Patterns of seed rain and regeneration in abandoned paddy fields in Bhadra Tiger Reserve

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Declaration

I declare that the thesis entitled "Patterns of seed rain and regeneration in abandoned paddy fields in Bhadra Tiger Reserve, Karnataka" comprises research work done by me under the guidance of Dr. Ankila Hiremath and co-guidance of Mr. Devcharan Jathanna. The work is original and has not been done earlier by anyone else. Part of this work, which is related to or similar to work done by other researchers, has been referred to in this thesis at appropriate places. The results presented in this thesis have not been submitted previously to this or any other University for an M.Sc. or any other degree.

Signature of the Guide
(Dr. Ankila Hiremath)

Signature of the Candidate
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Certificate

I declare that this thesis entitled "Patterns of seed rain and regeneration in abandoned paddy fields in Bhadra Tiger Reserve, Karnataka" comprises research work carried out by Karthik T. at the Centre for Wildlife Studies under my guidance and the co-guidance of Mr. Devcharan Jathanna during the period 2005-2006 for the Degree of Master of Science in Wildlife Biology & Conservation of the Manipal Academy of Higher Education (MAHE). The results presented in this thesis have not been submitted previously to this or any other University for M.Sc. or any other degree.

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Summary

Agricultural fields in 13 villages within Bhadra Tiger Reserve were abandoned following a relocation program in 2002. Patterns of seed rain and regeneration were studied in five of these sites which covered an area of about 130 ha from February, 2006 to May, 2006. Seed rain traps that collected wind-dispersed seeds were laid along five transects that radiated from forest edge into the fields in each site at distances of 0, 2, 4, 8, 16, 32 and 64 m, with a control trap within the adjoining forest to compare seed rain in the forest with the seed rain in the fields. Animal-dispersed seeds were collected monthly over three visits from plots adjoining the wind-dispersed seed rain traps. Wind-dispersed seed rain was collected fortnightly over seven visits from 200 traps. Artificial perches were erected in the fields along one transect in each site at the same distances as the wind-dispersed seed rain traps. Bird-dispersed seed rain below the perches was collected fortnightly from 35 traps over five visits. The total number of wind-dispersed seeds, animal-dispersed and bird-dispersed seeds of tree species collected during the study period was 5,563, 706 and 3,715 respectively. Wind-dispersed seed rain abundance and species richness was found to decline non-linearly with distance from the forest-field edge but few seeds dispersed upto 64 m. When I explored patterns by species, I found that seed rain of larger seeded species declined non-linearly, while smaller seeded species declined linearly and dispersed farther into the fields. Species richness of wind-dispersed seed rain was {mean (± SD)} 7.6 (±1.67) in the control traps in the forest and 5.34 (±1.76) in the fields. Distance from the edge had no effect either on animal-dispersed

seeds or on bird-dispersed seeds at the perches. Seed rain at perches was 20 times higher than seed rain at plots with no perches and the species richness was enhanced by about 50%. The lack of patterns in bird-dispersed seed rain with distance, and the enhancement in seed rain abundance and diversity suggests that bird-perching structures are effective in increasing seed arrival in open fields.

Vegetation was censused in 250 nested quadrats across the five sites for trees, seedlings and saplings. Cover variables (shrub cover, weed cover, bareground cover, grass cover and litter cover) were visually estimated from 250 plots across the five sites. The total number of seedlings and saplings recorded in the fields in 200 plots was 163 and the density was {mean (± SD)} 0.82 (±0.59) seedlings and saplings / 25 m^2. Compared to this, the seedling and sapling density in the adjoining forest plots was 5.68 (±3.26) seedlings and saplings / 25 m^2. Percent grass cover was found to increase with distance from the forest-field edge and weed cover was found to be highest at the edge. However, distance from the edge was found to have no effect on the shrub cover. Soil moisture was sampled at different distances from the forest-field edge in each site, and was found to show no clear pattern. Using generalized linear models with shrub cover, soil moisture and distance from the forest-field edge as the predictors, and seedling and sapling density as the response, it was found that distance from the forest-field edge had the strongest effect on the seedling and sapling density.

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Contents

Chapter I, Introduction

Over the past few decades, village relocation and rehabilitation programs have been perceived to be the most practical solutions for mitigating the impacts of anthropogenic disturbances on biodiversity across reserves in India (TTF 2005). Follow-up monitoring and documentation of habitat recovery, both in terms of the flora and the fauna, can provide vital information to assess the success of such relocation programs. In 2002, 457 families from 11 villages were relocated from within Bhadra Tiger Reserve (hereafter, Bhadra), Karnataka, India. Prior to relocation, these families were largely involved in growing paddy with incomes being supplemented by sales of various non-timber products collected from the forest (Karanth 2003). The relocation provides a unique opportunity to examine and understand patterns of forest recovery in the abandoned paddy fields after many decades of intense human use.

Documented examples of vegetation recovery or changes after relocation of villages in India come from Nagarahole and Kanha National Parks. In Nagarahole, paddy fields abandoned due to relocation of several hundred families about 30 years ago have now become short grass clearings and swampy fallows (Karanth *et al.* 1999). These areas, locally known as *hadlus,* are known to help maintain high densities of grazer species due to the year-round abundance of forage (Karanth & Sunquist 1992). Similarly, most of Kanha's grassy meadows are abandoned village sites. Some of these meadows date back to the desertion of villages during the famine of 1874; others that are more recent resulted from the relocation of villages subsequent to the declaration of Kanha as a Project Tiger Reserve in 1973. The surrounding forest has been prevented from recolonising these sites by periodic frosts, yearly fires and grazing by animals (Schaller 1967). These meadows have been referred to as "unique contributions to the Project Tiger network" (Dale & Haeuber 2001) because of their ability to help support high densities of tiger prey. The matrix of tall grass meadows interspersed with short grass meadows has been maintained by the Forest Department using annual burning, to provide habitat for the barasingha (*Cervus duvaucelii)* and the blackbuck (*Antelope cervicapra*).

Across the world, vegetation recovery following human-abandonment has been studied over a range of habitats such as dry tropical savanna (e.g. Donfack *et al.* 1995), temperate rain forests (e.g. McClanahan & Wolfe 1993, Reige & Moral 2004), and wet tropical and neo-tropical forests (Hooper *et al.* 2005, Holl 1999, Chapman & Chapman 1999, Willson & Crome 1989, Duncan & Chapman 1990, Cardoso da Silva *et al.* 1996, Uhl 1987, Buschbacher *et al.* 1988, Aide & Cavelier 1994, Zahawi & Augspurger 1999). Habitat recovery has also been examined at scales ranging from the patch (e.g. Cubina & Aide 2001, Willson & Crome 1989, Holl 1999) to the landscape (e.g. Thomlinson *et al.* 1996, Endress & Chinea 2001, Holl & Crone 2004). Habitat recovery studies have been carried out at sites with differing land-use histories such as shifting agriculture (Uhl 1987, Uhl *et al.* 1988), pastures (Aide *et al.* 1995, Holl 1999, Zahawi & Augspurger 1999) and agricultural fields (Donfack *et al.* 1995, Zhuang & Corlett 1997, Duncan &

Chapman 1999, Duncan & Duncan 2000), although a considerable overlap occurs between the latter two land-use types (i.e. abandoned agricultural lands used as pastures for cattle grazing). Seed dispersal limitations, competition from existing vegetation, harsh micro-climatic conditions, low soil-nutrient availability, and seed/ seedling-predation have been shown to inhibit recovery of habitats following intense human-use (Uhl 1987, Willson & Crome 1989, Holl 1998, Duncan & Chapman 1999, Chapman & Chapman 1999, Holl 1999, Cubina & Aide 2001, Aide & Caveliar 1994, Holl 2002, Hooper *et al.* 2005).

Succession and regeneration

With large areas of forest already converted to other land uses, it is increasingly pertinent to understand the processes underlying forest recovery on degraded lands, or lands abandoned following human-use. Several studies have attempted to address the above question, a large proportion of them from the neotropics. Most of these studies show that succession following abandonment is clearly related to site history (i.e. the intensity of past disturbances) (Uhl *et al.* 1988, Ewel 1980, Donfack *et al.* 1995, Kammesheidt 1999; but see Chapman & Chapman 1999). Buschbacher & others (1984) conclude from their study in Amazonia that forest recovery in pastures following abandonment is inversely proportional to the intensity of pasture use (Uhl 1987). In Puerto Rico, forest recovery quantified by biomass accumulation was shown to be much slower in pastures than in plantations and sites affected by natural disturbances such as hurricanes (Aide *et al.* 1995). In comparison to this, Gehring and others (2005) show that in Amazonia in a slash-and-burn agriculture scenario, biomass accumulation occurs with rapid initial increments followed by a gradual increase. Uhl (1987), through his findings from Amazonia, affirms that in contrast to slash-and-burn agriculture, elements influencing succession such as regeneration mechanisms, micro-habitats and soil nutrients fall below their critical levels in pastures.

The factors that have been shown to impede succession and regeneration can be broadly classified as proximate—seed arrival, seed and seedling predation, and seedling survival; and ultimate—distance from seed sources, competition from existing vegetation, low nutrient availability and harsh micro-climatic conditions (Uhl 1987, Willson & Crome 1989, Holl 1998, Duncan & Chapman 1999, Chapman & Chapman 1999, Holl 1999, Cubina & Aide 2001, Aide & Caveliar 1994, Holl 2002, Hooper *et al.* 2005).

Competition with existing grasses, herbs, shrubs and ferns for nutrients has been shown to be a crucial factor affecting tree regeneration in abandoned grasslands (Aide & Caveliar 1994, Holl *et al.* 2000, Slocum 2001, Reige & Del Moral 2004, Slocum *et al.* 2004). In fern thickets in a subtropical montane forest in the Dominican Republic, considered to be in a state of arrested succession, Slocum *et al*. (2004) found a significant increase in density and diversity of woody plants once fern thickets were cleared.

Distance from the forest edge has been shown to affect regeneration patterns (Aide & Caveliar 1994, Hooper *et al.* 2005; but see Donfack *et al.* 1995). For instance, a decrease in seedling density and species richness can be expected with increasing distance from the edge due to lower seed dispersal and harsher micro-climatic conditions farther from the forest (Duncan & Duncan 2000; but see Slocum 2001).

Various studies (Willson & Crome 1989, Duncan & Chapman 1999, McClanahan & Wolfe 1993, Cardoso da Silva *et al.* 1996, Galindo-Gonzalez *et al.* 2000, Holl *et al.* 2000, Slocum 2001) emphasise the importance of isolated trees as natural perches for birds and their role in succession in abandoned fields and pastures. Remnant trees have been shown to considerably increase seed dispersal (Willson & Crome 1989, Duncan & Chapman 1999, Galindo-Gonzalez *et al.* 2000) and buffer harsh micro-climatic conditions (Guevara *et al.* 1992, Zahawi & Augspurger 1999) thus improving seedling survival. Guevara *et al.* (1998) found that in pastures in Mexico, vegetation recovered rapidly under isolated trees with about 85 % of the seed rain dispersed by bats and birds (Galindo-Gonzalez *et al.* 2000).

