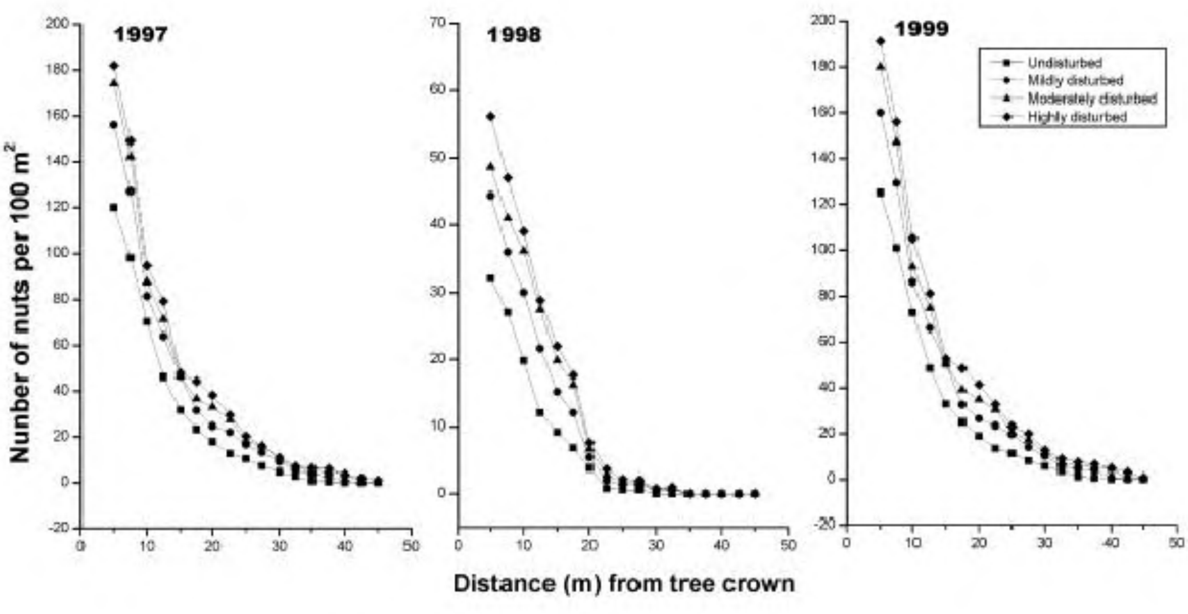

Figure 3. Dispersal curves of *E. ganitrus* in different forest stands.

greater in the moderately and highly disturbed stands than in the undisturbed stand.

Density of fruits on the forest floor decreased significantly ($F = 7065.2$; df = 16; $P < 0.001$) with increasing distance from the parent tree crown in all four forest stands (Figure 3). Maximum fruits (32–191 fruits per 100 m^2) were counted within 5 m of the tree crown.

During the post fruit-fall period, a large fraction (55–99%) of the remaining fruits disappeared. However, removal increased with the increase in disturbance index, and was

Table 4. Dispersed, disappeared, dormant and germinated seeds expressed as fraction (%, ±SD, $n = 5$ trees) of total number produced by *E. ganitrus* in four forest stands experiencing different degrees of disturbance (stands I, II, III, and IV are undisturbed, mildly disturbed, moderately disturbed and highly disturbed forest patches respectively)

