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Fruit predation and adaptive strategies of *Garcinia imberti*, an endangered species of southern Western Ghats

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The germination and seedling emergence capacity of partially predated seeds of *Garcinia imberti* Bourd., an endemic and endangered tree species of the southern Western Ghats, was assessed with differentially devoured seeds. Pre-dispersal, fruit/seed predation by arboreal mammals especially *Ratufa indica* (Malabar Giant Squirrel) and to a smaller extent by *Trachypithecus johnii* (Nilgiri Langur) was observed. The fragmented seeds of natural predation as well as manually cut seed pieces showed speedy germination. Seed fragments with more than 50% of seed tissues showed high seed vigour index. The germination behaviour of cut seeds indirectly conveyed the simulated effect of predated seed germination in natural habitat. Germination of fragmented seeds overcomes the inevitable prolific predatory problems by frugivores. This study showed that *G. imberti* seeds tolerate predation to a certain extent as an adaptive character ensuring seed dispersal and seedling establishment through a unique plant–animal mutuality.

Keywords: Agasthyamala Biosphere Reserve, *Garcinia imberti*, plant–animal interaction, seed germination, seed predation.

FRUIT and seed predation is an important interactive force in plant communities affecting the dynamics and spatial distribution of populations. Plant–animal interactions which occur during seed dispersal and predation are critical factors determining the success of recruitment and community structure^{1–3}. Seed predation usually resulted in entire seed loss, however, in many large seeded plants partial consumption has been reported⁴. Recent studies demonstrated that partial seed predation is a key reproductive adaptation in many tropical and temperate plants^{4,5}. The ability to germinate from partially damaged/predated seeds has been mentioned for some large seeded plant species^{4–6}.

Partial seed predation is always not lethal but is advantageous to those species which have no dispersers but have predators^{5,7,8}. Loayza *et al.*⁵ demonstrated that partially predated seeds of *Myrcianthes coquimbensis* have the capacity of germination and is a key reproductive strategy for its continuous survival. Seed mass

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removal up to 50% by insect infestation in *Gustavia superba* had no effect on the probability of germination⁸. Perea *et al.*⁷ studied the dispersal of acorns in *Quercus pyrenaica* and found that partially predated acorns dispersed to more distance and established quickly than normal acorns. Moreover, they commented that dispersal of partially predated seeds is an important event in the regeneration of *Q. pyrenaica*⁷. In addition to dispersing seeds, partial seed damage may also decrease or eliminate seed dormancy as described by Karban and Lowenberg⁹ in wild *Gossypium* species and Koptur¹⁰ in *Vicia sativa*. Moreover, in *Gossypium* faster germination may eliminate further damage to seed resource before its germination⁹.

Garcinia imberti Bourd. is an endangered tree species endemic to the southern Western Ghats^{11–13}. Their populations are highly fragmented due to habitat degradation and disturbances together with poor recruitment^{11,13}. It was observed that *G. imberti* suffered a high rate of fruit/seed predation and seed portions were scattered beneath the canopy and lacked an effective disperser. There were reports that seeds of *G. gummi-gutta* and *G. travancorica* are predated heavily by animals such as *Ratufa indica*, *Funambulus palmarum*, ants, etc., which resulted in poor recruitment of species^{13,14}. Rai¹⁴ observed that *Ratufa indica* fed on the cotyledon of *G. gummi-gutta* seed after removing the seed coat and is a major predator, but primates also disperse seeds. Joshi *et al.*¹⁵ reported that even though *Semnopithecus entellus* and *Maccaca radiata* fed on pulp and spat out the seeds, there is a probability that some seeds are destroyed due to bites using sharp teeth. Studies carried out in allied species of *Garcinia* revealed that cut seed portions have the ability to germinate^{15–17}. With this background, the present study is formulated to hypothesize the advantage of seed predation in dispersal, germination and survival of *G. imberti* with the following aspects: (i) to quantify the natural seed predation in *G. imberti*; (ii) germination response of naturally predated seeds with different level of predation; and (iii) its comparison with simulated seed damage of fresh seeds.