Seed rain

Patterns of seed rain in pastures and fields at different distances from the forest edge are variable across sites. Cubina & Aide (2001) have demonstrated that, in Puerto Rico, seed rain from the adjoining forest recedes to zero beyond 8 m from the forest edge, whereas Willson & Crome (1989) found both animal- and wind-dispersed seeds 100 m into fields in Queensland, Australia. In an abandoned pasture in Costa Rica, Holl (1999) found that few animal dispersed seeds of woody species were deposited beyond 5 m; however, distance was found to have no effect on wind dispersed seeds. Slocum & Horvitz (2000) report a lack of pattern in animal-dispersed seeds with distance from the forest edge.

Tropical forest seeds have been shown to have extremely short viability (Holl *et al.* 2000, Uhl 1987). Hence, the main seed arrival occurs from parent trees in the adjoining forests (Saulei & Swaine 1988, Aide *et al.* 1995, Holl *et al*. 2000) rather than the existing seed bank. This makes it critical to understand the dynamics of seed rain from adjoining forests in that seed arrival into fields and pastures is a major limiting factor. In this context, it is critical to understand if the incoming seed arrival can be enhanced. Only a few studies (McClanahan & Wolfe 1993, Aide & Caveliar 1994, Holl 1998) have introduced bird perches in fields and shown an increase in the diversity as well as abundance of seed arrival.

Goal of the study

In my study in Bhadra I examined patterns of seed rain in abandoned paddy fields from adjoining forest and investigated if the seed arrival can be enhanced using artificial bird-perches erected in the fields. I also explored patterns of regeneration, and factors affecting them, at different distances from the forest-field edge.

Specific questions

The questions that I posed were:

1) What are the patterns of seed rain in the fields from the adjoining forest at different distances from the forest-field edge?
2) Can the incoming seed arrival be enhanced by providing perches for birds in the fields?
3) What are the patterns in regeneration in the fields at different distances from the forest, and what are the spatial correlates of these patterns?

Chapter II, Study area and methods

Study site

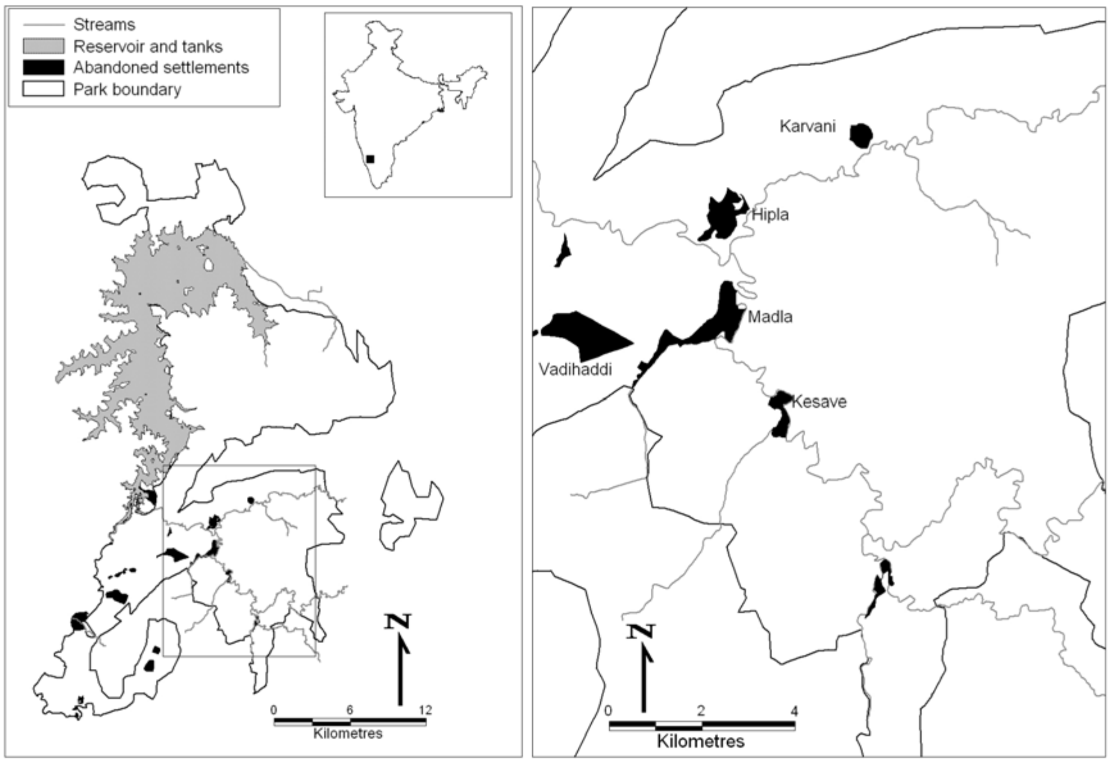

Figure 1: On left: Map of Bhadra Tiger Reserve showing the Bhadra reservoir to the northwest, and the location of abandoned settlements (Inset map shows location of Bhadra within peninsular India). On right: Five of the 13 abandoned settlements in Bhadra that were chosen as replicate sites for this study.

Bhadra ($13^0$22'N - $13^0$47'N and $75^0$29'S - $75^0$47'S) covers an area of 492 km^2 and is located in Chikamagalur and Shimoga districts of Karnataka state (Figure 1). The Babubudan Hills, an eastern arm of the Western Ghats, partially surround Jagara Valley, the southern portion of the reserve. Annual mean temperatures range between 10 and 32 ºC and the annual rainfall of 2000-2540 mm occurs mainly from June to September (Karanth 1982). The valley within the crescent formed by the Bababudans ranges between 670 –760 m above m.a.s.l, and is dissected by numerous perennial streams. The Bhadra river forms the western boundary of the reserve, flowing into the Bhadra Reservoir, which separates the northwestern part from the rest of the reserve. Bhadra was notified as a Tiger Reserve in 1998, subsequent to its declaration as a Wildlife Sanctuary in 1972 (Karanth 1982).

The reserve is predominantly covered by the *Tectona-Dillenia-Lagerstroemia* series (Meher-Homji 1990) moist deciduous forests. It gradually merges with southern tropical dry deciduous forests towards the north-eastern edges. The higher slopes of the Bababudans are covered by grassy meadows interspersed with evergreen 's*holas'* (Karanth 1982). Bhadra is characterized by an abundance of bamboo, mainly *Bambusa arundinaceae* and *Dendrocalamus strictus.* Tree species such as *Dalbergia latifolia, Terminalia alata, T. paniculata, T. bellerica, Pterocarpus marsupium, Schleichera oleosa* and various species of *Ficus* (Karanth 1982) comprise the top canopy of the moist deciduous parts of Bhadra. The mid canopy has species such as *Kydia calycina, Careya arborea, Emblica offiicinalis* and *Gmelina arborea*. Presently, *Bambusa arundinaceae* is regenerating subsequent to its mass flowering around 2001 (Jathanna 2001). Trees such as *Hydnocarpus pentandra, Syzigium cumini, Elaeocarpus tuberculatus* and *Trewia polycarpa* characterize the riverine semi-evergreen patches of Bhadra. Teak *Tectona grandis* plantations by the Forest Department cover about 6 % of the southern part of the Reserve (Jathanna 2001).

Bhadra has a diverse mammalian fauna, similar to other deciduous forests in peninsular India. The herbivore assemblage is comprised of species such as Asian elephant (*Elephas maximus)*, gaur (*Bos gaurus)*, sambar (*Cervus unicolor)*, chital (*Axis axis)*, muntjac (*Muntiacus muntjak)*, chevrotain (*Tragulus meminna)* and wild pig (*Sus scrofa)*. Arboreal mammals include langur (*Semnopithecus entellus)*, bonnet macaque (*Macaca radiata)*, Indian giant squirrel (*Ratufa indica)* and large brown flying squirrel (*Petaurista philippensis)*. Carnivores include the tiger (*Panthera tigris)*, leopard (*P. pardus)*, wild dog (*Cuon alpinus)*, sloth bear (*Melursus ursinus),* small Indian civet (*Viverricula indica),* common palm civet (*Paradoxurus hermaphroditus)*, mongooses (*Herpestes spp).* and jackal (*Canis aureus)* (Jathanna *et al.* 2003).

Settlements

Thirteen villages inhabited by about 4000 people were located within the reserve before their relocation in 2002 (Karanth 2005). A major irrigation project constructed in the sixties isolated these villages from the towns in the north-west of the Reserve. Similar to anthropogenic pressures in other protected areas in India, poaching, cattle grazing, logging, collection of firewood and non-timber products were extant in the Reserve before the relocation (Karanth 2005). The present study was carried out in the relocated village sites of Madla, Vadihaddi, Hipla, Kesave and Karvani. The paddy fields that have been abandoned in the five sites aggregate to about 130 ha of productive riparian habitat. All the fields adjoin the Somavahini and Hipla streams, which were the main source of irrigation for the paddy fields.

Figure 2 An abandoned paddy field in Vadihaddi, one of the relocated village sites in Bhadra Tiger Reserve