	1997				1998				1999				
	Stand				Stand				Stand				
	I	II	III	IV	I	II	III	IV	I	II	III	IV	F value
Dispersed	2.16 ±0.22	3.24 ±0.59	4.68 ±0.39	5.64 ±0.88	4.24 ±0.4	5.0 ±0.5	7.64 ±0.8	8.88 ±1.1	2.28 ±0.4	3.34 ±0.5	4.6 ±0.3	4.88 ±0.2	Stand = 97.8; P = 0.001 Year = 117.6; P = 0.001 Year × stand = 3.3; P = 0.008
Disappeared	66.14 ±1.93	73.58 ±1.93	77.28 ±2.16	80.36 ±3.97	72.9 ±2.2	79.5 ±1.0	83.5 ±2.0	85.7 ±2.3	65.5 ±1.4	72.4 ±2.2	75.9 ±2.0	78.1 ±2.0	Stand = 5.4; P = 0.001 Year = 0.5; P = 0.001 Year × stand = 0.9; P = 0.5
Dormant	31.7 ±1.79	23.18 ±2.0	18.04 ±2.37	14.0 ±4.27	22.8 ±2.3	15.5 ±1.1	8.84 ±2.7	5.4 ±2.9	32.2 ±1.3	24.3 ±1.9	19.5 ±2.1	17.0 ±2.0	Stand = 132.4; P = 0.001 Year = 100.8; P = 0.001 Year × stand = 0.3; P = 0.9
Germinated	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	

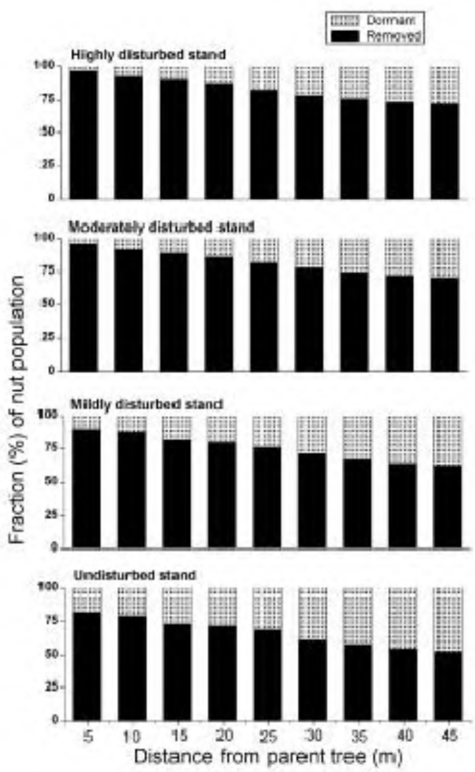

Figure 4. Percentage of nuts removed and dormant at different distances from parent tree of *E. ganitrus* in different forest stands.

maximum in the highly disturbed stand and minimum in the undisturbed stand (Table 3). During this period, no nut germinated.

In general, about 80% of the total fruits produced by *E. ganitrus* disappeared from the forest floor, including nuts damaged by insects, especially ants and termites. About 20% of nuts remained live and was dormant (Table 4).

Secondary dispersal

Removal of fruits from the soil decreased with increasing distance from the source tree ($F = 2015.7$, df = 8, $P < 0.001$; Figure 4). Removal also differed significantly ($F = 2765.5$, df = 3, $P < 0.001$) among forest stands, and was highest in the highly disturbed stand and lowest in the undisturbed stand (Figure 4). More than 85% of the sown fruits disappeared within a 5-m circle around the tree, while about 55% of fruits disappeared from the segment at a distance of 42.5–45 m from the tree. The remaining fruits lay dormant and none of them germinated during the study period in segment. Mostly rodents were noticed hoarding these fruits. A large number of nuts was found deposited in rotten logs (Figure 1*c*) rather than immediately eaten. The nuts were also found washed away by water run-off, especially in disturbed stands, and trapped in fallen branches or exposed roots of plants (Figure 1*d*). Seeds of about 90% of the hoarded nuts were eaten either by rodents or destroyed by ants[17].

Effect of fruit stage on removal

Removal of fruits differed significantly between fruit stages ($F = 695.5$; df = 2; $P = 0.001$). Ripe fruits were more likely to be removed than unripe fruits or nuts. Removal was greatest (>80%) in the highly disturbed stand and minimum (<60%) in the undisturbed stand ($F = 208.2$; df = 3; $P = 0.001$; Figure 5).

