Forest Ecology and Management 257 (2009) 1966–1975

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Spatial distribution, advanced regeneration and stand structure of Nepalese Sal (*Shorea robusta*) forests subject to disturbances of different intensities

Indra Prasad Sapkota *, Mulualem Tigabu, Per Christer Odén

Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, PO Box 49, SE-230 53, Alnarp, Sweden

ARTICLE INFO

Article history:
Received 19 October 2008
Received in revised form 1 February 2009
Accepted 4 February 2009

Keywords:
Nepal
Spatial distribution
Disturbance ecology
Sal forests
Morisita index

ABSTRACT

We investigated the spatial distribution, advanced regeneration and stand structure of five *Shorea robusta*-dominated forests in 25 1-ha plots subject to disturbances of different intensities. We aim to elucidate the relationships of advanced regeneration and spatial patterns of the tree species with degree of disturbance magnitude. Sixty-seven tree species were recorded in the forest plots; 41 species were found in the least disturbed forests, while only 10 species were found in the heavily disturbed forests. We found 5320 trees with >1.5 cm diameter at breast height, in total, and found that moderately disturbed forests contained the highest advanced regeneration (sapling)/pole densities. No significant differences were observed in stem basal area among forests. The overall stand density changed quadratically across the disturbance gradient. A strong inverse relationship was found between the overall stand density and diameter class in the least disturbed and moderately disturbed forests. Ten species showed variation in their dispersion patterns across the disturbance gradient. Most of the socio-economically important tree species analyzed showed little or no regeneration in the least and most heavily disturbed forests. Individual species showed different responses to disturbance ranging from ‘tolerant’ (*Shorea robusta*, *Lagerstroemia parviflora* and *Symplocos* spp.) to ‘sensitive’ (*Trewia nudiflora*, *Adina cardifolia* and *Terminalia alata*). We concluded that moderate disturbance intensity not only ensures high stand density, but also enhances the advanced regeneration of socio-economically important tree species and affects their dispersion patterns. Future management strategy must balance the consumptive needs of the local community with those of species conservation by allowing regulated access to the forests.

1. Introduction

Forest disturbance can alter environmental conditions by changing light availability and soil conditions (Fredericksen and Mostacedo, 2000). Disturbance also influences processes that can either augment or erode the ecological functions of a forest community (Sagar et al., 2003). Both natural and human disturbances influence forest dynamics and tree diversity at local and regional scales (Hong et al., 1995; Hubbell et al., 1999; Sheil, 1999; Ramirez-Marcial et al., 2001). However, the biology of specific species (such as their life history traits, physiology and behavior) also influence post-disturbance forest regeneration (Lawes et al., 2007).

Generally, post-disturbance changes in regeneration, dominance and diversity of woody species are related to characteristics of the overall disturbance regime, including the intensity, frequency and scale of disturbances (Kennard et al., 2002; Mori and Takeda, 2004; Zhu et al., 2007). Frequently, however, individual disturbance factors (e.g., selective logging) have been highlighted in attempts to explain the structural attributes of forests (Vetaas, 1997; Nagaike et al., 1999; Ramirez-Marcial et al., 2001; Sapkota et al., 2009). Despite multiple factors simultaneously altering ecosystem functioning, frequent and fluctuating disturbance factors (e.g., grazing, browsing, fuel-wood and fodder collection) have often been overlooked in explanations of post-disturbance changes in forest ecosystems.

Connell (1978) highlighted the spatio-temporal fluctuations observed in disturbance e.g., ‘type’ and ‘intensity’ of disturbance. He linked community richness with ‘time since’, ‘frequency of’ and ‘size of’ disturbance and proposed that disturbance of moderate intensity may support species diversity. In line with the Connell’s proposal, Sheil and Burslem (2003) argued that excessive disturbance leads to the loss of late-successional species, whereas too little leads to competitive exclusion of species adapted to colonize sites immediately following a disturbance. Therefore, an intermediate disturbance regime enables species to co-exist (Molino and Sabatier, 2001; Sheil and Burslem, 2003). However, Hubbell et al. (1999) argued that dispersal and recruitment limitations normally outweigh the role of disturbance. These authors emphasized that

---

* Corresponding author. Tel.: +46 40 41 53 97; fax: +46 40 41 53 98.
E-mail addresses: indra.sapkota@genfys.slu.se, isapkota@gmail.com (I.P. Sapkota), mulualem.tigabu@genfys.slu.se (M. Tigabu), per.oden@genfys.slu.se (P.C. Odén).

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.02.008

although disturbance in mature forests does increase the number of available niches, these niches may not necessarily be filled by the most adapted species, but by species whose propagules are sufficiently abundant at the right place and time.

Although the relationship between disturbance and species richness has extensively been explained (Vetaas, 1997; Sheil, 1999; Vandermeer et al., 2000; Molino and Sabatier, 2001; Sheil and Burslem, 2003), the studies that elucidate how disturbances influence stand structure, species composition and regeneration of tree species are very limited (Sapkota et al., 2009). In addition, these studies have produced contrasting conclusions. Some authors claimed that structure of a plant community in many natural ecosystems is largely determined by a disturbance (Rao, 1990; Kennard et al., 2002), while others emphasized the biology of specific species to be the main responsible factor (Pickett and White, 1985; Lawes et al., 2007). It has also not been well understood whether or not tree species exhibit micro-site variability following a disturbance for their niche differentiation (Barik et al., 1992).

Shorea robusta forests (hereafter referred to as Sal forests) are among the most disturbed types of forest in Southeast Asia (Sapkota et al., 2009), due to their high timber value and socio-economic importance for fodder, fuel-wood, leaf litter and minor forest products. The frequent and fluctuating type of disturbance in such forests, and its causes, have been investigated for decades in India (Pandey and Shukla, 2001; Sagar et al., 2003) and Nepal (Webb and Sah, 2003; Timilsina et al., 2007; Sapkota et al., 2009). Although these studies have highlighted the differential responses of tree regeneration to disturbance, further knowledge of the relationship between the degree of disturbance and tree species regeneration would be highly valuable. An understanding of this relationship is essential for developing forest management strategies in countries like Nepal, where more than 80% of the rural population (Webb and Sah, 2003) depends on such forests for subsistence needs, including fuel-wood, livestock feed, animal bedding, compost, and other minor forest products (Gautam and Devoe, 2006).

In this study we aimed to elucidate the relationships between frequent, fluctuating disturbance and stand structure, dispersion patterns and the advanced regeneration of selected species in Sal forests. Specifically, we propose that (i) mild levels of disturbance promote higher stand density; (ii) disturbance leads to changes in species dispersion patterns; and (iii) advanced regeneration of important tree species is enhanced by mild disturbance.

2. Materials and methods

2.1. Study area

This study was conducted in five seasonally dry deciduous Sal forests (Jackson, 1994) in Nawalparansi district of Nepal (Fig. 1). The location and elevation of these forests, which represent climatic climax vegetation in each locality (Anon., 1994; Webb and Sah, 2003), are shown together with current management regimes

Table 1
Geographical location and management regimes of study forests.