Field methods

i) Study design

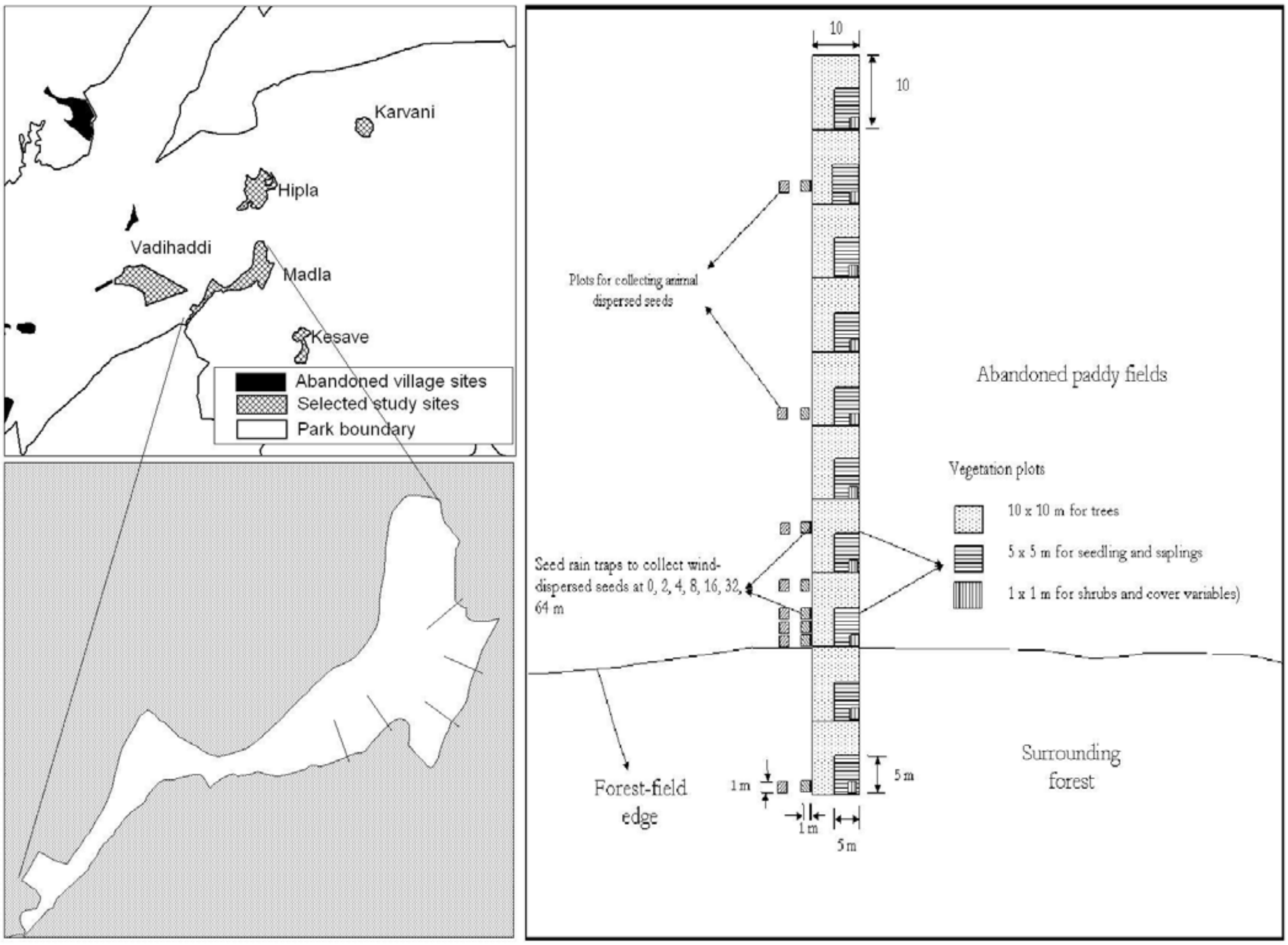

Figure 3 On the left: One of the settlements, Madla with a schematic of transects On right: A schematic of a transect showing the layout of seed rain traps, and nested quadrats used to sample vegetation. Wind-dispersed seeds were collected in 1x1 m pits at distances of 0, 2, 4, 8, 16, 32 and 64 m into the abandoned fields; an additional pit was located 20 m into the forest; 1x1 m plots to sample animal-dispersed seeds were arrayed parallel to the pit traps at a distance of 5 m from them. Vegetation was sampled along the entire length of the transect in nested quadrats of 10x10 m, 5x5 m, and 1x1 m for trees, seedlings and saplings, and per cent ground cover, respectively. There were 7 such transects in each of 5 replicate clearings.

Abandoned paddy fields in five village sites within Bhadra were selected for the study. In each of the clearings, a forest-field edge, 350 m long, was marked using a global positioning system (GPS). Along this edge, five points were marked at random, taking care to ensure that no two points were less than 50 m apart. Transects radiating into the clearing were established starting at each of these points for monitoring seed rain and to sample vegetation (Figure 3). Seed traps were set up along the transects at distances of 0, 2, 4, 8, 16, 32, and 64 m from the forest edge to collect wind-dispersed seeds arriving in the fields; additionally, a control seed trap was placed about 20 m within the forest to compare seed rain in the forest with that in the fields. Animal-dispersed seeds were collected from plots adjacent to the seed rain traps laid for collecting wind-dispersed seeds. Bamboo poles used as bird perches were erected at the same distances as the seed rain plots to compare seed rain at plots with and without perches. Vegetation in the fields and the surrounding forest was sampled using nested quadrats that ran along the transects. Each transect was divided into 10 m segments, within which tree data were recorded. Eight of these segments lay in the fields, with two of the segments in the adjoining forest. Seedlings and saplings were censused in 5 x 5 m quadrats nested within the 10 x 10 m tree plots. 1 x 1 m quadrats, nested within the 5 x 5 m plots, were used to record data on shrubs and ground cover variables.

ii) Seed rain

Seed traps for wind-dispersed seeds initially consisted of plastic pots, 35.5 cm in diameter and depth, embedded into the soil to a depth of 15 cm to prevent them from being overturned by the wind. These pots were nested within a 1 x 1 m plot and used to collect small, wind-dispersed seeds, especially those of shrubs; in addition, the 1 x 1 m patch of ground around the pot was searched for larger seeds during each visit to collect the seed rain. The number of seeds collected from the pots was subsequently expressed as total (over 7 visits) seed rain/ m^2. Seed traps were visited fortnightly, starting 1st March, 2006 for a total of 7 collections till the end of May 2006. Given that most trees flower and fruit during the February-May dry season in Bhadra, the sampling period coincided with the main window of seed dispersal in this forest.

Within the first two samplings, it was found that at least 5% of pots had been damaged due to large mammals, mainly elephants. Consequently, from the second month onward, pots were replaced by pits, 1 x 1 m wide and 10 cm deep. The pits were lined with cloth to ensure that small seeds were not overlooked during collections.

Animal-dispersed seeds were collected from 1 x 1 m plots placed at a distance of 5 m from each of the seed traps. These plots were established away from the seed traps for wind-dispersed seeds to minimise disturbance that might deter animals from visiting these plots. In addition, care was taken to avoid disturbing ground vegetation in these plots at the time of seed collection. Plots for animal-dispersed seeds were checked monthly, for a total of 3 collections, from 1st of March to 31st of May, 2006.

iii) Bird perches

At each site, seven bamboo poles (7 m in height, with at least 10 lateral branches on each pole), were selected from the clumps of dead bamboo (*Bambusa arundanaceae*) and erected at 0, 2, 4, 8, 16, 32 and 64 m from the forest edge, along one of the seed rain transects. The seed traps dug (1 x 1 m, 10 cm deep) below the perches trapped both wind and bird-dispersed seeds for comparison. The perches were laid after a month of monitoring wind-dispersed seed rain, in order to examine the degree to which their introduction enhances seed arrival into the paddy fields. Five fortnightly visits were made to each of the five abandoned village clearings during the study period, and bird dispersed seed rain was collected from 35 traps during each visit.

Bird visitation rates and diversity of visiting birds were expected to have a significant effect on the incoming seed arrival. Therefore, the artificial perches were monitored for visitation by birds on five consecutive days in each of the five sites between 0700 to 0900 hrs and 1600 hrs to 1800 hrs.

Figure 4 Bird-perches at different distances from the forest-field edge in Karvani, one of the abandoned village sites in Bhadra Tiger Reserve

iv) Vegetation composition

Data on vegetation composition and structure within the abandoned fields were recorded in nested quadrats along five transects in each site, with 10 quadrats in each site, eight of which lay in the fields and two in the adjoining forest (Figure 2). All the vegetation transects were adjacent to the transects along which seed rain was collected. The total area covered for vegetation sampling was 5,000 m^2 in each site and 25,000 m^2 across all the sites.

All live and dead trees were identified and their height, and girth at breast height were measured in the 10 x 10 m segments along each transect. Seedling (height below 25 cm) and saplings (height between 25 and 100 cm) were identified and their height and basal diameter were measured in 5 x 5 m segments and their height and basal diameter were measured. All the shrubs were identified in the 1 x 1 m segments. In addition, percent grass cover, shrub cover, exotic shrub cover, litter cover and bare ground cover were visually estimated in these plots. Percent canopy cover in each of the segment was measured using a spherical densiometer.

v) Soil moisture, wind direction and speed

Seed rain transects across sites were not aligned towards the same direction. Hence, difference in the patterns of wind across sites was expected to influence the abundance of seed arrival. In order to assess if the pattern of prevailing wind influenced seed arrival, wind direction and speed were recorded using an anemometer over one day in each site at hourly intervals between 0700 hours to 1800 hours.

Soil moisture was expected to affect seedling and sapling abundance since lower levels of moisture may be available in the soil farther from the forest edge. Twenty soil samples were collected from each site from two of the five lines in which the vegetation was sampled. The moisture in the soil was estimated gravimetrically. The soil samples were weighed in the field, dried at 105˚ C for 24 hours and reweighed. A subset (20 of the 100) samples collected were dried at 105˚ C for an additional 24 hours and weighed to check for further reduction in weight. Soil moisture was calculated using the following equation: % Soil moisture = (Wet weight of soil)-(Dry weight of soil) / (Wet weight of soil) x 100

Analytical methods

Given the problems pointed out with inference based on hypothesis testing (Burnham & Anderson 1998, Johnson 1999), especially with observational studies (as opposed to controlled experiments where treatment levels are fully randomised), I chose to base inferences using an information-theoretic model selection approach (Burnham & Anderson 1998, Johnson & Omland 2004). The approach stresses confronting a set of competing *a priori* models with empirical data, rather than choosing between a null and an alternative hypothesis based on unknown test distributions and arbitrary significance levels unrelated to biological significance. In this approach models are ranked based on an objective criterion, usually Akaike's Information Criterion (AIC), computed as

AIC = -2log{£(model | data)} + 2k, where £(model | data) is the likelihood of the model given the data, at the maximum likelihood estimates of model parameters, and k is the number of parameters. If parameter estimates are based on least squares estimation rather than maximum likelihood estimation, £(model | data) may be estimated as:

£(model | data) = $-\frac{n}{2}\log(\frac{RSS}{n})$, where RSS is the residual sum of squares for a model.

AIC thus trades off model fit against complexity, selecting the simplest (lowest AIC) model which best explains the patterns in the data. I used a small sample correction for AIC, computed as AIC_C= AIC+$\frac{2k(k+1)}{n-k-1}$. The AIC_C differences, ΔAIC_C were computed for each model as $\Delta_i = AIC_i - AIC_{minimum}$. AIC weights were then computed as $W_i = \frac{e^{(-\frac{1}{2}\Delta_i)}}{\sum \sum_{j=1}^{R} e^{(-\frac{1}{2}\Delta_j)}}$. AIC weights can be interpreted as the probability that model *i* is the best model for the observed data, given the candidate set of models (Burnham and Anderson 1998, Johnson and Omland 2004). Further, AIC weights, summed over all the models which contain a particular predictor, are a measure of the relative importance of that predictor.

Response variables (e.g. seed density, species richness) were modelled as a function of predictors (e.g. distance from field-forest edge, perch/ no perch) using linear and non-linear functions, and generalised linear models (GLMs). GLMs are a generalisation of analyses such as linear regressions and ANOVA, allowing predictors to be either metrics (as in regressions) or categories (as in ANOVA).