Fate of dispersed nuts

The number of nuts remaining on the soil surface decreased significantly with increasing disturbance ($F = 663.4$; df = 3; $P < 0.001$). The number of nuts on the soil surface was greatest in the undisturbed stand and lowest in the highly

Table 5. Nut bank on soil surface (per 100 m^2) and fraction (%) of depredated and undamaged nuts in total nut population of *E. ganitrus* before next fruit-fall crop in four forest stands (stands I, II, III and IV are undisturbed, mildly disturbed, moderately disturbed and highly disturbed forest patches respectively). ± indicates SD values (n = 5 trees)

	1997				1998				1999				
	Stand				Stand				Stand				
	I	II	III	IV	I	II	III	IV	I	II	III	IV	F value
Total nut bank	347 ±23	337 ±21	216 ±15	97.8 ±9.7	257 ±19	225 ±9.7	107 ±7.2	33.4 ±9.3	348 ±26	337 ±23	218 ±14	94.8 ±13	Stand = 663.3; P = 0. 001 Year = 202.8; P = 0. 001 Year × stand = 2.9; P= 0.01
Depredated (%)	89.7 ±4.1	87.4 ±3.6	79.2 ±6.6	88.4 ±4.9	90.38 ±2.5	86.48 ±2.2	80.44 ±9.9	82.12 ±4.8	90.5 ±4.3	87.6 ±3.6	80.4 ±8.4	89.9 ±6.9	Stand = 8.02; P = 0. 001 Year = 0.44; P = 0.7 Year × stand = 0.3; P = 0.9
Undamaged (%)	10.3 ±4.1	12.6 ±3.6	20.8 ±6.6	11.6 ±4.9	9.62 ±2.5	13.52 ±2.2	19.56 ±9.9	17.88 ±4.8	9.5 ±4.3	12.4 ±3.6	19.6 ±8.4	10.1 ±6.9	Stand = 8.7; P = 0. 001 Year = 0.8; P = 0.5 Year × stand = 0.7; P = 0.7

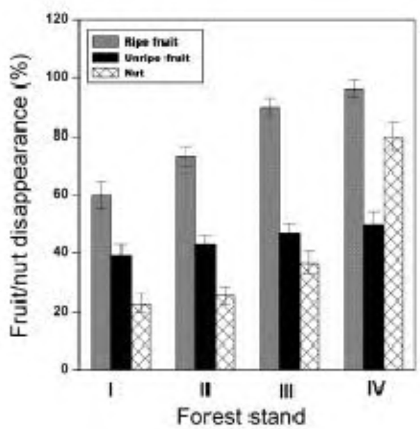

Figure 5. Removal of fruits of *E. ganitrus* as influenced by their ripeness and pulp in the undisturbed (I), mildly disturbed (II), moderately disturbed (III) and highly disturbed (IV) forest stands.

disturbed stand (Table 5). During the poorest fruit production year (1998), the number of nuts remaining on the soil surface was also low. More than 85% (damaged severely by insects, especially ants and termites) of the nuts was predated (Table 5).

Discussion

Several factors, including tree age, size, light and climatic conditions are known to affect the initiation, frequency, intensity and duration of flowering and fruiting in tropical tree species [16,20]. In *E. ganitrus* also patterns of these reproductive phenological events varied greatly in time and space. Fruiting trees of *E. ganitrus* with greater girth and height produced more flowers and fruits. It is generally accepted that tall, dominant trees with large crowns, which receive a lot of light, produce maximum seeds[20]. Tall individuals may offer more foraging opportunities and thereby increased chances of pollination and also increased protection from predators of flowers and fruits[21].