Forests	Latitude	Longitude	Elevation (m)	Management regime
Sushta Triveni	27° 28.342′	83° 56.495′	105–175	Buffer zone forest (BZF)
Chautari	27° 42.948′	84° 14.481′	305–360	Community forest (CF)
Nandan	27° 42.606′	84° 21.544′	195–295	Community forest (CF)
Danda Chisapani	27° 42.948′	84° 03.534′	160–186	State managed forest (SMF)
Shree Shanti	27° 38.490′	84° 08.667′	170–200	Buffer zone forest (BZF)

The management responsibilities and ownership are recently assigned to the local community in CF and BZF. Government owns and manages the entire forests in SMF. Buffer zone is a forest area between settlements and the core protected forests.

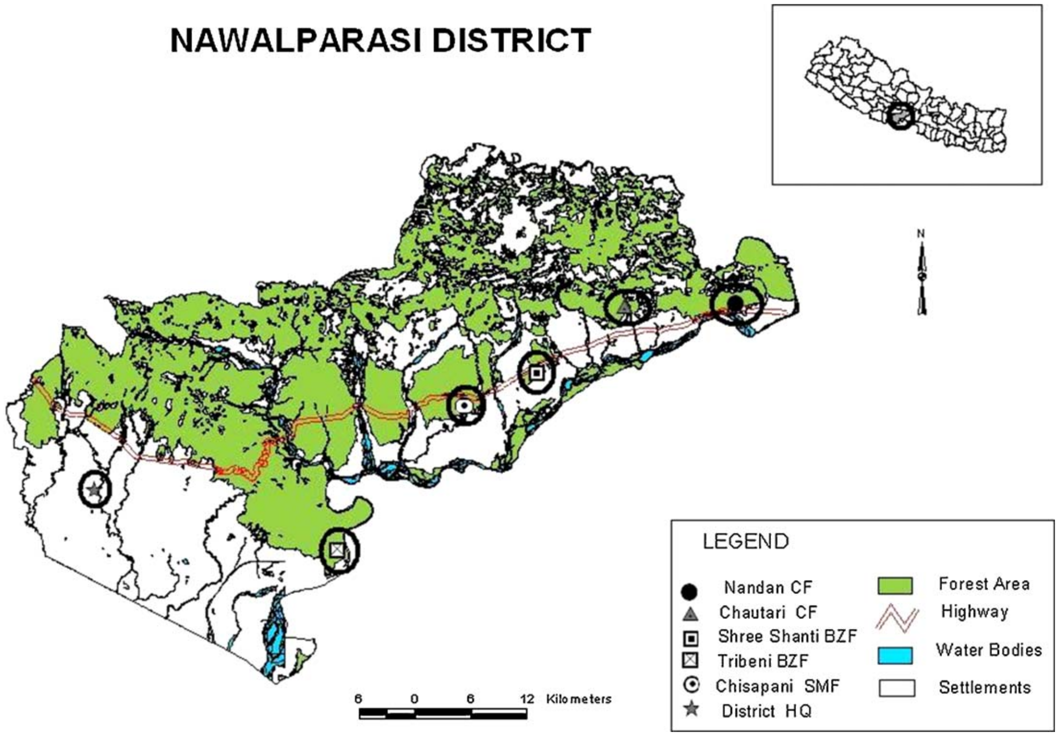

Fig. 1. Locations of five seasonally dry deciduous Sal forests.

Table 2
Physico-chemical properties of study forests (Mean ± SE).

Soil parameters	Forests				
	Sushta Triveni	Chautari	Nandan	Danda Chisapani	Shree Shanti
pH	6.3 ± 0.30	5.2 ± 0.07	5.2 ± 0.10	5.5 ± 0.10	5.2 ± 0.09
Organic matter (%)	0.79 ± 0.19	2.1 ± 0.15	1.2 ± 0.13	2.0 ± 0.2	1.5 ± 0.21
N (%)	0.06 ± 0.01	0.13 ± 0.01	0.28 ± 0.2	0.13 ± 0.01	0.26 ± 0.15
P (kg/ha)	12.2 ± 0.4	3.0 ± 0.5	4.1 ± 1. 1	26.1 ± 9.7	18.6 ± 5.7
K (kg/ha)	173.0 ± 49.3	413.2 ± 40.8	236.0 ± 73.6	471.2 ± 54.4	346.1 ± 20.0
Sand (%)	52.4 ± 3.1	41.9 ± 1.3	47.3 ± 3.9	40.2 ± 5.5	43.4 ± 2.3
Silt (%)	36.2 ± 3.8	35.7 ± 1.1	33.6 ± 1.8	34.2 ± 2.9	38.0 ± 1.9
Clay (%)	11.4 ± 1.01	22.4 ± 1.07	19.1 ± 3.4	25.6 ± 3.5	18.6 ± 1.9
Moisture (%)	6.3 ± 0.9	12.3 ± 1.3	7.1 ± 1.1	11.0 ± 1.0	11.7 ± 1.2
Type	Sandy	Sandy-clay loam	Sandy-clay loam	Loam	Loam

in Table 1. The study forests are growing on an alluvial plain with similar geological characteristics to the Gangetic plain of India in the south, while the underlying sediments originate from tertiary Siwalik material in the north (Anon., 1994). The Siwalik hills are composed of coarsely bedded stones, crystalline rocks, clays and conglomerates. The physico-chemical properties of the soil (from 0 to 10 cm depth) in each forest are shown in Table 2. The climate in the area is tropical to sub-tropical, as shown by the climatic data presented in Fig. 2. A typical year can be divided into three main seasons: cold, hot and rainy. May and June have the highest mean maximum temperature (34.6 °C), while the coldest months are December and January (9.9 °C). Maximum rainfall occurs during the monsoon season (June–September) with an average monthly rainfall of 531.3 mm. Dew falls from December to February.

Prior to 1963, the forests in the study area were intact and near 'pristine' with high faunal and floral diversity. Later, malarial eradication programs, construction of the East–West national highway and political disturbances reduced the forest cover considerably. The continuous flow of migrating people from the hills to these areas has caused further forest degradation and encroachment. According to the forest management plan for this region (Anon., 1994), the annual deforestation rate between 1964 and 1990 was 2–2.4%. In this 25-year period, approximately half of the forest area in the district was either degraded or converted to other land uses. Recently, the management and ownership rights of some forests have been transferred from the state back to the local communities. Although protection rules have been imposed following this transfer of ownership, no specific management tools have been applied in these forests. All forests are managed with the same approach, of protection with selective logging of dead and diseased trees. Moreover, no major changes in forest use patterns have been observed following the ownership change.