Prior to modelling, exploratory data analyses were carried out to check for normality, homeoscedasticity and intercorrelated predictors (to prevent multicollinearity) using histograms, scatter plots, and box and whiskers plots. Non-normally distributed variables and those exhibiting heteroscedasticity were log-transformed (base 10) (e.g. Figures 5, 6). All analyses were carried out using MS Excel, S-Plus 6.0 version and SPSS .

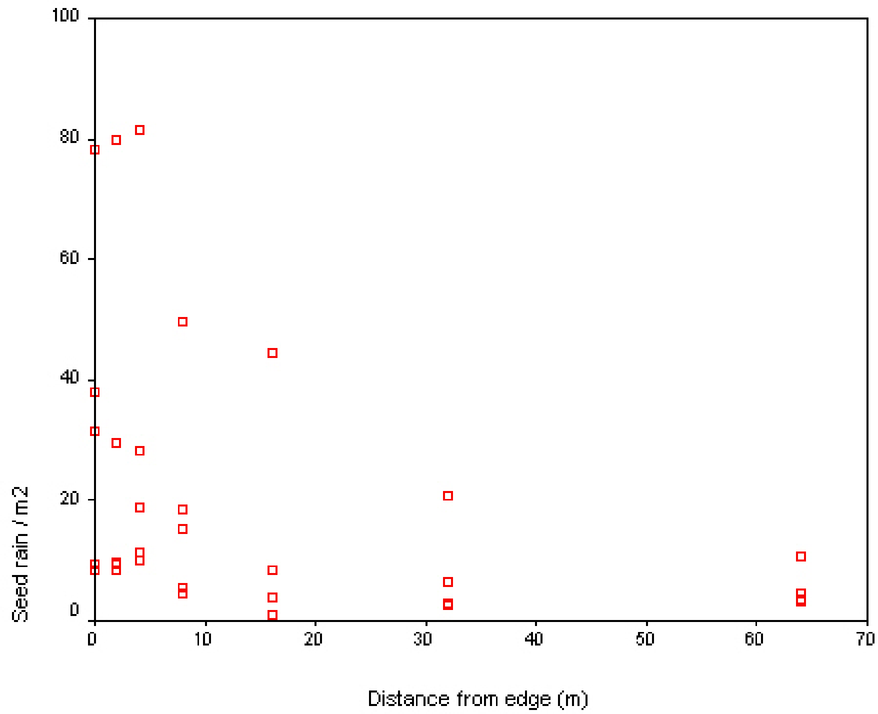

Figure 5 Seed rain data across all the five paddy field sites in Bhadra Tiger Reserve showing heteroscedasticity prior to log transformation

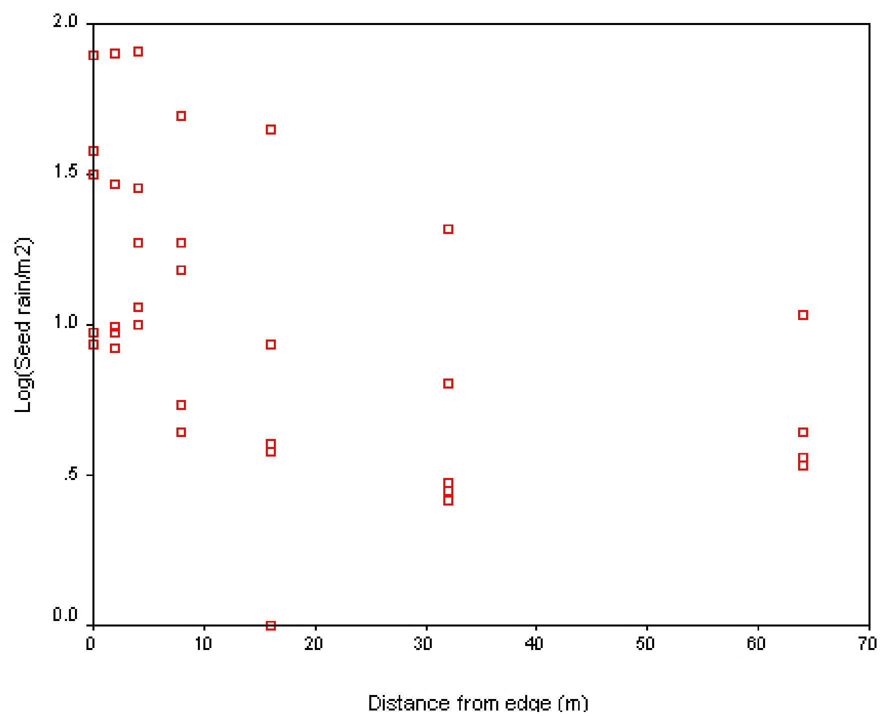

Figure 6 Seed rain data across all the five paddy field sites in Bhadra Tiger Reserve showing homeoscedasticity after log transformation.

i) Seed rain

Sites were considered as replicates and seed rain data from all the lines in each site were pooled together for analysis. Mean seed rain/m^2/ 7 fortnights was log-transformed (base 10) to achieve normal distribution of errors, and to remove heteroscedasticity in the data (Figures 5, 6). Using distance to the forest-field edge as the predictor variable and $\log_{10}$mean seed rain/m^2 as the response variable, linear, quadratic, cubic and exponential functions were fit to the data. The model that best fit the data was determined using Akaike's Information Criterion, corrected for small samples (AIC_C).

To examine if seed size affects seed rain patterns with distance from the forest-field edge, the five most abundant species were selected. Linear, quadratic, cubic and exponential functions were fit to the seed rain data for these species and the best model selected using AIC_C. The effect of distance on the species richness of the incoming seed arrival was also modeled using linear, quadratic, cubic and exponential equations with the response variable species richness of the seed rain and the predictor variable distance from the forest-field edge. The appropriate model was selected using AIC_C.

Animal-dispersed data across the lines within each site were pooled to obtain a single mean value of seed rain at each plot. The seed rain data were log-transformed and modelled as a function of distance from forest-field edge using linear, quadratic, cubic and exponential functions. The appropriate model was selected based on AIC_C.

ii) Bird perches

Generalized linear models were used to model the effects of perches and distance from edge on seed arrival. Log_{10} seed rain/ m^2/ 5 fortnights was used as the response variable and the predictor variables used were perch/ no perch (categorical variable) and distance from the edge (metric). AIC_C was used to compare the following models: (a) seed rain as a function of perches, (b) seed rain as a function of distance, (c) seed rain as a function of perches + seed rain, and (d) seed rain as a function of perches + seed rain + an interaction between perches and seed rain

iii) Soil moisture

Percentage soil moisture was plotted on the X-axis and the distance from the forest-field edge on the Y-axis to explore the effect of distance from the forest-field edge on percentage soil moisture.

iv) Cover variables

The cover variables (i.e. shrub cover, grass cover, weed cover, bareground cover and litter cover) were expressed as percentage values and were plotted with distance from the forest-field edge on the X-axis and percentage cover variable on the Y-axis using stacked bar graphs. This plot was used to observe the patterns of each of the cover variables with increasing distance from the forest-field edge. Additionally, percentage shrub cover was plotted on the Y-axis with distance from the forest-field edge on the X-axis to examine patterns in percentage shrub cover with distance. Percent shrub cover was also plotted against soil moisture to check for possible correlations.

v) Vegetation composition

Generalised linear models were used to examine the factors affecting regeneration in the fields. The response variable used was seedling/sapling density and the predictor variables used were:

1) Distance from the edge
2) Percentage soil moisture
3) Percentage shrub cover
4) Distance + Percentage soil moisture
5) Distance + Percentage shrub cover
6) Percentage soil moisture + Percentage shrub cover

The model that best described the observed pattern was determined using AIC_C. AIC_C weights were computed and summed over all the models containing each individual predictor to determine the relative importance of each predictor.

Chapter III, Results

I) Wind-dispersed seeds

A total of 5,563 wind-dispersed seeds were collected from 200 traps over 7 visits during the study period from March 1st to May 31st, 2006. 3,505 seeds were collected from traps in the fields and 2,058 seeds from the control traps in the adjoining forest. The average seed rain density in the forest was 82.32 seeds / m^2/ 7 fortnights whereas it was 20.03 seeds/ m^2/ 7 fortnights in the fields.

Since sites were considered replicates, seed rain abundance data were first averaged across lines within each site and then summed over all visits (7 fortnights) to a get seed rain/ m^2/ 7 fortnights at each distance and site. Using $\log_{10}$seed rain/ m^2/ 7 fortnights as the response variable and distance from the forest-field edge as the predictor, I fit linear, quadratic, cubic and exponential functions to the data. Based on lowest AIC_C values, it was determined that the patterns of seed rain decline with increasing distance from the edge were best described by a quadratic function (Table 1). Table 2 shows estimated parameter values for the selected model. Figure 7 is a plot of seed rain against distance, with a quadratic function fitted.

Model	Δ AIC_c	Model likelihood	AIC_c weights
Quadratic	0	1	0.6191
Lineat	2.3263	0.3124	0.19349
Cubic	2.3909	0.3025	0.18733
Exponential	27.61779	1.00664E-06	6.233E-07

Table 1: AIC_C Weights for linear, quadratic, cubic and exponential equations with distance from the forest-field edge as the response and log_{10} seed rain/m^2/ 7 fortnights as the predictor variable. Data from abandoned village sites in Bhadra Tiger Reserve.

R^2: 0.3527

Model parameter	Value ± SE
B_0	1.371± 0.1098
B_1	-0.0367 ± 0.012
B_2	0.0004 ± 0.0001

Table 2: Parameter values for the quadratic equation with log_{10}seed rain/m^2/ 7 fortnights as response variable and distance from the forest-field edge as predictor variable for wind-dispersed seed rain. Data from abandoned village sites in Bhadra Tiger Reserve.

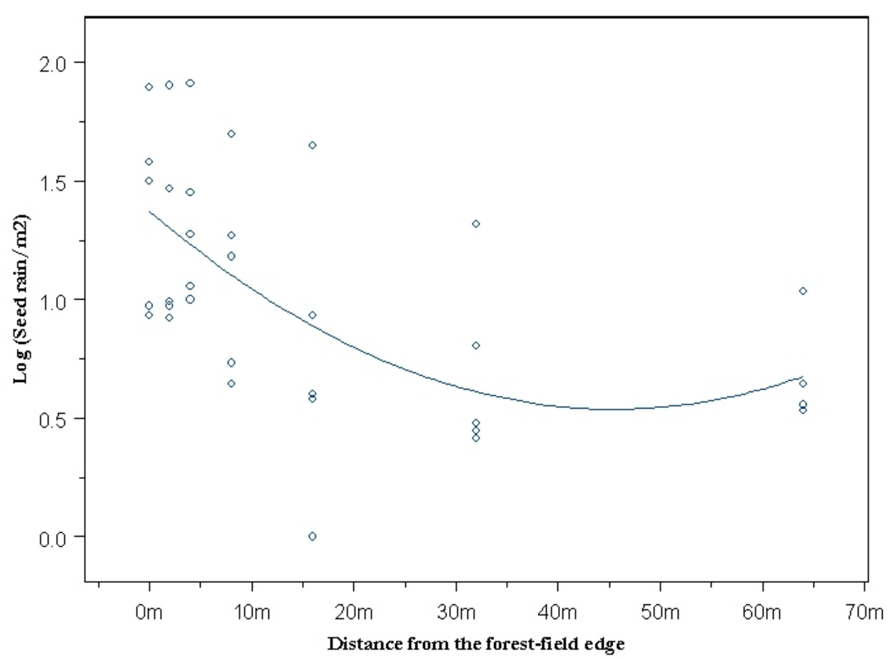

Figure 7: Wind-dispersed seed rain across all 5 abandoned village sites in Bhadra Tiger Reserve. Data averaged across transects within each site.