Garcinia imberti of the Clusiaceae family is confined to the valleys and river courses in specific pockets of submontane evergreen forests in Agasthyamala Biosphere Reserve (ABR) (08°39'0"N, 77°13'0"E). They are distributed to an altitudinal range of 900–1200 m. This dioecious species reaches a height of 30–40 feet occupying sub-canopy area¹⁸. The wood is yellowish grey and hard. The bark is brownish white and smooth. Leaves are simple, opposite with elliptic or lanceolate lamina. The major tree associates in the study sites include *Agrostistachys borneensis*, *Cullenia exarillata*, *Cinnamomum sulphuratum*, *C. chemmunjiyanam*, *Elaeocarpus tuberculatus*, *G. travancorica*, *G. rubro-echinata*, *Humboldtia unijuga*, *Myristica dactyloides*, *Litsea leavigata*, *Palaquium ellipticum*, *Popowia* sp., *Vateria indica*, etc. The male and female trees are distributed in the ratio 1 : 1.2 respective-

ly. Male flowers are smaller than female flowers. Flowering occurs annually and extends from February to May. Fruits have characteristic beak with thin rind and pulp normally bearing one or two seeds (Figure 1a and b)¹⁷. Fruits matured during the months of August–October. Seeds are recalcitrant and exhibit hypogeal ‘Garcinia type’ of germination¹⁷. In the natural habitat, seeds are dormant for more than six months and removal of seed coat alleviate dormancy¹⁷.

The studies were conducted during peak fruiting seasons from 2014 to 2016 in three populations of *G. imberti* at ABR: Bonacaud (943 m amsl, 8°45'25"N, 77°11'20"E), Chemunji (1186 m amsl, 8°41'28"N, 77°11'04.8"E) and Ponmudi (1003 m amsl, 8°45'50.2"N, 77°06'48.5"E). Fruit development was monitored on randomly selected trees by tagging female flowers. Fruit and seed measurements (length, breadth and thickness) were recorded using vernier callipers from randomly collected 50 mature single and double seeded fruits from different trees. Total fruit production in a tree was directly counted using Nikon 10× binoculars from 15 marked trees at Chemunji and 5 each from Bonacaud and Ponmudi. Direct and indirect observations were carried out on two focal trees at each site for frugivore predator activity. Direct observations were made during morning hours (0700–1130 h). Mammalian frugivore predators were identified following Prater²⁰. Indirect observations were based on the characteristic incision marks of predators on the rind and seed remains observed beneath the trees²¹. The frequency of predation was assessed by counting entire and predated fruit/seed portions from ten 1 × 1 m fruit traps established beneath five mother trees at each site^{21,22}. Predated seeds were counted and classified with various percentages of seed remains such as 10, 30, 50, 70 and 90 predation (90, 70, 50, 30 and 10 seed tissues respectively). The percentages of predated fruits were estimated from the pooled data. The difference between total fruit crops and the fruits that fell beneath the tree crown was used as a measure for complete predation assuming that all missing fruits were taken by predators²².

For seed germination trials, fresh predated seeds were collected from fruit traps. Fresh ripened fruits collected from the tree were used as control. Seeds/seed portions were separated from their rind and were sterilized with 0.1% HgCl₂ for 5 min followed by free rinse in distilled water and then dried at 28 ± 2°C. The naturally predated seeds were named P1 to P5 on the basis of extent of predation (10%, 30%, 50%, 70% and 90% of predation affected seeds respectively). The mature fresh seeds were used as such (C, Control) decoated (C1 – to overcome dormancy)¹⁰ and cut into sections of 30%, 50% and 90% of seed remains such as coated proximal section of seeds (C2 – 50% predation), decoated proximal section (C3 – 50% predation), decoated proximal section (C4 – ± 30% seed content simulating 70% predation of distal end),



Figure 1. *a*, *Garcinia imberti* fruits. *b*, Cross section showing single and double seeded fruit. *c*, Mature seeds. *d*, Predated fruit/seed portions.

decoated middle section (C5 – 30% seed content simulating 70% predation of proximal and distal ends), decoated distal section (C6 – \pm 50% predation of proximal end), decoated distal section (C7 – \pm 30% seed content simulating 70% predation of proximal end) and decoated distal portion chipped (C8 – 90% seed content simulating 10% predation of proximal ends) simulating the different modes of predation^{4,5}. Thus the germination trials consisted of 14 treatments: P1 to P5 for naturally predated seeds, C1 to C8 for simulated treatments of predated seeds and C as control.