Flower and fruit production in *E. ganitrus* increased with disturbance. This is in line with the findings of Barik *et al.*[18]. Greater flower and fruit production in disturbed stands may be attributed to increased availability of resources (sunlight, nutrients) and less intense pre-dispersal seed predation[6,22]. Wycherley[23] also reported increase in seed set with increase in irradiance in Borneo. High light intensity may elevate bud temperature, which may lead to increase in the concentration of growth regulators, particularly gibberellins[24], stimulating flowering and fruiting. Due to high light regime in disturbed stands, temporary water stress may be created, which is known to stimulate bud initiation in some forest trees[25].

While fruit production increased with increase in disturbance index, fruit and nut weight decreased. The ovary of *E. ganitrus* is five-celled, and may thus produce 1, 2, 3, 4 or 5 seeds depending upon pollination and abortion during development. Correspondingly, mature fruits vary in weight/size and in seediness (number of seeds within a fruit). Such variations in production of fruits and their weight among different stands could be due to differential environmental influences in these four stands[18]. Ovule abortions may be higher in fragmented habitats due to failure of pollination[2]. Strong winds and drier conditions may cause physiological stress and resource limitation on trees in fragmented forests, and thereby failure of pollination of some of the ovules[26]. This might have been the reason for the production of lighter fruits of *E. ganitrus* in fragmented forests. However, De Viana[27] argued that plants may adjust resource allocation to fruit and seed production under various environmental conditions via plasticity in fruit/seed mass and in the several traits that affect flower number, ovules per flower, and fruit and seed abortion. Further, the magnitude and pattern of these traits vary in response to environmental conditions[28]. It is generally held that fruit size is inversely related to fruit number, and environmental conditions such as reduced irradiance may cause reduction in fruit number and lead to the production of heavier fruits[29].

The nuts of *E. ganitrus* have low dispersal ability without transportation by animals. Therefore, nut-dispersing animals are important for this species as they may reduce sibling competition by removing them from high mortality areas, decrease genetic-relatedness of patches and enable *E. ganitrus* to colonize new areas. During the course of our experiment not a single nut was found germinated up to 45 m distance from the parent tree. This may be due to the hardness of the nuts, which take 2–3 years to germinate. Also ants and termites consume the seeds as soon they are softened by microbial activity. In this study, germination of the hoarded nuts was not directly examined, but partial damage to nuts may prove beneficial by making them permeable to water. The few studies that have looked at the ultimate fate of cached seeds have, however, reported very low numbers of finally established seedlings (2 seedlings out of 923 seeds[30]; 1 seedling out of 489 seeds[31]).

The ripeness of exocarp of fruits and presence or absence of exocarp seem to have greatly influenced fruit dispersal. Fruits with ripe exocarp were more preferred by dispersers than fruits with unripe exocarp and those without exocarp. Many studies have revealed that fruit colour, nutritional content, pulpiness, aroma or presentation attract dispersal agents[32,33] in a variety of ways. It is a known fact that rodents discriminate among food types[34]. Most large and ripe fruits are more nutritionally rewarding than unripe fruits and nuts[33]; they be preferred by rodents and hence might face greater risks of predation[35].

Hornbills and bats, which normally take the fruits of *E. ganitrus* to a greater distance from the crown, appear to be much better dispersal agents than flying squirrels and monkeys, which drop the fruits beneath the tree crown after eating the pulp[17]. Though some animals such as deer, wild pig, buffalo, mithun, etc. were seen to eat the ripe fruits fallen on the forest floor, the nuts were not swallowed and were usually regurgitated under the crown. This suggests the low species dispersal ability[36]. However, rodents such as *V. oleracea*, *R. pruinosus*, *M. musculus*, *R. rattus rufescens*, *R. rattus brunneusculus*, and *M. minutus erythrotis*, are the main secondary consumers, dispersers and hoarders of fruits of *E. ganitrus*[17].