Data from the five most abundant species were used to examine patterns of seed rain based on seed size and weight. For each of the five species, an appropriate model describing the observed patterns was selected based on lowest AIC_C (Tables 4-13, Figures 8-12).

Weight category	**Species**
High	*Terminalia alata, Pterocarpus marsupium*
Medium	*T. paniculata, Dalbergia latifolia*
Low	*Lagerstroemia lanceolata*

Table 3: Size categories for the five most abundant wind-dispersed species collected from fields in the 5 abandoned villages sites in Bhadra Tiger Reserve.

Model	**ΔAIC_C**	**Model likelihood**	**AIC_C weight**
Quadratic	0	1	0.4654
Cubic	0.2858	0.8668	0.4034
Linear	2.5339	0.2816	0.1311
Exponential	26.4317	1.82E-06	8.48E-07

Table 4: AIC_C weights for linear, quadratic, cubic and exponential equations with $\log_{10}$*T. alata* seeds/m^2/ 7 fortnights as the response and distance from the forest-field edge as the predictor. Data from abandoned village sites in Bhadra Tiger Reserve.

T. alata : R^2: 0.15347

Model parameter	**Value ± SE**
B_0	0.9199 ± 0.1721
B_1	-0.0396 ± 0.0188
B_2	0.0005 ± 0.0003

Table 5: Parameter values for the quadratic equation with $\log_{10}$*T. alata* seeds /m^2/ 7 fortnights as the response variable and distance from the forest-field edge as predictor variable. Data from abandoned village sites in Bhadra Tiger Reserve.

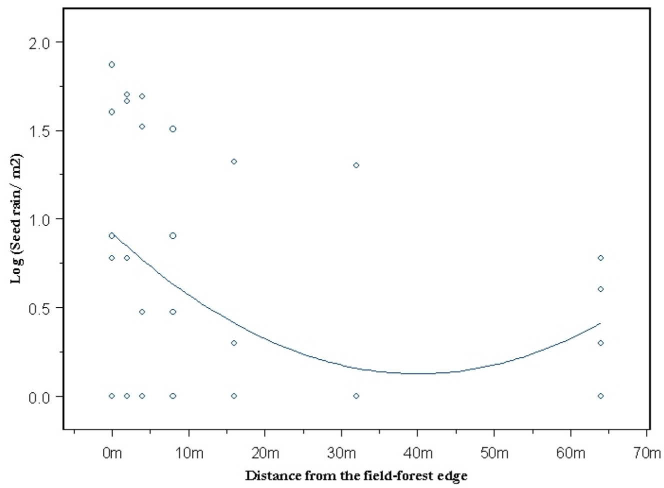

Figure 8: Plot of *Terminalia alata* seed rain at different distances from the forest-field edge. Function fitted: quadratic. Data from abandoned village sites in Bhadra Tiger Reserve.

Model	**ΔAIC_C**	**Model likelihood**	**AIC_C weight**
Quadratic	0	1	0.4687
Cubic	0.4547	0.79664	0.3734
Linear	2.1786	0.3364	0.1577
Exponential	21.3326	2.33E-05	1.09E-05

Table 6: AIC_C weights for linear, quadratic, cubic and exponential equations with $\log_{10}$*T. paniculata* seeds/m^2/ 7 fortnights as the response and distance from the forest-field edge as the predictor. Data from abandoned village sites in Bhadra Tiger Reserve.

T. paniculata :	R^2: 0.26799
Model parameter	**Value ± SE**
B_0	1.2194 ± 0.1544
B_1	-0.0397 ± 0.0169
B_2	0.0004 ± 0.0003

Table 7: Parameter values for the quadratic equation with $\log_{10}$*T. paniculata* seeds /m^2/ 7 fortnights as the response variable and distance from the forest-field edge as predictor variable. Data from abandoned village sites in Bhadra Tiger Reserve.

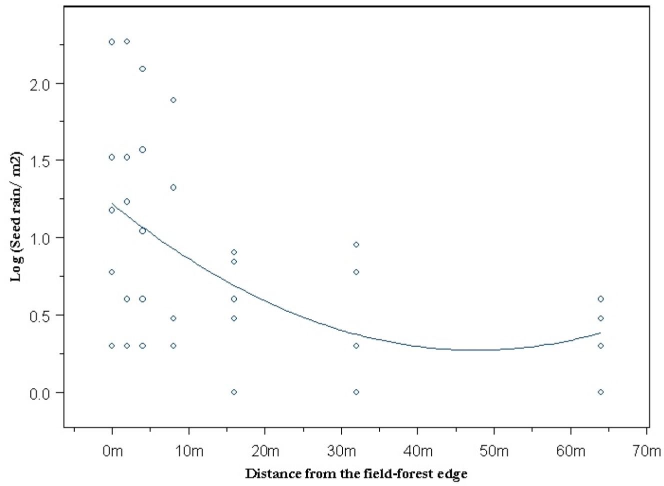

Figure 9: Plot of *Terminalia paniculata* seed rain at different distances from the forest-field edge. Function fitted: quadratic. Data from abandoned village sites in Bhadra Tiger Reserve.

Model	ΔAIC_C	Model likelihood	AIC_C weight
Quad	0	1	0.3705
Cub	0.015	0.9925	0.3677
Lin	0.6944	0.7067	0.2618
Exp	26.0382	2.22E-06	8.22E-07

Table 8: AIC_C weights for linear, quadratic, cubic and exponential equations with $\log_{10}$ *P. marsupium* seeds/m^2/ 7 fortnights as the response and distance from the forest-field edge as the predictor. Data from abandoned village sites in Bhadra Tiger Reserve.

P. marsupium : R^2: 0.12702

Model parameter	Value ± SE
B_0	0.4878
B_1	-0.0161
B_2	0.0002

Table 9: Parameter values for the quadratic equation with $\log_{10}$ *P. marsupium* seeds /m^2/ 7 fortnights as the response variable and distance from the forest-field edge as predictor variable. Data from abandoned village sites in Bhadra Tiger Reserve.

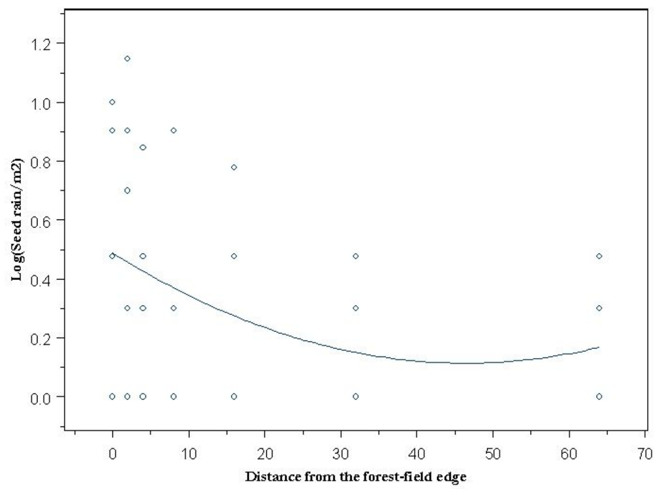

Figure 10: Plot of *Pterocarpus marsupium* seed rain at different distances from the forest-field edge. Function fitted: quadratic. Data from abandoned village sites in Bhadra Tiger Reserve.

Model	ΔAIC_C	Model likelihood	AIC_C weight
Lin	0	1	0.6333
Quad	1.565	0.4573	0.2896
Cub	4.2140	0.1216	0.0770
Exp	30.3932	2.51E-07	1.59E-07

Table 10: AIC_C weights for linear, quadratic, cubic and exponential equations with $\log_{10}$ *D.latifolia* seeds/m^2/ 7 fortnights as the response and distance from the forest-field edge as the predictor. Data from abandoned village sites in Bhadra Tiger Reserve.

D. latifolia: R^2: 0. 098

Model parameter	Value ± SE
B_0	0.8925
B_1	-0.0066

Table 11: Parameter values for the linear equation with $\log_{10}$ *D.latifolia* seeds /m^2/ 7 fortnights as the response variable and distance from the forest-field edge as predictor variable. Data from abandoned village sites in Bhadra Tiger Reserve.

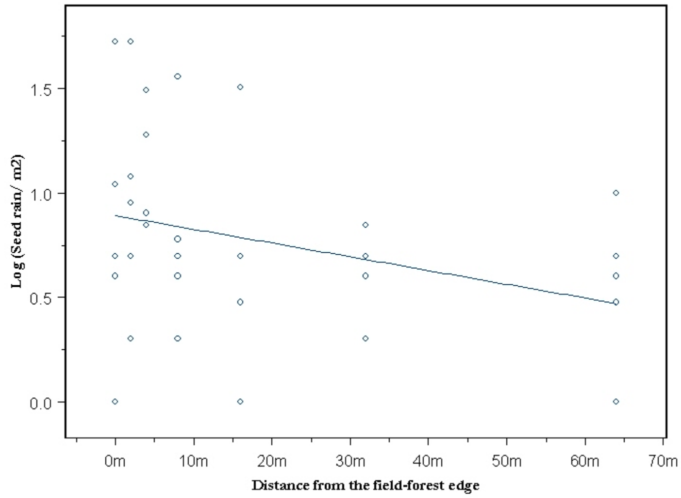

Figure 11: Plot of *Dalbergia latifolia* seed rain at different distances from the forest-field edge. Function fitted: linear. Data from abandoned village sites in Bhadra Tiger Reserve.

Model	ΔAIC_C	Model likelihood	AIC_C weight
Lin	0	1	0.6333
Quad	1.565	0.4573	0.2896
Cub	4.2140	0.1216	0.0770
Exp	30.3932	2.51E-07	1.59E-07

Table 12: AIC_C weights for linear, quadratic, cubic and exponential equations with $\log_{10}$*L. lanceolata* seeds/m^2/ 7 fortnights as the response and distance from the forest-field edge as the predictor. Data from abandoned village sites in Bhadra Tiger Reserve.