Germination tests were carried out for all seed treatments of five replicates of twelve seeds/seed fragments each, rolled in an acid free moist germination paper (A.R. Industries, Bangalore, India) kept in a seed germinator without light ($30 \pm 2^\circ\text{C}$, 80% RH)^{17,22}. Germination trials of five replicates of twelve seeds/seed fragments each were noted at weekly intervals¹⁷. Seed viability was inferred with the percentage of germinated seeds. The seeds were considered as germinated when the length of the primary root or shoot was ≥ 5 mm (refs 17, 22). From the sixth month onwards, percentage of seedlings survived was calculated and Seed Vigour Index (SVI) was determined by multiplying germination percentage and seedling length (cm)²³ before being planted in the field. Along with germination trials, nutritive analysis (protein, carbohydrates, starch and lipids) of fresh mature seeds that influences frugivory was carried out.

Pooled data on predated and non-predated seeds, germination rate, seedling survival and SVI were statistically evaluated year-wise with control seeds by one way

ANOVA (Welch's) and significance of differences between means at $\alpha = 0.05$ were tested by least significant difference (LSD) (Tukey).

Fruits of *G. imberti* took approximately 6–8 months for maturity after pollination. They are greenish yellow. Single seeded fruit measures $29.07 \pm 0.87 \times 14.12 \pm 0.27 \times 13.33 \pm 0.55$ mm (length, breadth and thickness respectively) and weighs 2.60 ± 0.15 g, while double-seeded fruit measures $32.47 \pm 0.41 \times 18.25 \pm 0.43 \times 14.67 \pm 0.23$ mm and weighs 3.49 ± 0.19 g. Mature seeds measures $21.97 \pm 0.76 \times 11.66 \pm 0.96 \times 11.92 \pm 0.52$ mm and weigh 1.49 ± 0.88 g (Figure 1 c). Mature fruit production rates are highly variable ranging from 40 to 1456 per tree. Field observations revealed that fruits/seeds of *G. imberti* suffered with high rate of predation especially from arboreal mammals such as *Ratufa indica* (Malabar Giant Squirrel) and *T. johnii* (Nilgiri Langur) from immature stage onwards. During the peak fruiting period, predated seed portions of various sizes left by the predators were found carpeted beneath the mother trees and adjacent areas (Figure 1 d). About $53.23 \pm 2.3\%$ of fruit were predated at immature stage (within 80 to 120 days after pollination) while up to $74.48 \pm 2.27\%$ of fruits were predated at mature stage (Table 1) leaving less seeds available for the next seedling generation. The pooled data from the seed traps also showed a similar trend of only less than 8% of seeds escaping predation (range 2.8 ± 1.2 to 6.2 ± 1.8) (Table 2). However, a majority of seeds (74% to 85%) were only partially predated which means they escaped from predation with different proportions of seed kernels. More than 40% of seed remains were with

Table 1. Total fruit production and percentage of fruit predation during 2014–16

Year	Immature fruits	Immature fruits predated (%)	Mature fruits	Mature fruits predated (%)
2014	1009.6 ± 15.2	57.5	623.3 ± 16.3	73.25
2015	971.6 ± 14.6	52.9	449.2 ± 11.1	77.6
2016	1456.5 ± 19.4	49.2	516.6 ± 16.4	72.6
Mean	1145.3 ± 12.4	53.2	529.3 ± 12.4	74.48

Table 2. Rate of different seed predation levels in *G. imberti* (pooled data from seed traps in %)