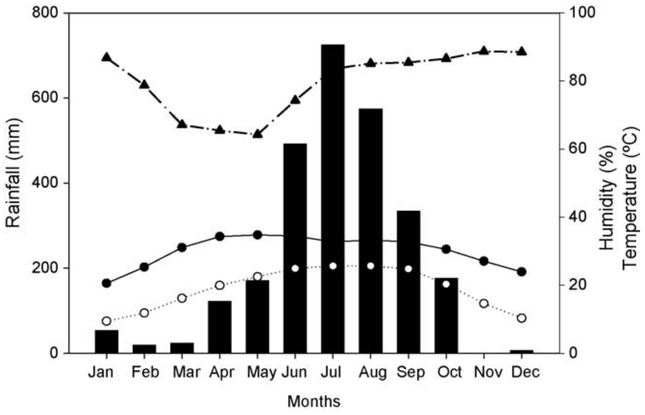

Fig. 2. Rainfall, relative humidity and temperature data for the study area from January to December (mean of years 2003–2005): average rainfall (vertical bars); relative humidity (triangles); mean maximum temperature (points); and mean minimum temperature (circles).

2.2. Sampling and inventory

Five sample plots were selected in each of the five forests using satellite images and field observations. All forests were ranked according to the degree of disturbance they have been subjected to. Detailed inventories for each forest were carried out from October 2006 to March 2007, using the quadrat method. In each forest, a constant azimuth (320°, 360°, 40°, 300° and 20° for the five forests shown, respectively, in Table 1) was chosen and a transect line was laid out. Using the satellite images, each azimuth for each forest was set towards the forest core zone from corresponding settlements, and five 1-ha plots were established along the right-hand side of each transect, at successive 200 m intervals from the settlements. Each 1-ha plot was then divided into 25 sub-plots (each 20 m × 20 m) for sampling individuals with >20 cm diameter at breast height (dbh). A square quadrat of 25 m^2 was also laid out at the left corner of each sub-plot for sampling individuals of tree species only with 1.5–20 cm dbh. The dbh of each individual was measured using a digital caliper and a D-tape (when possible). Based on the dbh of each individual, we grouped individuals of tree species into three categories: advanced regeneration or sapling (1.5–10 cm dbh), pole (>10–20 cm dbh) and tree (> 20 cm dbh). The dbh of some buttressed trees was measured above the buttress point. Species were identified *in situ* when possible, and by comparison with voucher specimens from the National Herbarium.

2.3. Assessment of disturbance

All of the forests had been subjected to natural and/or anthropogenic disturbance regimes of varying intensities. Prior to the inventory, all possible disturbance regimes and their severity were discussed with local forest users. All disturbance regimes and their intensities were then identified, and their indicators or sources were recognized. The major sources or indicators of disturbance that were believed to occur in a frequent and fluctuating manner, and showed multiple and simultaneous effects on vegetation ecology, were taken into account. Individuals damaged by windthrow, harvesting, cutting, lopping, breakage, browsing, uprooting, and/or damage associated with crown openness, footpaths, cart trails, animal feces and wallowed or disturbed soil, were considered to have experienced major disturbance. Harvesting, illegal cutting and windthrow were more common in adult individuals, while lopping, breaking and (in a few cases) illegal cutting were mainly associated with saplings and poles. In contrast, browsing, lopping and uprooting were associated with seedlings. No major fire disturbances have previously been observed in these forests, thus not considered in this study. During the forest inventory, all individuals showing signs of damage were identified and counted, and their collar diameters were measured in the same sub-plots and quadrats. 'Time since' disturbance was estimated and categorized as 'recent' (<2 years), 'old' (>2 years to <10 years) or 'very old' (>10 years). These categories were based on visual inspection of the bark, stem and leaf residues around the stumps, stump freshness, stump color, termite mounds and cracks in the remaining stumps. Crown openness was estimated using a densiometer. Disturbance due to herbivores was estimated by counting the number of wallowed and/or disturbed spots (e.g., by rhinos, wild pigs, deer, rodents, hedgehogs etc.) and animal feces (as indicators of their presence). Footpaths and trails were measured using a linear tape.

A modified method of Sagar et al. (2003) was used to estimate a disturbance impact factor (DIF). The DIF was derived from the relative impact of major disturbance sources or indicators for each forest (see Sagar et al., 2003 for detail method). DIF values for browsing, cutting, lopping, breaking and uprooting were obtained from estimates of relative disturbed densities and basal areas, defined as the ratio of total disturbed density and basal area of seedlings, saplings, poles and trees to their total density and basal area in each forest. The forests with the lowest values were assigned an impact factor of 1 for each disturbance indicator. For other forests, the relative impact factor was calculated as the ratio of the relative disturbed density and basal area of the respective forests to that of the forest with the lowest value. The impact factor was also calculated according to 'time since disturbance' for each disturbance indicator. The relative impact factor of other disturbances (crown openness, herbivory and footpath/trails etc.) was also estimated by assigning 1 to a forest with the lowest number of cases and proportionally higher values to the other forests. By summing the impact factors for each disturbance source, the forests were placed along a disturbance gradient from I (least disturbed) to V (heavily disturbed) (Table 3).

2.4. Data analysis

The total number of species, the number of species represented by a single individual and the number of quadrats with more than 15 individuals in each forest, were calculated. For each growth form (advanced regeneration, pole and adult tree), stem density and basal area data were calculated and subjected to one-way ANOVA to examine significant differences in these variables among forests. Means that exhibited differences were compared using Tukey's test with a 5% probability significance threshold. While performing the one-way ANOVA, missing data (of which there were very few) were substituted with average values in order to assure a plot-wise balanced design. The effect of disturbance on advanced regeneration and their establishment of some selected socio-economically important tree species of high fodder, fuelwood, timber and/or medicinal values were analyzed by examining the density of advanced regeneration and poles. Since many of the plots did not contain these species (except *S. robusta*), parametric tests would have been difficult to perform, due to an unbalanced design, therefore a pair-wise Mann–Whitney *U* test was performed to compare the density of advanced regeneration and poles among forests (Zar, 1999). In addition, a number of parametric tests were performed to examine the impact of disturbance on the *S. robusta* population, due to its frequent occurrence in all the sample plots.

The dispersion of each species was studied using the standardized form of Morisita's index (Krebs, 1999) in order to determine if any significant changes occurred in the dispersion patterns of species with respect to disturbance. We concluded that changes or shifts in the dispersion pattern of a species had occurred if it showed a dissimilar pattern of dispersion along the disturbance gradient. At the scale of a 5-ha plot, the index was calculated for species with ≥ 5 individuals in each forest found in at least two sampling plots. To calculate this index, the Morisita's index of dispersion (I_d) was first calculated, along with two critical values, the uniform index (M_u) and the clumped index (M_c). The calculations are performed as follows:

$$I_d = n\left[\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x}\right] \quad M_u = \frac{\chi^2_{0.975} - n + \sum x}{(\sum x) - 1} \quad M_c = \frac{\chi^2_{0.025} - n + \sum x}{(\sum x) - 1}$$

where n is the sample size (5 × one-ha plots), x is the number of individuals, $\chi^2_{0.025}$ and $\chi^2_{0.975}$ are the values of chi-squared with $(n-1)$ degrees of freedom that have 2.5% or 97.5% of the area to the right. The standardized Morisita's index (I_p) is then calculated by one of the four following formulae:

(a) When $I_d \geq M_c > 1$,

$$I_p = 0.5 + 0.5\left[\frac{I_d - M_c}{n - M_c}\right]$$

(b) When $M_c > I_d \geq 1$,

$$I_p = 0.5\left[\frac{I_d - 1}{M_u - 1}\right]$$

Table 3
Estimated disturbance impact factor (DIF) for each forest.