L. lanceolata	R^2: 0. 098
Model parameter	**Value ± SE**
B_0	1.0690
B_1	-0.0067

Table 13: Parameter values for the linear equation with $\log_{10}$ *L. lanceolata* seeds /m^2/ 7 fortnights as the response variable and distance from the forest-field edge as the predictor variable. Data from abandoned village sites in Bhadra Tiger Reserve.

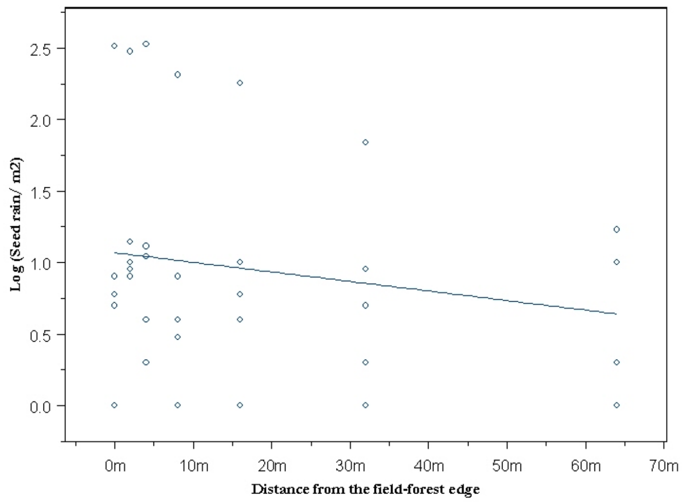

Figure 12: Plot of *Lagerstroemia lanceolata* seed rain at different distances from the forest-field edge. Function fitted: linear. Data from abandoned village sites in Bhadra Tiger Reserve.

Seeds of 19 wind-dispersed tree species were collected from the seed rain traps during the study period. The species richness of seed rain was (mean ± SD across sites) 7.6 ± 1.67 in the control traps in the forest and 5.34 ± 1.76 in the fields. The effect of distance on the species richness of the incoming seed arrival was examined from data across all lines and sites. Based on lowest AIC_C values, a quadratic function with distance from the forest-field edge as the predictor variable and mean species richness as response was found to best describe the data (Figure 13, Tables 14 &15).

Model	Delta AIC_C	Model likelihood	AIC_C weights
Quad	0	1	0.5851
Cub	1.9789	0.3717	0.2175
Lin	3.0914	0.2131	0.1247
Exp	4.1741	0.1240	0.0725

Table 14: AIC_C weights for linear, quadratic, cubic and exponential functions with distance from the forest-field edge as the response and mean species richness as the predictor

R^2: 0.235

Variables	Value ± SE
B_0	5.917 ± 0.31
B_1	-0.0724 ± 0.023
B_2	0.0009 ± 0.0004

Table 15: Parameters values for a quadratic equation with mean species richness of seedlings and saplings recorded in paddy fields in the five abandoned village sites in Bhadra Tiger Reserve

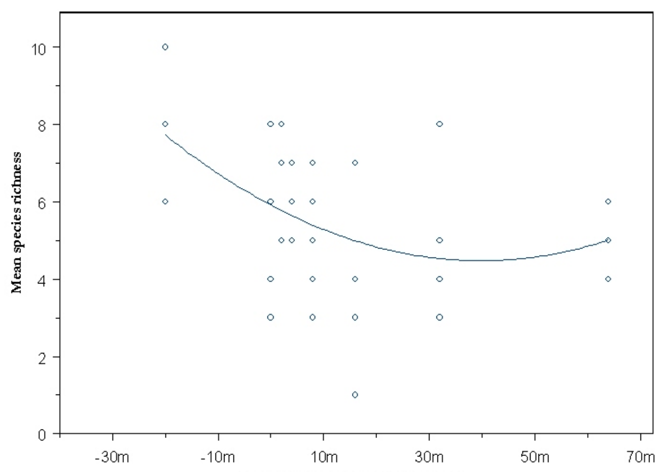

Figure 13: Species richness in seed rain with distance from the forest-field edge Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

II) Animal-dispersed seeds

A total of 706 animal-dispersed seeds of 11 species were collected during the study period. The species richness of animal-dispersed seed rain in the forest was (mean ± SD across sites) 1.6 ± 1.51 and the species richness in the fields was 1.225 ± 1.07. The number of seeds that were encountered in the adjoining forest was 109, with a density of 4.36 seeds/ m^2 / 3 months and 660 seeds were collected from the fields with a density of 3.77 seeds/ m^2 / 3 months. Data within each site i.e. data from different lines, were pooled to produce a single value of the mean seed rain over each point in each site. When the $\log_{10}$animal dispersed seeds/ m^2/ 7 fortnights were plotted against distance from forest-field edge, there was no evidence of any pattern. This is also supported by the extremely low R^2 value (0.031), as well as slope parameter (0.0037) obtained when a linear model was fit to the data (Figure 14).

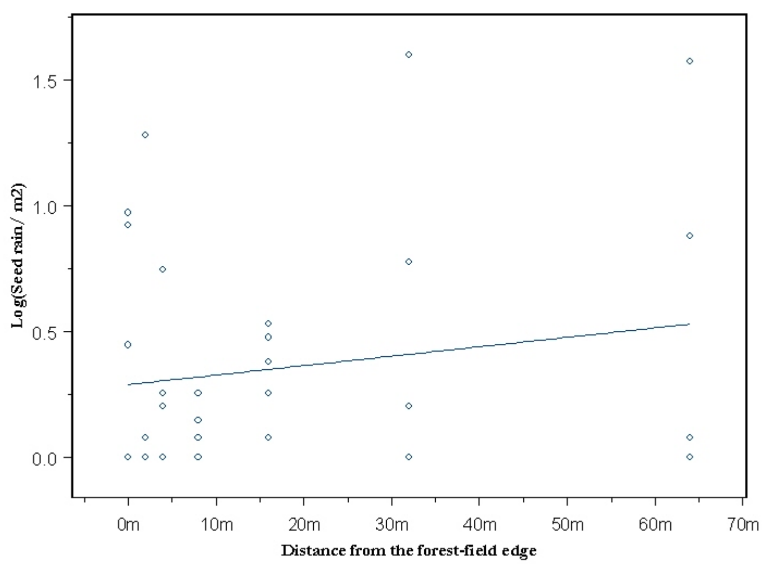

Figure 14: Animal-dispersed seed rain with distance from the forest-field edge. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

III) Bird perches

A total of 3,715 bird-dispersed seeds of 10 tree species were collected from 35 traps (from one transect in each of 5 village sites) with a density of 26.53 seeds/ m^2 / 5 fortnights from April 1^{st} to May 31^{st}, 2006.

Generalized linear models (GLM) were used to model the effects of perches on the seed rain. The response variable was $\log_{10}$seeds/ m^2/ 5 fortnights, and the predictors were i) Presence/ absence of perches (as a 2 level categorical variable) and ii) Distance from the forest-field edge (as a metric). I constructed all three possible models: (a) seed rain as a function of perches (Figure 15), (b) seed rain as a function of distance (Figure 16), (c) seed rain as a function of perches + seed rain, and (d) seed rain as a function of perches + seed rain + an interaction between perches and seed rain; and these were ranked based on AIC_C values. The best model was found to be model (a) (Table 16), though model (c) had a relatively low Δ AIC_c, indicating that presence or absence of perches had a strong effect on seed rain, while the effect of distance from edge was much weaker in the presence of perches.

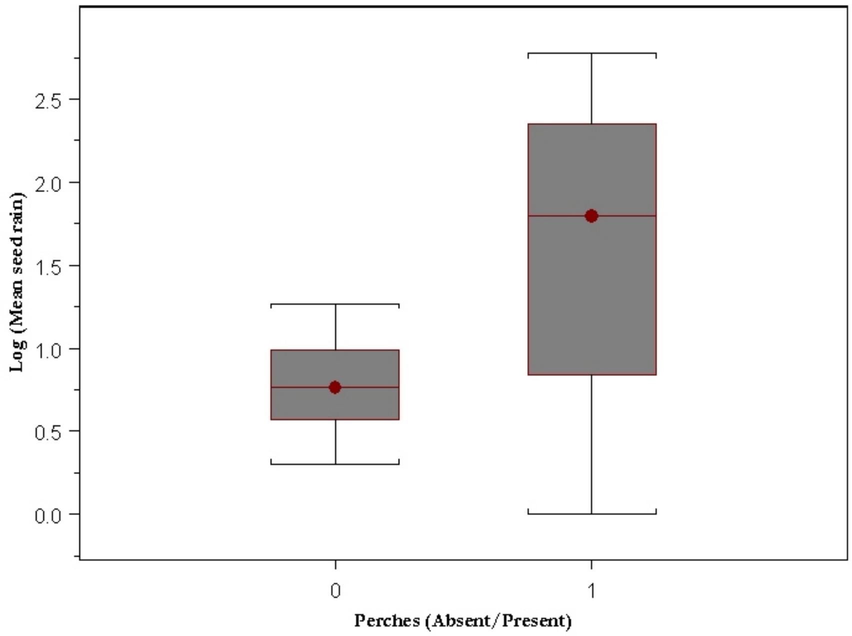

Figure 15: Seed rain comparison at sites with and without bird-perches. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

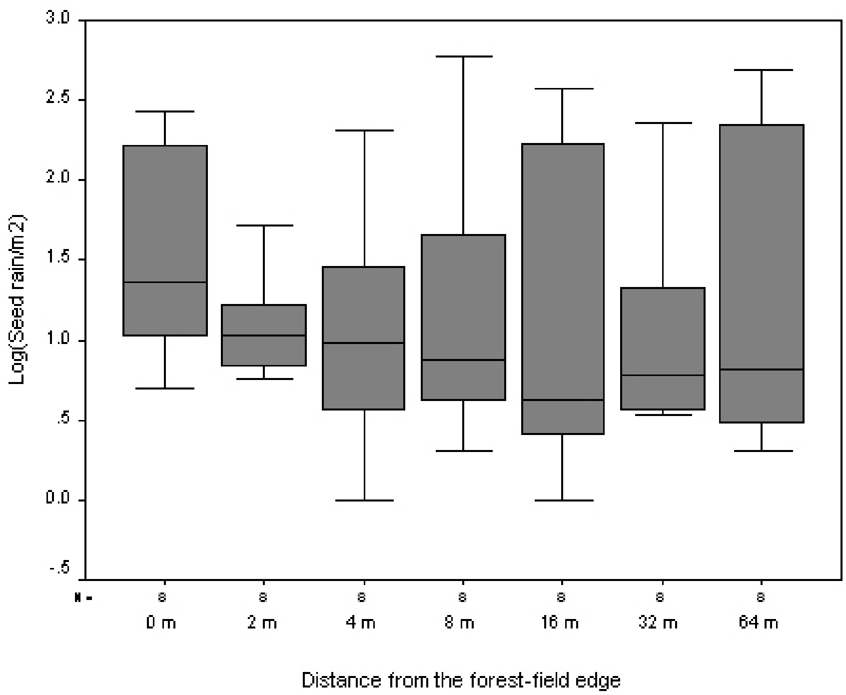

Figure 16: Seed rain at different distances from the forest-field edge. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

Model	Δ AIC_C	Model likelihood	AIC_C weights
Perch	0	1	0.731
Perch+Distance	1.9999	0.3678	0.2689
P+D+P*D	2.8361	0.2421	7.9E-05
Distance	18.2593	0.0001	7.9E-05

Table 16: AIC_C weights for the GLMs using log_{10}seed rain/ m^2/ 5 fortnights as the response and a) Perch: present/ absent, b) Distance from the forest field edge and c) Both Perch and distance from edge as predictor variables. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

IV) Soil moisture

Soil moisture data from 250 plots (across all transects and sites) was plotted on the Y-axis with distance from the field-forest edge on the X-axis. Soil moisture was found to show no clear patterns with distance from the forest-field edge as evidenced by the extremely low R^2 and slope parameter (Table 17, Figure 17).