Seed fate	2014	2015	2016
Np	2.3 ± 0.1	3.1 ± 0.5	6.3 ± 0.2
P1	5.1 ± 0.7*	7.4 ± 0.2*	10.4 ± 1.3*
P2	11.1 ± 0.1*	10.4 ± 1.2*	12.4 ± 1.5*
P3	18.2 ± 0.7*	13.6 ± 1.5*	18.4 ± 1.9*
P4	29.2 ± 0.5*	24.2 ± 2.3*	21.2 ± 4.3*
P5	21.2 ± 1.3*	18.4 ± 2.6*	17.3 ± 3.1*
LSD (0.05)	0.18	0.35	0.22

Np, Non-predated fruits/seeds (control); P1–P5, 10%, 30%, 50%, 70% and 90% predation affected seeds respectively. *Significant at α 0.05 based on LSD following Welch's ANOVA.

little seed tissue ($\geq 66\%$ predation) that might be of the scraped tissues escaped while feeding (Table 2). Observations showed that the Malabar Giant Squirrel is the main predator of *G. imberti* (71.23%) in the study areas followed by *Rattus rattus* (2.04%) and the *T. johnii* (1.21%) to a small extent. All these animals feed on seeds and not the pericarp which is thin (1 mm thickness) and not juicy like other *Garcinia* fruits. *Ratufa indica* is a major seed predator in the Western Ghats tropical forests^{20,24}. During the fruit maturation period of *G. imberti*, most other wet evergreen forest trees²⁴ ceased their flowering and fruiting and the animals experienced dearth of food resources which may prompt *Ratufa indica* to depend more on *G. imberti* fruits. Seeds are rich in nutrients like proteins (16.16 ± 0.5 mg/g) and lipids (127.7 ± 6.2 mg/g) which may attract more animals especially rodents²⁵.

Irrespective of the recalcitrant nature, *G. imberti* seeds showed low germination rate with 5 to 8 months of dormancy due to the presence of double layered impermeable seed coat¹⁷. Many *Garcinia* species exhibited seed coat induced dormancy, by preventing water uptake, gas exchange, light diffusion and escape of any inhibitors from the seed^{16,26,27}.

Germination experiments on partially predated seeds with more than 50% of seed content significantly showed high percent of germination, germination period and SVI (Table 3) compared to control seeds (Figure 2). Predated seed portions generally were incompletely covered with seed coat, and may evade the seed coat imposed dormancy. Also predation leads to exposure of more seed tissues which increase surface area of water absorption. Increased surface area may also help in metabolic activities for germination resulting in increased seed growth

and vigour. Seed portions of *G. imberti* are thus adventitiously tolerant to germination. Tolerance is the ability to develop and reproduce seedlings after herbivore damages of seeds^{4,28}. Even though there was no significant difference in the number of days for predated seed germination, 10% and 30% predated seeds (P1 and P2) showed more germination rate, seedling survival and higher SVI (699.5) compared to high rate of predation-affected seeds (P4 and P5) and control seeds (C) (Table 3). This may be because the seed coat removal/partial removal and increased absorption area during predation accelerated quick germination (reduced dormancy) that could survive effectively as they are with more seed tissues. For those germinating seeds higher SVI is considered more vital²⁹. The present observations were similar to the observations made by Vallejo-Marin⁴ in *Pouteria campechiana* and *Pseudolmedia oxyphyllaria*, where partial predation increased the number of seeds germinated with reduced dormancy. The seed cut simulation experiments also exhibited more or less similar results like those of predated seeds (Table 3).