Sources/indicators of disturbance	Forests				
	Shusta Triveni	Chautari	Nandan	Chisapani	Shree Shanti
Browsing etc. (seedling density)	1	4	6	5.9	5.5
Lopping etc. (sapling/pole density)[a]	2.6	6.4	13.8	8.8	23
Lopping etc. (sapling/pole stump basal area)[a]	2.5	4.5	18.4	9.9	9.4
Harvesting etc. (adult tree density)[a]	3	7.1	7	16	8.7
Harvesting etc. (adult tree stump basal area)[a]	3	6	8.2	25.8	10.9
Crown openness	1	1.2	1.3	1.4	1.2
Wild-lives and herbivores	14.1	15.7	3.5	1	32.8
Foot path and trails	1	31.6	30.1	34.3	64.4
Animal feces	1	3.7	2.3	1.3	5.1
Total	29.2	80.2	90.6	104.4	161
Disturbance category/gradient	I	II	III	IV	V

[a] Impact factor for these disturbances was first computed for recent, old and very old groups separately and then summed up.

Table 4
The stand structure of seasonally dry Sal forests along a disturbance gradient (mean ± SE). Means followed by the same letter across rows are not significantly different.

Structural attributes	Disturbance gradient				
	I	II	III	IV	V
Advanced regeneration/pole density (no./ha)	1066 ± 70a	2263 ± 186b	2744 ± 142c	2720 ± 175c	1590 ± 101d
Adult trees density (no./ha)	101 ± 4a	45 ± 8b	88 ± 7a	54 ± 6b	54 ± 4b
Total stem density (no./ha)	1167 ± 81a	2308 ± 218b	2831 ± 55c	2774 ± 183c	1644 ± 123d
Adult tree basal area (m^2/ha)	15.5 ± 1.4a	19.3 ± 3.5a	12.5 ± 1.6a	15.8 ± 1.3a	15.7 ± 1.9a
No. of species with single individual	12	14	8	6	5
No. quadrats with >15 individuals	1	14	22	8	1

(c) When $1 > I_d > M_u$,

$$I_p = -0.5\left[\frac{I_d - 1}{M_u - 1}\right]$$

(d) When $1 > M_u > I_d$,

$$I_p = -0.5 + 0.5\left[\frac{I_d - M_u}{M_u}\right]$$

I_p values range from −1 to +1. A value of zero indicates a random dispersion pattern, a value higher than zero indicates a clumped pattern, and a value below zero indicates a uniform pattern.

For all growth forms combined, curve estimation was performed to examine the density (y) and diameter (x) relationships for each forest. This was also repeated for adult trees. Log-transformation of the stem density was used where appropriate. The relationship between the overall stem density (y) and DIF (x) and between the advanced regeneration/pole density of *S. robusta*

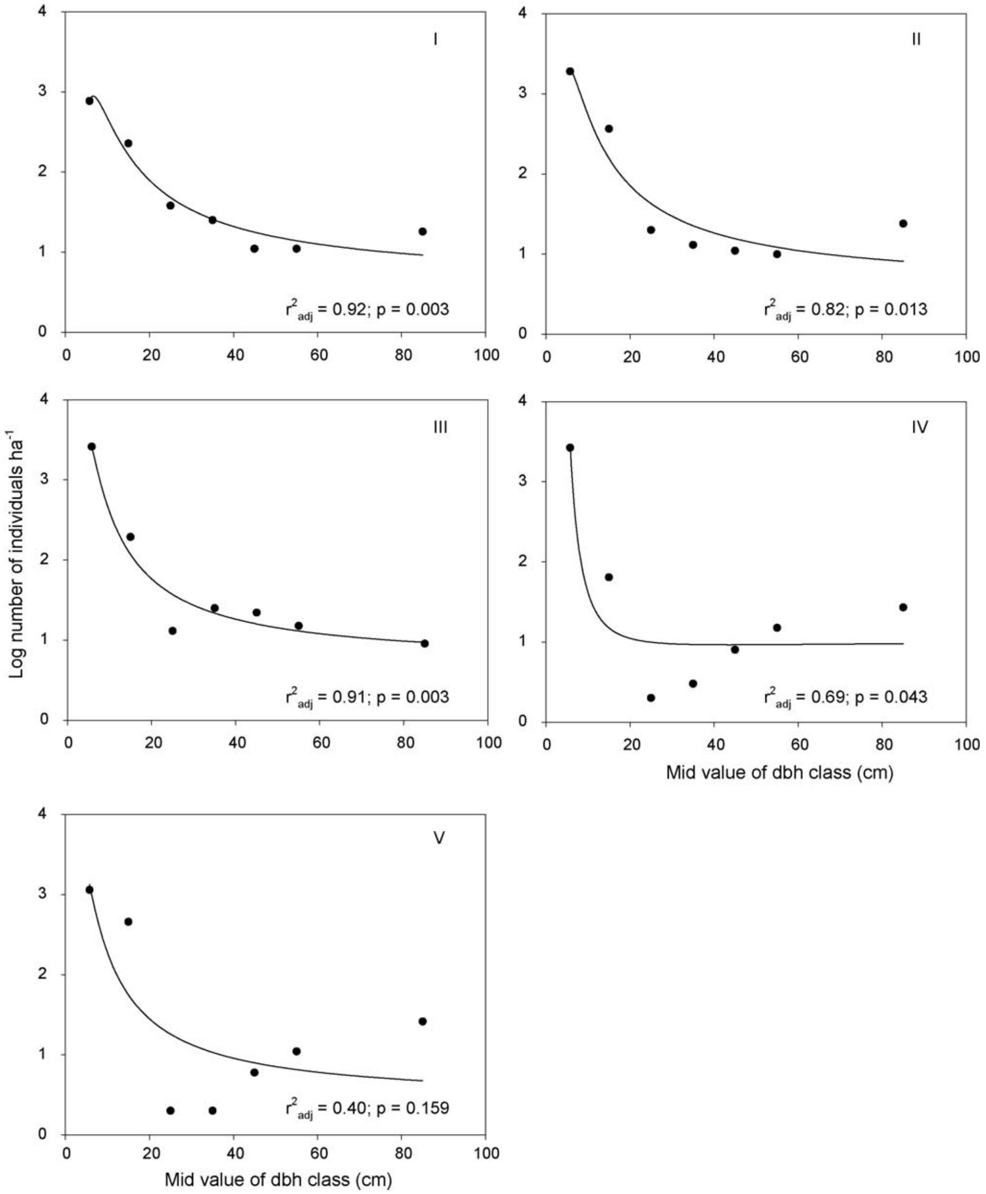

Fig. 3. Relationship between mid value of seven dbh classes and stand density in five forests. Roman numerals assigned in five graphs represent least disturbed (I) to severely disturbed (V) forests.