R^2: 0.007	
Variables	Value ± SE
B_0	8.36 ± 1.143
B_1	0.0203 ± 0.0273

Table 17: Parameter values for the linear equation with % soil moisture as the response variable and distance from the forest-field edge as the predictor variable. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

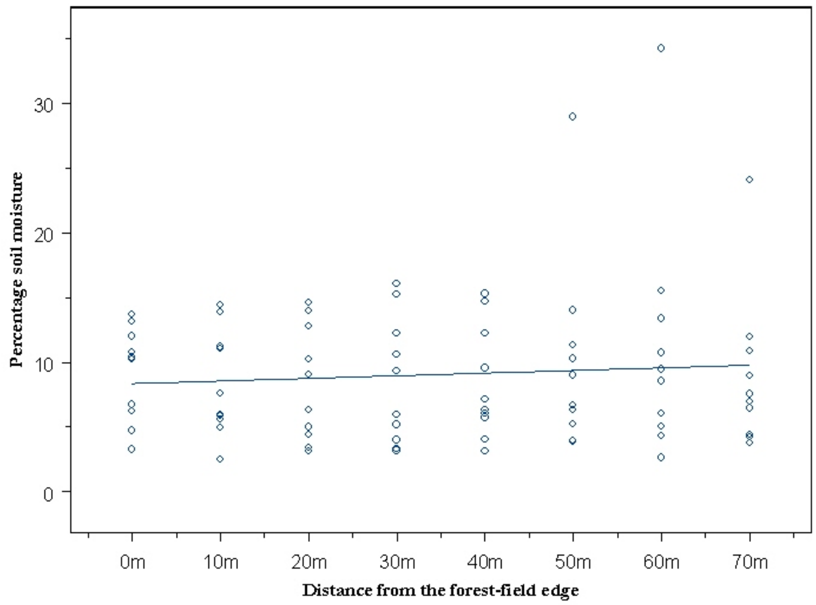

Figure 17: Percentage soil moisture across all sites with distance from the forest-field edge. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

V) Percentage cover

The cover variables collected from the 1 x 1 m plots (n=250) were plotted using the distance from the forest-field edge across the X-axis and percent mean cover on the Y-axis as a stacked bar graph (figure 18). Distance from the forest-field edge had no effect on the mean percent shrub cover across plots (Figure 19). Mean percent shrub cover was plotted against mean percent soil moisture and it was found that there was no relation between the two variables (Figure 20)

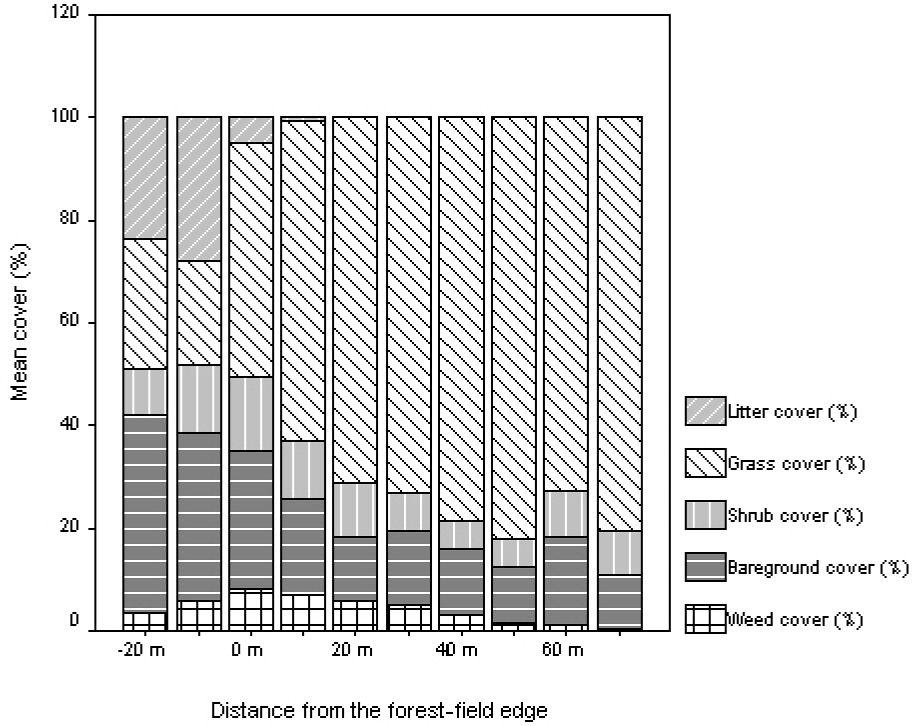

Figure 18: Average percent cover across all the plots in the five abandoned paddy fields in Bhadra Tiger Reserve

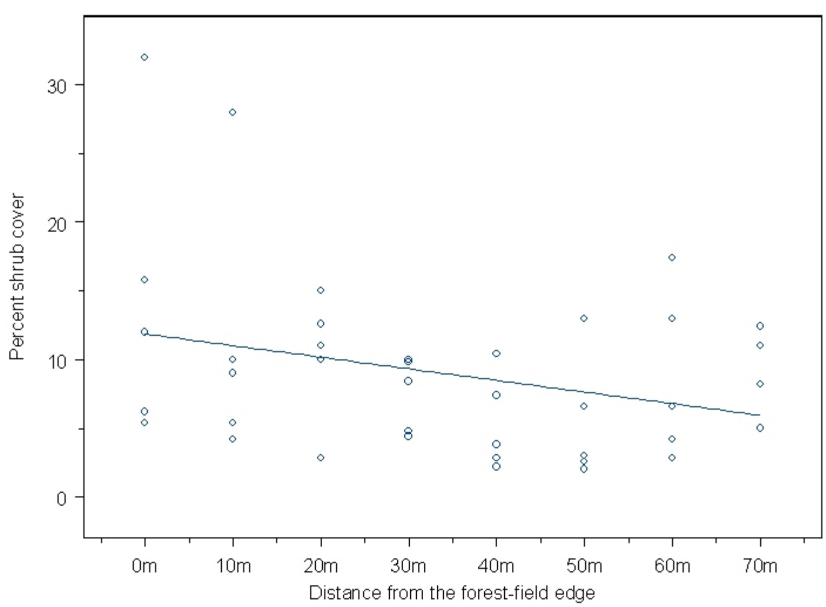

Figure 19: Average percent shrub cover with distance from the forest-field edge in plots in all the five abandoned fields in Bhadra Tiger Reserve

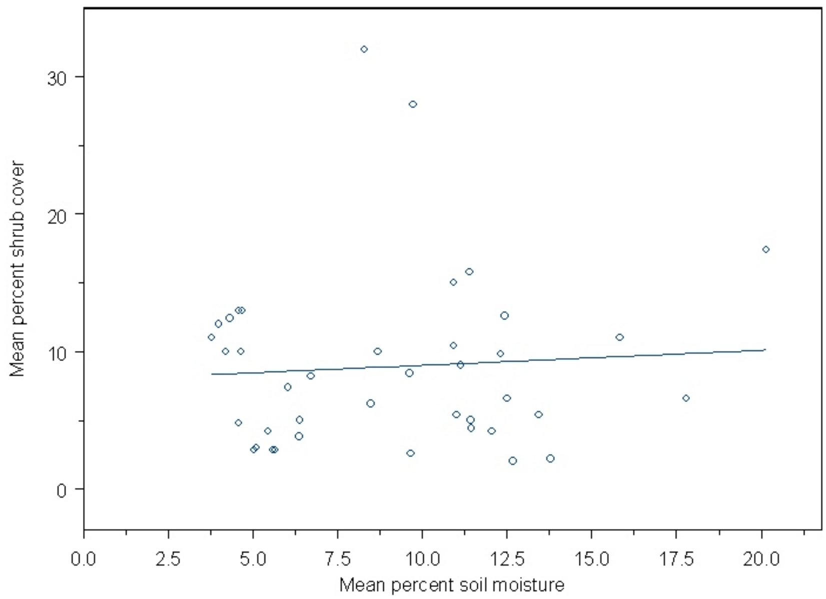

Figure 20: Mean percent shrub cover with mean percent soil moisture in plots in all the five abandoned paddy fields in Bhadra Tiger Reserve

VI) Vegetation composition

The total number of seedlings and saplings counted in the 5 x 5 m plots (250) was 447 representing 48 species. The mean seedling and sapling density in the fields was 0.815 seedlings and saplings / 25 m^2 and in the adjoining forest it was 5.68 seedlings and saplings / 25 m^2. Before constructing models, predictors were checked for multicollinearity using scatter plots (Figures 17, 19-20). To explore the possible factors determining seedling and sapling density, I built generalized linear models of seedling sapling density as a function of the following predictors, which were then assessed on the basis of lowest AIC_C value:

1) Distance from the edge

2) Percentage soil moisture

3) Percentage shrub cover

4) Distance + Percentage soil moisture

5) Distance + Percentage shrub cover

6) Percentage soil moisture + Percentage shrub cover

It was determined that the best model in the candidate set had distance from the forest-field edge as the predictor of seedling and sapling density (Tables 18-20, Figure 21). The AIC_C weights were summed for all the models containing a particular predictor, to help assess the relative importance of different predictors.