Like other species of *Garcinia*^{16,29}, *G. imberti* also exhibits polarity in seed germination¹⁷. During germination, shoot tip originated from proximal end (end towards the peduncle) and primary root from the opposite distal end. However, it is difficult to distinguish the different poles morphologically¹⁵ after dispersal (Figure 1c). Seed cut treatments showed that the distal portion with 30% seed tissue (C6 and C7) produced only the primary root and not shoot, like seeds of *G. kola*²⁹. All types of proximal sections show both shoot and adventitious roots in their proximal portion, and primary roots in their distal cut end (Figures 2f, 2g, 3). But those cut portions with

Table 3. Germination period (number of days), total germination (%), seedling survival rate (%) and seed vigour index calculated from different germination treatments of *G. imberti* seeds ($n = 12$)

Treatments	Germination period (days)	Germination (%)	Seedling survival (%)	Seed vigour index
P1	52.3 ± 4.3	83.2 ± 2.4*	77.4 ± 3.24*	699.5 ± 9.7*
P2	43.3 ± 1.9	79.4 ± 2.2*	70.3 ± 4.28*	462.29 ± 9.6*
P3	36.4 ± 3.5	70.5 ± 3.5*	61.4 ± 3.8*	353.03 ± 7.2*
P4	29.5 ± 3.2	65.1 ± 2.48*	22.5 ± 1.13*	287.2 ± 6.35*
P5	47.3 ± 3.9	31.2 ± 3.35*	9.2 ± 0.34*	79.47 ± 4.2*
Control	152 ± 8.3	14.8 ± 1.4	63 ± 2.60	92.12 ± 4.49
C1	15.4 ± 2.3	100*	93.7 ± 4.3*	879 ± 12.7*
C2	24.1 ± 2.4	25.01 ± 1.47*	55.7 ± 2.79*	38.1 ± 1.7*
C3	16.4 ± 1.1	84.4 ± 3.83*	77.9 ± 4.3*	502.8 ± 11.4*
C4	22.3 ± 2.2	74.6 ± 2.63*	64.4 ± 3.2*	318.3 ± 9.9*
C5	28.2 ± 3.4	47.2 ± 2.35*	51.3 ± 2.6*	221.4 ± 11.2*
C6	42.3 ± 3.2	75.4 ± 3.32*	–	–
C7	46.7 ± 2.9	32.6 ± 0.82*	–	–
C8	24.3 ± 2.1	89.1 ± 0.52*	52.6 ± 1.4*	439.05 ± 3.1*
LSD (0.05)	–	0.70	0.49	1.61

P1–P5, 10%, 30%, 50%, 70% and 90% predation affected seeds respectively; C, Control entire seed; C1, Decoated fresh seeds (100%); C2, Coated proximal section of seeds (50%); C3, Decoated proximal section of seeds (50%); C4, Decoated proximal section of seeds ($\pm 30\%$ seed content simulating 70% predation of distal end); C5, Decoated middle section of seeds (30% seed content simulating 70% predation of proximal and distal ends); C6, Decoated distal section of seeds ($\pm 50\%$ predation of proximal end); C7, Decoated distal section of seeds ($\pm 30\%$ seed content simulating 70% predation of proximal end) and C8, Decoated distal portion chipped seeds (90% seed content simulating 10% predation of proximal ends).

*Significant at $\alpha 0.05$ based on LSD following Welch's ANOVA.

more seed tissue portions ($>60\%$) can produce both stem and root (C8 treatment). However, the SVI is more in those seed portions with proximal end (Table 3). From the simulation experiments, it can be assumed that those predated seeds with proximal end have more ability to germinate and survive in their habitat. An interesting observation of the present study was that the germination of partially predated seeds was more efficient and vigorous than control seeds. This may be an advantage to *G. imberti* which experience high rate of predation. Joshi *et al.*¹⁵ also opined that the ability of *G. gummi-gutta* fragmented seeds to germinate into seedlings is an adaptation to overcome the death of seeds by frugivory.

There was no significant role for the primary root in growth and development of the seed, but to conduct water just before the emergence of the adventitious root²⁹ and hold the seeds in the soil temporarily. In *G. imberti*, this primary root collapses after the adventitious roots are developed. The primary roots of randomly predated seeds were also well developed than control seeds as an advantage for seed fragments in its initial water conduction. The last sign of seed germination is the appearance of a thick and brittle adventitious root from the base of the shoot. In this experiment, the predated seed had the maximum significant difference observed in the length of adventitious roots (4.59 ± 0.21) (Figure 3). Moreover, all measurements were significantly higher in predated seeds and exhibited $82.73 \pm 1.50\%$ of germination irrespective of their size ($\approx >40\%$ seed tissue). Thus the partial seed