(y) and DIF, were further examined by curve fitting. A linear model was fitted to examine the relationship between the frequency of occurrence of *S. robusta* in quadrats (y) and DIF (x). All statistical analyses were performed using SPSS version 15 (SPSS for Windows, Chicago: SPSS Inc.).

3. Results

3.1. Stand structure and advanced regeneration

We found 67 species representing 60 genera and 37 families in the five seasonally dry *S. robusta*-dominated forests; of which 41, 37, 28, 22 and 10 species were found across the disturbance gradient types from I to V, respectively. Some species were represented by only a single individual, which were large and found in the least and moderately disturbed forests (I and II) (Table 4). The total number of stems recorded in all forests was 5320, of which 3254 individuals were advanced regeneration and poles and 1966 were adult trees. Significant variations in the mean stem density of advanced regeneration/poles ($F_{[4,620]} = 27.95$; $p < 0.0001$), adult trees ($F_{[4,620]} = 25.66$; $p < 0.0001$) and total population ($F_{[4,620]} = 21.40$; $p < 0.0001$) were observed among forests. The least (I) and the most heavily disturbed (V) forests had significantly lower densities of advanced regeneration/poles, as well as total stem density, than forest types II, III and IV. The density of adult trees was higher in the least (I) and moderately disturbed (III) forests, compared with the other forests (Table 4). The number of individuals varied from 1 to 33 per quadrat, and the

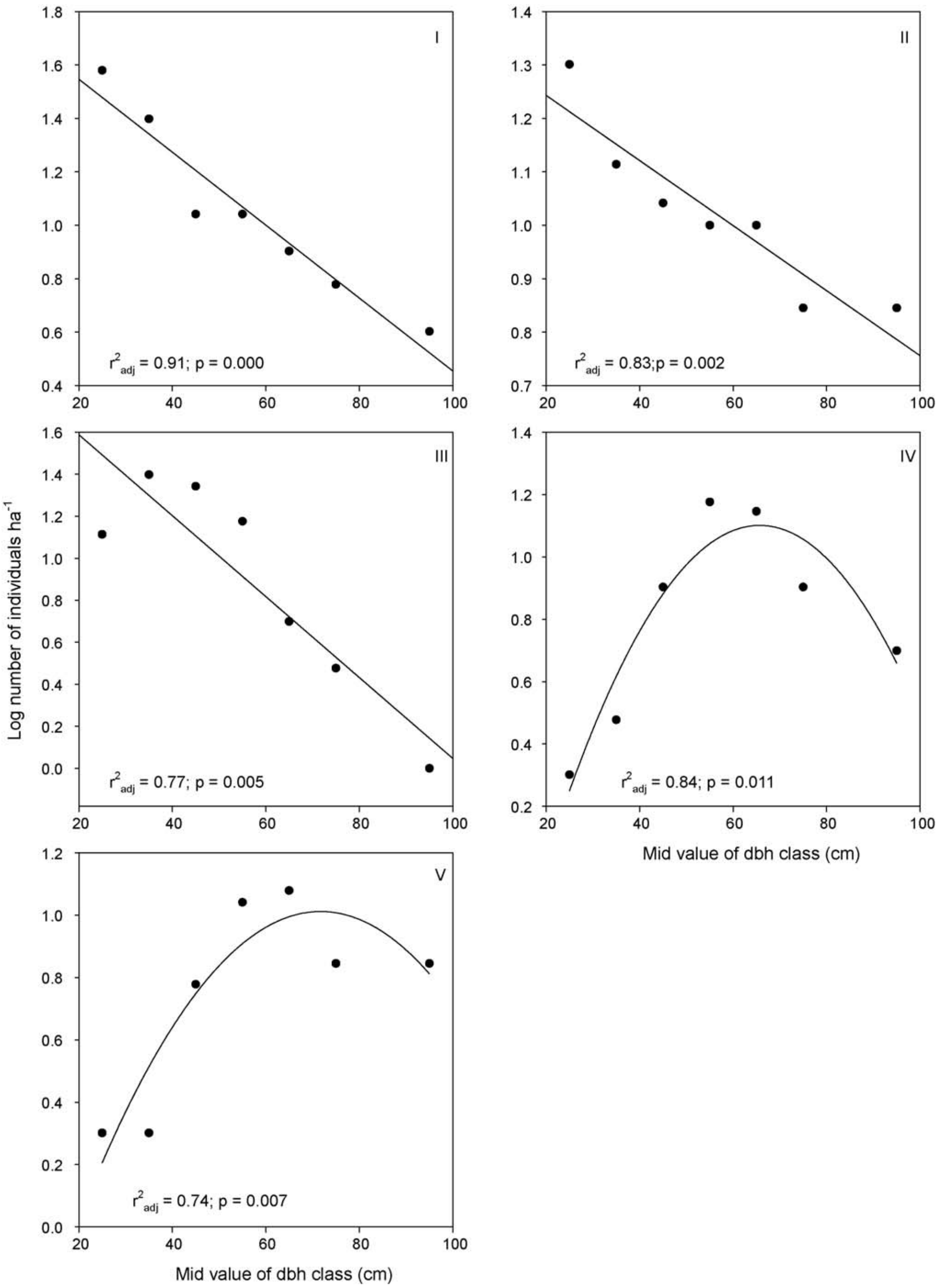

Fig. 4. Relationship between mid value of seven dbh classes and density of adult trees in five forests. Roman numerals assigned in five graphs represent least disturbed (I) to severely disturbed (V) forests.