Greater removal of fruits from the undisturbed stand than the disturbed stand during the fruit-fall period may be linked with higher populations of wildlife and their more frequent visits to hoard pulpy fruits in the former stand[17]. Wright and Duber[37] have also reported that ecologically effective seed dispersal distances were greater at fully protected sites than in the fragmented site. Anthropogenic disturbances may lower the abundance and diversity of seed dispersal agents. This in turn may lower the effective seed dispersal distances and levels of seed predation by rodents[37]. To summarize, anthropogenic disturbance may indirectly reduce seed dispersal and seed predation. However, as has been noticed, collection of nuts by people from the forest floor of the disturbed stand might have caused greater removal during the post fruit-fall period.

Analysis of nut bank dynamics of *E. ganitrus* indicated that there were two important stages at which nut losses could occur in this species. First, predators removed a large proportion of fruits shed below the crown immediately after fruit fall. Secondly, there was a rapid decline in the nut density on the forest floor throughout the year due to secondary predators. In the present study, density-dependent predation was clearly indicated. Below the crown of trees, about 89% of nuts was found to be predated and the remaining was dormant. The high degree of postdispersal nut predation reported in this study is not unusual[30]. Recent reviews have found 90–100% losses of seeds to predators in 22 of the 62 studies[38,39]. Studies on seed predation of Lauraceae found 96–100% predation[40]. The high level of nut predation in our study especially in undisturbed and mildly disturbed stands could be explained by dense vegetation and cloudy conditions, providing rodents protection from predators[41]. During the day, light levels in the study area are often reduced because of cloudy weather as well as due to dense vegetation. Indeed, on a few occasions, rodents were seen and some marked fruits/nuts were removed by them. More rodents were seen on misty or rainy days and nights than during clear weather[17]. Thus, the high levels of predation for *E. ganitrus* could be the result of longer rodent activity, especially small ones and such levels may be typical for many large-seeded tree species in tropical wet and cloud forests[30]. The dormant fraction might give rise to seedlings in the near future. This prediction is supported by the presence of a few established seedlings around the trees.

A clear influence of dispersal ability on the distribution and persistence of threatened plant has significant conservation implications. Anthropogenic disturbances may lower the abundance and diversity of seed dispersal agents and may indirectly alter plant regeneration, especially of threatened plants. The findings on dispersal of *E. ganitrus* may have great implications for regeneration of the species. Prolonged nut dormancy may increase the risk of predation and ultimately reduce the chances of germination. Further, ants damage a large fraction of the nut population hoarded by rodents by eating cotyledons of seeds inside. Due to ethnic importance, nuts of *E. ganitrus* are also collected in huge quantities from the forest floor, causing shrinkage in its seed bank. These factors are directly responsible for the threatened status of the species. As argued by Quinn *et al.*[42], the distribution of such threatened plant species with poor dispersal ability could be enhanced by artificial introduction in suitable habitat conditions. Though such a course of action is justified and clearly requires careful evaluation, introductions and re-introductions are becoming an important tool of conservation of plants and other organisms.

1. Asquith, N. M., Terborgh, J., Arnold, A. E. and Riveros, C. M., The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *J. Trop. Ecol.*, 1999, **15**, 229–235.
2. Forget, P.-M., Kitajima, K. and Foster, R. B., Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae):