predation of *G. imberti* may be an important reproductive adaptation in which the damage is often non-lethal. According to Loayza *et al.*⁵, seeds that are damaged during frugivory have a better chance to germinate than non-damaged seeds. Mack³⁰ reported that, larger seeds act as a buffer for their survival even when the predation is crucial which is true in the case of *G. imberti* as demonstrated by our experiments. The middle section of *G. imberti* seeds showed germination of multiple shoots (Figure 2h) like other related species such as *G. gummi-gutta*¹⁵, *G. cambogia* and *G. xanthochymus*¹⁶ and *G. mangostana*³¹. According to Malik *et al.*¹⁶, multiple seedlings from the seed pieces of *G. indica*, *G. cambogia* and *G. xanthochymus* indicated the apomictic nature.

The seeds of *Garcinia* are not true seeds as they have no differentiated embryo and the embryo is represented by the swollen hypocotyl traversed by embryonic axis with vascular bundles^{15,16}. The regeneration capacity of *G. imberti* predated seeds may be an evolved character to exploit the predation as an advantage for seed dispersal since our observations revealed that there were no effective seed dispersers for the tree as the fruit is less attractive to frugivores because of greenish-yellow pericarp with less pulpy rind. However, the lipid and protein-rich seeds attract rodents²⁵, and *Ratufa indica* is the main seed predator of *G. imberti*. There are chances that these animals may carry seed portions/seeds far away from the parent tree while foraging and deposit at some safe zones to facilitate germination. Our experiments using seed