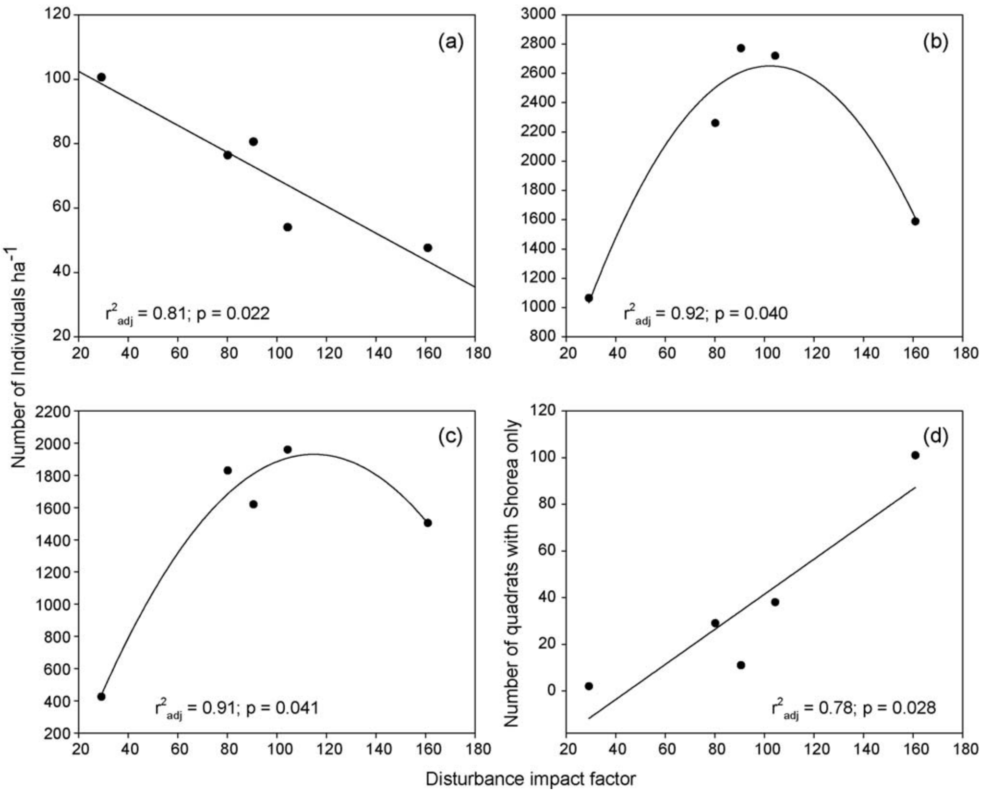

Fig. 5. Relationships of disturbance impact factor with (a) density of adult trees; (b) overall stand density; (c) advanced regeneration/pole density of *Shorea robusta*; and (d) frequency of *Shorea robusta* population occupancy.

number of quadrats with more than 15 individuals was substantially lower in the least (I) and the most heavily disturbed (V) forests, compared with the moderately disturbed (II and III) forests (Table 4). With regard to stand basal area, no significant variation was observed ($F_{[4,620]} = 1.865$; $p = 0.123$) across the disturbance gradient (Table 4).

An inverse relationship was found between the overall stand density and the diameter class in all forests, except type V (Fig. 3). For adult trees, the diameter–density relationship differed among forests. For forest types I–III, the density of adult trees was linearly related with diameter class, while for forest types IV and V, the relationship was quadratic (Fig. 4). Regression analyses also revealed that the density of adult trees linearly declined across the disturbance gradient (Fig. 5a), while the change in overall stand density across the disturbance gradient was quadratic (Fig. 5b). An analysis of species occurrence showed that *S. robusta*, *Lagerstroemia parviflora* and *Symplocos* spp. were present in all 25 of the 1-ha plots, while *Trewia nudiflora* only occurred in one sampling location. Further analysis of the most dominant species, *S. robusta*, showed that the change in its advanced regeneration/pole density across the disturbance gradient was quadratic (Fig. 5c), while its occupancy increased linearly as the intensity of disturbance increased (Fig. 5d).

3.2. Spatial patterns of selected tree species

Of 14 species appeared in more than two disturbance intensities, 10 showed changes in their dispersion patterns with changes in disturbance intensity (Table 5). *Terminalia alata*, *Sapium insigne*, *Mallotus philippensis* and *Pterospermum lanceaefolium* showed consistent dispersion patterns, while those of *Careya arborea* and *Cassia fistula* changed from clumped to uniform, and that of *Adina cardifolia* changed from clumped to random, along the

Table 5
Dispersion pattern and abundance of species across a disturbance gradient.

Species	Disturbance gradient				
	I	II	III	IV	V
Shorea robusta	297^{c}	815^{c}	834^{c}	875^{r}	704^{c}
Lagerstroemia parviflora	119^{c}	30^{u}	32^{c}	14^{u}	10^{c}
Symplocos spp.	25^{u}	16^{c}	14^{u}	82^{c}	8^{u}
Terminalia alata	35^{c}	19^{c}	45^{c}	37^{c}	
Semecarpus anacardium	35^{u}	15^{c}	62^{c}	22^{c}	
Eugenia operculata		6^{u}	10^{c}	9^{u}	
Syzigium cumini		13^{u}	50^{c}		
Mallotus philippensis	58^{c}	67^{c}			
Adina cardifolia	5^{c}		10^{r}		
Careya arborea		13^{c}		6^{u}	
Pterospermum lanceaefolium	6^{u}		8^{u}		
Sapium insigne		10^{u}		17^{u}	
Cassia fistula		14^{c}		11^{u}	
Cornus oblonga			5^{r}	22^{c}	
Anogeissus latifolius	33^{c}				
Anthocephalus cadamba		11^{c}			
Myrsine semiserrata			7^{u}		
Mariscus sumatrensis	22^{c}				
Acacia catechu	14^{c}				
Gmelina arborea	11^{c}				
Schleichera oleosa	23^{u}				
Stereospermum chelonoides	10^{u}				
Wendlandia exserta			75^{c}		
Desmodium oojeinense	32^{c}				
Dalbergia latifolia	14^{u}				
Grewia elastica	13^{c}				
Dillenia pentagyna	16^{u}				
Semecarpus spp.			71^{c}		
Sterculia villosa	6^{u}				
Wendlandia coriacea			81^{c}		
Spondias cytheria		18^{c}			
Unidentified	17^{u}				

c: clumped; u: uniform; r: random.

Table 6
Advanced regeneration/pole density ha^{-1} of seven socio-economically important tree species together with their uses (Fo, Fu, T and M refer to fodder, fuel wood, timber and medicine, respectively), and pair-wise Mann–Whitney *U* test.

Species	Uses	I	II	III	IV	V
(A) Advanced regeneration/pole density						
1. *Terminalia alata*	Fo, Fu, T, M	192	32	432	544	0
2. *Lagerstroemia parviflora*	Fu, T, M	656	176	368	224	160
3. *Syzigium cumini*	Fo, Fu, T, M	0	112	544	32	0
4. *Adina cardifolia*	Fu, T	48	0	96	0	0
5. *Careya arborea*	Fo, Fu, T, M	32	0	32	96	0
6. *Eugenia operculata*	Fo, Fu, T, M	32	96	128	96	0
7. *Cassia fistula*	Fu, M	32	176	48	176	0

	Disturbance gradient			
	II	III	IV	V
(B) A matrix of pair-wise significant differences in advanced regeneration/pole density				
I	1, 2, 7*	1, 6*	1, 2, 7*	2*
II		1, 2, 3*	1*	–
III		–	3*	2*
IV				–
V				

* $p < 0.05$; Mann–Whitney *U* test; number corresponds to species above.

disturbance gradient. In contrast, dispersion patterns of *Semecarpus anacardium* and *Syzigium cumini* changed from uniform to clumped, while that of *Cornus oblonga* changed from random to clumped with increasing disturbance. The dispersion patterns of *S. robusta*, *Symplocos* spp., *L. parviflora* and *Eugenia operculata* also changed with increasing disturbance intensity.

3.3. Advanced regeneration of socio-economically important tree species

The Mann–Whitney *U* test used to compare each possible independent forest pair identified significant differences in the density of advanced regeneration for five of the seven commonly used species (Table 6). All species, except *L. parviflora*, were absent in forest type V. The advanced regeneration of most of the species we analyzed was poor in the least disturbed forest (I). The population density of *T. alata* was significantly higher in forest types III and IV, than in other forests. The population density of *S. cumini* was significantly higher in forest type III, compared to the other forests. The population density of *E. operculata* did not significantly differ among forest types, except between types I and III. Forest type I had a significantly lower population density of *C. fistula* than forest types II and IV.