effects of timing of fruiting and variation among trees. *J. Trop. Ecol.*, 1999, **15**, 61–81.
3. Janzen, D. H. and Vazquez-Yanes, C., Aspects of tropical seed ecology of relevance to management of tropical forested wildlands. In *Rainforest Regeneration and Management, Man in the Biosphere Series* (eds Gomez-Pompa, A., Whitmore, T. C. and Hadley, M.), UNESCO-MAB, Paris, France, 1991, vol. 6, pp. 137–157.
4. Silva, J. M. C. and Tabarelli, M., Tree species impoverishment and the future of flora of the Atlantic Forest of Northeast Brazil. *Nature*, 2000, **6773**, 72–74.
5. Schupp, E. W., Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.*, 1995, **82**, 399–409.
6. Jansen, P. A. and Forget, P. M., Scatterhoarding rodents and tree regeneration. In *Dynamics and Plant–Animal Interactions in a Neotropical Rainforest* (eds Bongers *et al.*), 2001, pp. 275–288.
7. Willson, M. F. and Whelan, C. J., Variation in post-dispersal of vertebrate-dispersed seeds: effects of density, habitat, location, season and species. *Oikos*, 1990, **57**, 191–198.
8. Chandrasekharan, C., Forest types of Kerala State. Special paper submitted for Diploma in Forestry, New Forest, Dehra Dun, 1960.
9. Rao, R. R. and Haridasan, K., Threatened plants of Meghalaya – a plea for conservation. In *An Assessment of Threatened Plants of India* (eds Jain, S. K. and Rao, R. R.), Botanical Survey of India, Howrah, 1983, pp. 94–103.
10. Kanjilal, U. N., Kanjilal, P. C., Das, A. and Purkayastha, C., *Flora of Assam*, Published under the authority of the Government of Assam, India, 1935, vol. 1, pp. 174–182.
11. Bhuyan, P., Khan, M. L. and Tripathi, R. S., Tree diversity and population structure in undisturbed and human-impacted stands of tropical wet evergreen forest in Arunachal Pradesh, Eastern Himalayas, India. *Biodivers. Conserv.*, 2003, **12**, 1753–1773.
12. Bhuyan, P., Khan, M. L. and Tripathi, R. S., Regeneration status and population structure of Rudraksh (*Elaeocarpus ganitrus*) in relation to cultural disturbances in tropical wet evergreen forest of Arunachal Pradesh. *Curr. Sci.*, 2002, **83**, 1391–1394.
13. Kaul, R. N. and Haridasan, K., Forest types of Arunachal Pradesh – a preliminary study. *J. Econ. Taxon. Bot.*, 1987, **9**, 379–388.
14. Champion, H. G. and Seth, S. K., *Revised Survey of the Forest Types of India*, Manager of Publications, New Delhi, 1968.
15. Rao, P., Barik, S. K., Pandey, H. N. and Tripathi, R. S., Community composition and tree population structure in a subtropical broad-leaved forest along a disturbance gradient. *Vegetatio*, 1990, **88**, 151–162.
16. Lee, D. W., The biology of Rudraksha. *Curr. Sci.*, 1998, **75**, 26–30.
17. Bhuyan, P., Ecological studies on seed production, dispersal, germination and seedling fitness of Rudraksh (*Elaeocarpus ganitrus* Roxb.), Ph D thesis, North-Eastern Hill University, Shillong, 2002.
18. Barik, S. K., Tripathi, R. S., Pandey, H. N. and Rao, P., Tree regeneration in a subtropical humid forest: effect of cultural disturbance on seed production, dispersal and germination. *J. Appl. Ecol.*, 1996, **33**, 1551–1560.
19. Hurdbert, S. H., Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.*, 1984, **54**, 187–211.
20. Harmer, R., Natural regeneration of broadleaved trees in Britain: II seed production and predation. *Forestry*, 1994, **67**, 275–286.
21. Duncan, R. S. and Chapman, C. A., Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecol. Appl.*, 1999, **9**, 998–1008.
22. Jansen, P. A. and Zuidema, P. A., Logging, seed dispersal by vertebrates, and natural regeneration of tropical timber trees. In *The Cutting Edge. Conserving Wildlife in Logged Tropical Forests* (eds Fimbel, R. A., Robinson, J. G. and Grajal, A.), Columbia University Press, New York, 2001, pp. 35–59.