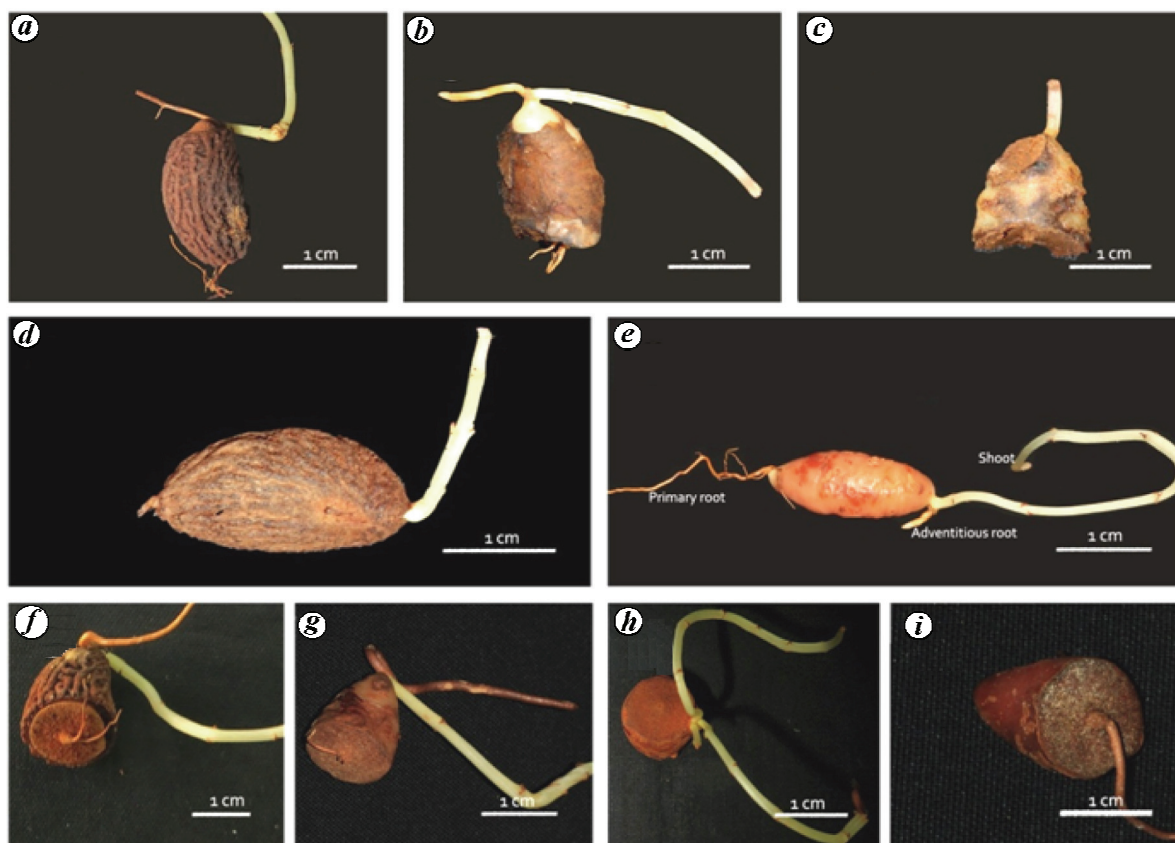


Figure 2. Different germination treatments of *Garcinia imberti* seeds. *a*, 10% predation-affected seed. *b*, 30% predation-affected seed. *c*, 50% predation-affected seed. *d*, Fresh coated seed (control). *e*, Decoated fresh seed. *f*, Coated proximal section of seed. *g*, Decoated proximal section of seed. *h*, Decoated middle section of seed with multiple shoots. *i*, Decoated distal section of seed.

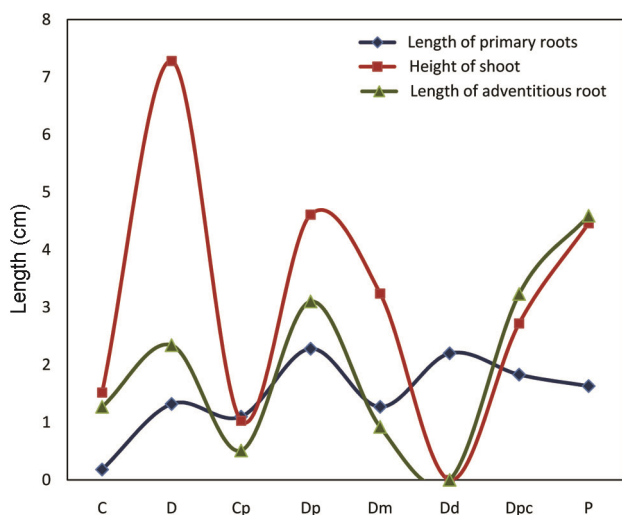


Figure 3. Germination responses of different treatments. C, Entire seed (control); D, Decoated entire seed; Cp, Proximal section with seed coat; Dp, Proximal section decoated; Dm, Middle section decoated; Dd, Distal section decoated; Dpc, Distal portion chipped seeds; P, Predated seeds.

fragments also confirmed the germinability of fragmented seeds. Thus the predatory behaviour of *Ratufa indica*, *Rattus rattus* and *Trachypithecus johnii* indirectly assists

seed dispersal and germination. Such types of antagonistic mutualism between predator and prey in plant–animal interactions were demonstrated by Tella *et al.*³² in endangered tree *Araucaria angustifolia* and parrots and Loayza *et al.*⁶ in *Myrcianthus coquimbensis* and rodents. Moreover the ability of partially predated seeds to germinate in short period has a chance to germinate early in the current wet season (August–November) itself, contrary to intact seeds that took approximately five to eight months to germinate. The observed high SVI of partially predated seeds was also useful for the successful establishment of seedlings. Alternatively, if the seeds germinate after dormancy period (next May–June) seedlings were exposed to high competition with other forest tree seedlings as majority of them germinate during early monsoon season.

In conclusion, the present study showed that partial seed predation in *G. imberti* is not always lethal, but a benefit in terms of speedy germination and seed dispersal. Even though fruit production rate varies, the year’s predation rate remains almost the same. Tolerance to partial predation exhibited by *G. imberti* seeds is likely a key reproductive strategy, which enables recruitment of this endangered species. Ecologically this study provides an example of how antagonistic interactions of seed predation turn into a positive interaction result.

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