4. Discussion

Our results suggest that frequent and fluctuating disturbances, acting simultaneously with multiple impacts, were responsible for striking differences in the number of species among forests, and the substantially higher stem density in forests subject to moderate disturbance (Table 4). Recurrent human intervention for the collection of fuel-wood, fodder, litter, and minor forest products, as well as grazing, browsing and trampling, can substantially alter species' habitats (Pandey and Shukla, 1999). Therefore, the species richness of a site subject to disturbance depends on the differential responses of species to such disturbances; some species may tolerate the disturbances, while others may become locally extinct (Sagar et al., 2003). Although the stem density of adult trees was significantly higher in forest types I and III, the basal area was similar in each forest type (Table 4). This may have been due either to most trees in all forests being within the 40–60 cm dbh class (Fig. 4), or the occurrence of a substantially higher number of adult trees in the 20–40 cm dbh class in forest types I and III.

We found that the dispersion patterns of most of the species changed with changes in disturbance intensities (Table 5), reflecting their responses to disturbance along with changes in their habitat condition (Sagar et al., 2003) and competition (Rozas and Fernandez Prieto, 2000). Our results are consistent with findings of Sagar et al. (2003), who observed a shift from clumped to uniform dispersion patterns associated with a change from higher to lower stem density. The dispersion pattern of *A. cardifolia* changed from clumped to random across the disturbance gradient, supporting the hypothesis that the existence of a random pattern is normally a result of transformation from an initially clumped pattern caused by self-thinning or some other disturbance (Rozas and Fernandez Prieto, 2000). Clumped dispersion patterns of species with high abundance (e.g., *L. parviflora* and *S. robusta* in our study) may be related to profound coppicing ability (Sagar et al., 2003). As succession proceeds with some intervention, population spatial patterns shift from highly aggregated to more random or uniform distributions (He et al., 1997). Nevertheless, combined effects of many biotic and abiotic disturbance factors affect species' distribution patterns (He et al., 1997; Rozas and Fernandez Prieto, 2000).

In all of the forests we studied, a large number of individuals were found in the 1.5–10 cm diameter size class or in advanced regeneration stage (Fig. 3). A pattern of decreasing overall stem density with increasing diameter size class is a typical characteristic of secondary dry tropical forests (González-Rivas et al., 2006; Timilsina et al., 2007). For adult trees, the stem density decreased linearly in the least disturbed forests, while in the heavily disturbed forest it was lowest for the smaller size class (20–40 cm dbh), but then increased in the 50–70 cm dbh size class. Finally, density declined in the higher diameter size classes (Fig. 4). Since illegal cuttings were a major disturbance factor affecting adult trees, this relationship was expected. However, the intensity of illegal cutting in the least disturbed forests could be low, and hence stem density declined gradually. In contrast, the illegal cutting of adult trees in heavily disturbed forests could be concentrated more in the lower diameter size class (20–40 cm dbh). Trees of this size have often been felled due to their suitability for house construction and, to some extent, for fuel wood. Furthermore, it may also be easier to fell relatively small trees with an axe. The low number of adult trees in the larger diameter classes in most of the studied forests could be related to the extraction of large-sized trees for timber production, which was also supported by an inverse linear relationship between the density of adult trees and DIF that we observed (Fig. 5a). Similar observations have been made in other tropical forests in India (Muthuramkumar et al., 2006).

The overall stem density (i.e., density of advanced regeneration, poles and adult trees) was higher in the moderately disturbed forests than in either the least or heavily disturbed forests (Fig. 5b), as was the density of young *S. robusta* individuals (Fig. 5c), indicating that mild disturbance supports species regeneration. The positive linear relationship between DIF and the single species occupancy of *S. robusta* in our study (Fig. 5d) supports earlier findings of Pandey and Shukla (2001), who recognized *S. robusta* as a disturbance-tolerant species. However, the higher population density of all species, including *S. robusta*, in moderately disturbed forests, could be attributed to a number of interacting factors. Firstly, vegetation cover in moderately disturbed forests may have been maintained by prolific ramet producers (e.g., *S. robusta*, *L. parviflora* etc.), particularly through rhizomes or root-stocks, as forest openings created by disturbance accelerate these processes (Jackson, 1994; Pandey and Shukla, 2001; Sapkota et al., 2009). Secondly, disturbance caused by selective logging in the past has created gaps in the stand (Sapkota et al., 2009), which generally increase light intensity and soil temperature, while reducing competition for water and nutrients, compared with undisturbed sites (Denslow et al., 1998). Therefore, we propose that the combined effects of increased light intensity, increased soil temperature and reduced competition for resources, might favor the entire regeneration process of many species. Thirdly, wildlife, particularly mega herbivores (e.g., rhinos, deer, cows, goats etc.) and dung beetles, may facilitate seed dispersion, germination and growth of many tree species through defecation (Pradhan et al., 2007). Following defecation, dung beetles have been frequently observed to facilitate seed germination and seedling growth as they generally maintain a favorable micro-environment (Shepherd and Chapman, 1998).

No advanced generation of any of the socio-economically important species analyzed in our study, except *L. parviflora*, was observed in highly disturbed forests (Table 6), indicating that these species have been over-exploited, and that their fitness for their habitats may have declined. At a critical level of disturbance species lacking asexual regeneration may gradually become rarer or even locally extinct (Daniels et al., 1995; Pandey and Shukla, 2001). The occurrence of *S. robusta, L. parviflora* and *Symplocos* spp. in all sample locations and the absence of *T. nudiflora* in 24 sample plots may support this hypothesis. The ubiquitous group of species shows extensive coppicing ability (Jackson, 1994; Sagar et al., 2003), while *T. nudiflora* appears to be very poor at vegetative propagation (personnel communication Chaudhary). We therefore consider *T. nudiflora* to be on the verge of local extinction due to lack of local seed availability. The significantly higher density of young individuals of *T. alata* in moderately disturbed forests can be attributed to the species' high light demands (Jackson, 1994). Despite their high fodder value, the populations of *S. cumini* and *E. operculata* were substantially larger in forest type III, which could be attributed to low wildlife or herbivore feeding pressure (Table 3). The population density of *S. cumini* was low in forest type IV too. Even if the herbivore pressure was also low in this forest, this result may be partly due to excessive fodder collection by local people, since the forest is managed by the state with relaxed protection. *S. cumini* has been considered a preferred fodder for some wild animals in similar forests of Nepal (Pradhan et al., 2007), which could explain the low population density (or absence) of this species in other forests. It is possible that some herbivores, like rodents, also act as seed predators (Blate et al., 1998). The lower population of *C. fistula* in forest type I, may reflect its slow germination and growth in undisturbed habitats due to deep seed dormancy (Jackson, 1994). Nevertheless, most of the species that we analyzed showed poor regeneration in the least and most heavily disturbed forests; most species favored forests that had been subject to disturbance of moderate intensity.