23. Wycherley, P. R., The phenology of plants in the humid tropics. *Micronesica*, 1973, **9**, 75–96.
24. Ross, S. D., Pharis, R. P. and Binder, W. D., Growth regulators and conifers: their physiology and potential uses in forestry. In *Plant Growth Regulating Chemicals* (ed. Nickell, L. G.), CRC Press, Florida, 1983, vol. II, pp. 35–78.
25. Kozlowski, T. T. (ed.), *Water Deficit and Plant Growth*, Academic Press, New York, 1981, vol. 6.
26. Kapos, V., Ganade, G., Matsuie, E. and Victoria, R. L., C^{13} as an indicator of edge effects in tropical rainforest reserves. *J. Ecol.*, 1993, **81**, 425–432.
27. De Viana, M. L., Seed production and seed bank of *Trichocereus pasacana* (Cactaceae) in Northwestern Argentina. *Trop. Ecol.*, 1999, **40**, 79–84.
28. Stephenson, A. G., The regulation of maternal investment in plants. In *Fruit and Seed Production* (eds Marshall, C. and Grace, J.), Cambridge University Press, Cambridge, 1992, pp. 151–171.
29. Khan, M. L., Bhuyan, P., Singh, N. D. and Todaria, N. P., Fruit set, seed germination and seedling growth of *Mesua ferrea* Linn. (Clusiaceae) in relation to light intensity. *J. Trop. For. Sci.*, 2002, **14**, 35–48.
30. Wenny, D. G., Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol. Monogr.*, 2000, **70**, 331–351.
31. Jansen, P. A., Bartholomeus, M., Bongers, F., Elzinga, J. A., Den Ouden, J. and Van Wieren, S. E., The role of seed size in dispersal by scatterhoarding rodent. In *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds Levey, D. J., Silva, W. R. and Galleti, M.), CAB International Press, Wallingford, UK, 2002, pp. 209–225.
32. Howe, H. F. and Westley, L. C., *Ecological Relationships of Plants and Animals*, Oxford University Press, UK, 1988.
33. Howe, H. F., Schupp, E. W. and Wesley, L. C., Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology*, 1985, **66**, 781–791.
34. Pena-Claros, M. and De Boo, H., The effect of forest successional stage on seed removal of tropical rain forest tree species. *J. Trop. Ecol.*, 2002, **18**, 261–274.
35. Osunkoya, O. O., Postdispersal survivorship of north Queensland rainforest seeds and fruits: Effects of forest, habitat and species. *Aust. J. Ecol.*, 1994, **19**, 52–64.
36. Hegde, S. G., Uma Shaanker, U. and Ganeshaiah, K. N., Evolution of seed size in bird-dispersed tree *Santalum album* L.: A trade-off between seedling establishment and dispersal efficiency. *Evol. Trends Plants*, 1991, **5**, 131–135.
37. Wright, S. J. and Duber, H. C., Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica*, 2001, **33**, 583–595.
38. Crawley, M. J., Seed predators and plant population dynamics. In *Seed: The Ecology of Regeneration in Plant Communities* (ed. Fenner M.), CAB International, Wallingford, UK, 1992, pp. 157–191.
39. Hulme, P. E., Post-dispersal seed predation by small mammals. *Symp. Zool. Soc. London*, 1993, **65**, 269–297.
40. Holl, K. D. and Lulow, M. E., Effects of species, habitat, and distance from edge on postdispersal seed predation in a tropical forest. *Biotropica*, 1997, **29**, 459–468.
41. Vasquez, R. A., Patch utilization by three species of Chilean rodents differing in body size and mode of locomotion. *Ecology*, 1996, **77**, 2343–2351.
42. Quinn, R. M., Lawton, J. H., Eversham, B. C. and Wood, S. N., The biogeography of scarce vascular plants in Britain with respect to habitat preference, dispersal ability and reproductive biology. *Biol. Conserv.*, 1994, **70**, 149–157.

ACKNOWLEDGEMENTS. The work was supported by a research grant to M.L.K. from the Department of Science and Technology, New Delhi. We thank Dr Patrick A. Jansen, Alterra – Centre of Ecosystems, Wageningen University, The Netherlands for helpful comments on the manuscript.

Received 3 March 2004; revised accepted 2 September 2004