Model	**Δ AIC_C**	**Model likelihood**	**AIC_C weights**
Distance	0	1	0.490
Distance+Shrub cover	2.1417	0.342	0.168
Distance+Moisture	2.3900	0.302	0.148
Shrub cover	3.1791	0.204	0.100
Moisture	4.2653	0.118	0.058
Moisture + Shrub cover	5.2870	0.071	0.035

Table 18: AIC_C weights for different models (see text) of factors determining seedling and sapling density. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

Predictor	**Summed AICc weight**
Distance	0.8069
Shrub cover	0.3029
Moisture	0.2414

Table 19: Summed AIC weights for each predictor in the candidate model set (see text). Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve

R^2: 0. 107

Model parameter	Value ± SE
B_0	1.4055 ± 0.3119
B_1	-0.0159 ± 0.0074

Table 20: Parameter values for the generalised linear model with mean number of seedlings and saplings / 25 m^2 as the response variable and distance from the forest-field edge as predictor variable. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

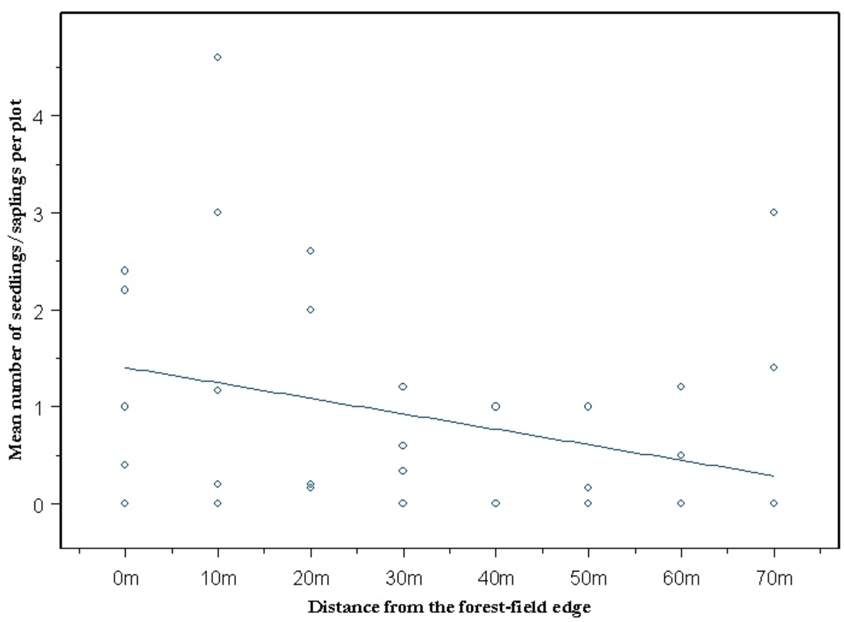

Figure 21: Seedling/ sapling density as a linear function of distance from the forest-field edge. Data from paddy fields in the five abandoned village sites in Bhadra Tiger Reserve.

Chapter IV, Discussion

Patterns of seed rain

In the abandoned paddy fields, the density and species richness of animal-dispersed seeds was found to be lower than that of wind-dispersed seeds. This pattern has been recorded in other studies as well, suggesting that wind-dispersed species are usually over-represented in pastures and fields (Cubina & Aide 2001, Holl 1999). The animal-dispersed seed density in the fields was comparable to the seed density in the adjoining forest, whereas the wind-dispersed seed density was about four times higher in the adjoining forest than in the fields. The species richness of both wind- and animal-dispersed seed rain was not very different between forest and the fields.

The findings from this study conform to those reported by Willson & Crome (1989), who found that both wind- and animal- dispersed seeds even 100 m into fields. Though wind-dispersed seed rain abundance in this study site declined with distance from the forest-field edge, seeds were found even 64 m into the fields. Habitat structure such as tree height and abiotic variables such as wind could have contributed to farther dispersal of seeds into the fields. Also, the shape of the paddy fields is such that the farthest seed rain plots in one of the lines was closer to the opposite forest-field edge. The trees from the opposite edge may have contributed to the seed rain in these plots.

Seed size and weight can also play a role in their dispersal into the fields. The patterns of seed rain with distance from forest edge for the three largest-seeded species were best described by a quadratic function, similar to the patterns of seed rain for all species taken together; patterns of seed rain for the two smaller-seeded species, on the other hand, were better described by linear functions._A quadratic function indicates a rapid decline in seed rain near the forest-field edge, with the rate of decline decreasing with increasing distance from edge. A linear function indicates that seed rain declines at the same rate over the distance range sampled, and the shallow slopes observed indicate that seeds disperse farther into the field. The differential patterns in seed dispersal as a function of seed size and weight that I observed suggest possible tradeoffs between investing in larger seeds as opposed to wider dispersal.

While some studies have found a lack of patterns in animal-dispersed seeds with distance from the forest edge (Willson & Crome 1989, Slocum & Horvitz 2000), others have found no seed dispersal by animals beyond 30 m (Aide & Caveliar 1994, Holl 1999, Cubina & Aide 2001). I found that, animal-dispersed seeds showed no patterns with distance from the forest-field edge, and found seeds even 64 m into the fields. Animal-dispersed seeds in the fields were found to have a highly clumped spatial distribution. My findings are very likely due to the presence of large mammalian herbivores in Bhadra, unlike in these other studies, most of which have been conducted in the neotropics. Large mammals probably take shelter in open areas such as abandoned fields to avoid predation by large carnivores, consequently dispersing seeds into the fields.

Bird perches

In the present study, the seed rain in plots with bird perches was about 20 times higher than the seed rain in plots without perches, and the species richness increased by about 50 %. Three of the 10 bird-dispersed species were of the genus *Ficus*, which are of considerable value to the forest as keystone species. Distance was found to play a minor role in bird-dispersed seed rain, i.e. the bird-dispersed seed rain in traps at the edge and the traps farther into the fields had similar abundance and diversity (Figure 14). Since most studies, including my own, demonstrate that seed arrival declines with increasing distance from the edge (Willson & Crome 1989, Holl 1999, Cubina & Aide 2001, Aide & Caveliar 1994), perches can play a considerable role in mitigating this limiting factor of seed arrival.

I found very little seeds dispersal by birds at perches in one of my sites (Hipla), which had many remnant trees, unlike the other 4 sites. Since bird-dispersed seed rain was significantly higher than wind-dispersed seeds in the other four open sites, artificial perches are more effective in relatively open sites.

Vegetation composition

Seedling and sapling density was five times higher in the adjoining forest than in the fields. As others have shown (Aide & Caveliar 1994, Hooper *et al.* 2005), the seedling and sapling density was found to linearly decrease with increasing distance from the edge. Factors such as seed and seedling predation, competition from existing vegetation, harsh micro-climatic conditions and low nutrient availability (Uhl 1987, Willson & Crome 1989, Holl 1998, Duncan & Chapman 1999, Chapman & Chapman 1999, Holl 1999, Cubina & Aide 2001, Aide & Caveliar 1994) have been shown to affect regeneration in fields. This study examined the effects of seed arrival, the presence of existing ground cover and soil moisture on regeneration. Amongst the factors examined, it was found that distance from the forest edge was the best predictor of seedling and sapling density, followed by the percentage shrub cover. Contrary to expectations, I found no pattern in gravimetric soil moisture content with distance from the edge in the study site. Grass cover was found to increase with distance from the forest-field edge and weed cover was found to be maximum at the edge. However, distance from the edge was found to have no effect on the shrub cover.

Implications for restoration

Considering a history of intense anthropogenic disturbance such as agriculture in the reserve and the fact that the fields were abandoned only four years ago, this study recorded considerable regeneration. Especially, closer to the forest edge, I found seedling and sapling densities as high as {mean (± SD)} 1.34 ± 1.52 individuals per 25 m^2, respectively; although the saplings may pre-date the abandonment of these clearings, the numbers of seedlings, especially, are an indicator of regeneration in the time since abandonment. Both animal-dispersed and wind-dispersed seeds and seedlings were found in the fields suggesting that the arrival of seeds, per se, may not be an impediment to forest regeneration, at least close to the forest edge. However, others have found (Aide & Caveliar 1994, Holl *et al.* 2000, Slocum 2001, Reige & Del Moral 2004) that existing grass cover can frequently be a barrier to tree regeneration, and may require restoration interventions to overcome. Other potential barriers to regeneration could include factors such as seed and seedling predation, and limiting soil nutrient availability.

A few other studies have introduced perches and shown increased seed arrival (McClanahan & Wolfe 1993, Holl 1999) into clearings and abandoned pastures. I too found that the introduction of bird perches increased the rate of seed arrival into the clearings and this effect is of increasing significance with distance from the edge. Thus, introducing perches for birds could help to accelerate vegetation recovery in abandoned clearings.

Remnant trees—like artificial perches—have been shown to considerably increase seed dispersal (Willson & Crome 1989, Duncan & Chapman 1999, Galindo-Gonzalez *et al.* 2000). They also have the added advantage of buffering harsh micro-climatic conditions (Guevara *et al.* 1992, Zahawi & Augspurger 1999) thus improving seedling survival. A judicious planting of trees, therefore, may facilitate succession in more ways than one. Native fruiting trees, especially, may serve to attract animals and birds and increase seed rain, while also ameliorating microclimatic conditions that facilitates and enhances seedling establishment and survival.

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Appendix

Checklist for tree species of seeds collected during the study period

Species	**Mode of dispersal**
Albizzia lebek	Wind
Albizzia odoratisima	Wind
Alstonia scholaris	Wind
Butea monosperma	Wind
Cassia spp	Wind
Cassia tora	Wind
Dalbergia latifolia	Wind
Dysoxylum binectarifurum	Wind
Erythrina indica	Wind
Erythrina spp	Wind
Largestromia spp	Wind
Pongamia pinnata	Wind
Pterocarpus marsupium	Wind
Tectonia grandis	Wind
Terminalia alata	Wind
Terminalia paniculata	Wind
Atlantia monophyla	Bird
Ficus glommerata	Bird / animal
Ficus mysorensis	Bird / animal
Ficus religiosa	Bird / animal
Grewia tillaefolia	Bird
Ziziphus xylocarpus	Bird
Artocarpus hirsuta	Animal
Elaeocarpus tuberculatus	Animal
Gmelina arborea	Animal
Mangifera indica	Animal
Melia dubia	Animal
Spondias mangifera	Animal
Sterespermum personatum	Animal
Syzigium cumini	Animal
Terminalia bellerica	Animal
Trewia polycarpa	Animal

Checklist for seedling and sapling species recorded from the abandoned paddy fields in five village sites in Bhadra Tiger Reserve

Bauhinia malabarica
Albizzia odoratissima
Butea monosperma
Cassia fistula
Dalbergia latifolia
Dillenia pentagyna
Dyospyros montana
Ficus exaspirata
Ficus glomerata
Grewia tilaefolia
Helectris isora
Hydnocarpus pentandra
Erythrina indica
Largestromia spp
Stereospermum personatum
Mangifera indica
Erythrina spp
Persea macrantha
Pongamia pinnata
Mallotus spp
Psidium gujava
Pterocarpus marsupium
Schleichera oleosa
Syzigium cumini
Terminalia elata
Terminalia paniculata
Bridelia spp
Tamarindus indicus
Ziziphus xylocarpus