5. Conclusion

In summary, advanced regeneration and spatial patterns of the tree species we examined in this study exhibited clear relationships with disturbance regimes. Furthermore, the total stem density of advanced regeneration and poles increased as the disturbance intensity increased to a certain level, while most of the tree species in the community showed fluctuating dispersion patterns along the disturbance gradient. The advanced regeneration of important tree species such as *S. robusta*, *T. alata*, *S. cumini*, *E. operculata*, and *C. fistula* exhibited different responses to disturbance and showed stronger regeneration performance in forests subject to moderate disturbance. Over-exploitation of tree species, for timber, fodder, fuel-wood and non-timber forest products by local people, and extreme browsing, trampling and uprooting by herbivores, may lower their regeneration ability in heavily disturbed sites. In contrast, reductions in light intensity, decreases in soil temperature and increased competition for water and nutrients due to low gap creation in the past, could account for the poor or absent advanced regeneration of most species in the least disturbed forests.

Since the rural population in Nepal depends on these forests for their subsistence needs, any management strategy must balance the consumptive needs of the human population with those of species conservation by allowing regulated access. Special attention should be paid to the extraction intensity of forest products, since we have found heavy disturbance to be detrimental to the composition and structure of the forests.

Acknowledgements

We thank Bijaya Raj Paudel and Padam Prasad Nepal for their help with logistics. We are grateful to Shesh Kanta Bhandari, Bishnu Bahadur Thapa, Shyam Sundar Bhandari and Tek Bahadur Rayamajhi for their constant support during the forest inventory. Meena Kunwar and Poorneshwor Subedi provided the satellite images. We also thank Chaudhary, Dr. Sushim Ranjan Baral and Puran Prasad Kurmi for their help with species identification in the field and at the Herbarium. We appreciate the comments from two anonymous reviewers. Dr. John Blackwell edited the manuscript. This work was financially supported by Sida.

References

Anon., 1994. Operational forest management plan for Nawalparansi district (1995–2000). Forest Research and Survey Centre, Kathmandu.

Barik, S.K., Pandey, H.N., Tripathi, R.S., Rao, P., 1992. Microenvironmental variability and species diversity in treefall gaps in a subtropical broadleaved forest. Vegetatio 103, 31–40.

Blate, G.M., Peart, D.R., Leighton, M., 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a southeast Asian rainforest. Oikos 82, 522–538.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. High diversity of trees and corals is maintained only in a nonequilibrium state. Science 199, 1302–1310.

Daniels, R.J.R., Gadgil, M., Joshi, N.V., 1995. Impact of human extraction on tropical humid forests in the Western Ghats in Uttara Kannada, south India. J. Appl. Ecol. 32, 866–874.

Denslow, J.S., Aaron, M.E., Sanford, R.E., 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. J. Ecol. 86, 597–609.

Fredericksen, T.S., Mostacedo, B., 2000. Regeneration of timber species following selection logging in a Bolivian tropical dry forest. Forest Ecol. Manage. 131, 47–55.

Gautam, K.H., Devoe, N.N., 2006. Ecological and anthropogenic niches of Sal (*Shorea robusta* Gaertn. f.) forest and prospects for multiple-product forest management—a review. Forestry 79, 81–101.

González-Rivas, B., Tigabu, M., Gerhardt, K., Castro-Marín, G., Odén, P., 2006. Species composition, diversity and local uses of tropical dry deciduous and gallery forests in Nicaragua. Biodiversity Conserv. 15, 1509–1527.

He, F.L., Legendre, P., LaFrankie, J.V., 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. J. Veg. Sci. 8, 105–114.

Hong, S.-K., Nakagoshi, N., Kamada, M., 1995. Human impacts on pine-dominated vegetation in rural landscapes in Korea and western Japan. Plant Ecol. 116, 161–172.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., de Lao, S.L., 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283, 554–557.

Jackson, J.K., 1994. Manual of afforestation in Nepal, second edition. Forest Research and Survey Center, Kathmandu, Nepal.

Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S., Morales, F., 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. Forest Ecol. Manage. 162, 197–208.

Krebs, C.J., 1999. Ecological Methodology, 2nd ed. Addison-Wesley Educational Publishers, p. 620.

Lawes, M.J., Joubert, R., Griffiths, M.E., Boudreau, S., Chapman, C.A., 2007. The effect of the spatial scale of recruitment on tree diversity in afromontane forest fragments. Biol. Conserv. 139, 447–456.

Molino, J., Sabatier, D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science 294, 1702–1704.

Mori, A., Takeda, H., 2004. Effects of undisturbed canopy structure on population structure and species coexistence in an old-growth subalpine forest in central Japan. Forest Ecol. Manage. 200, 89–100.

Muthuramkumar, S., Ayyappan, N., Parthasarathy, N., Mudappa, D., Raman, T.R.S., Selwyn, M.A., Pragasan, L.A., 2006. Plant community structure in tropical rain forest fragments of the Western Ghats, India. Biotropica 38, 143–160.

Nagaike, T., Kamitani, T., Nakashizuka, T., 1999. The effect of shelterwood logging on the diversity of plant species in a beech (*Fagus crenata*) forest in Japan. Forest Ecol. Manage 118, 161–171.

Pandey, S.K., Shukla, R.P., 1999. Plant diversity and community patterns along the disturbance gradient in plantation forests of Sal (*Shorea robusta* Gaertn.). Curr. Sci. 77, 814–818.

Pandey, S.K., Shukla, R.P., 2001. Regeneration strategy and plant diversity status in degraded Sal forests. Curr. Sci. 81, 95–102.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego.

Pradhan, N.M.B., Wegge, P., Moe, S.R., 2007. How does a re-colonizing population of Asian elephants affect the forest habitat? J. Zool. 273, 183–191.

Ramirez-Marcial, N., Gonzalez-Espinosa, M., Williams-Linera, G., 2001. Anthropogenic disturbance and tree diversity in montane rain forests in Chiapas, Mexico. Forest Ecol. Manage 154, 311–326.

Rao, P., 1990. Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. Vegetatio 88, 151–162.

Rozas, V., Fernandez Prieto, J.A., 2000. Competition, mortality, and development of spatial patterns in two cantabrian populations of *Fagus sylvatica* L. (Fagaceae). Anales del Jardín Botánico de Madrid 58, 117–131.

Sagar, R., Raghubanshi, A.S., Singh, J.S., 2003. Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. Forest Ecol. Manage. 186, 61–71.

Sapkota, I.P., Tigabu, M., Oden, P., 2009. Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation. J. For. Res. 20, 7–14.

Sheil, D., 1999. Tropical forest diversity, environmental change and species augmentation: after the intermediate disturbance hypothesis. J. Veg. Sci. 10, 851–860.

Sheil, D., Burslem, D.F.R.P., 2003. Disturbing hypotheses in tropical forests. Trends Ecol. Evol. 18, 18–26.

Shepherd, V.E., Chapman, C.A., 1998. Dung beetles as secondary seed dispersers: impact on seed predation and germination. J. Trop. Ecol. 14, 199–215.

Timilsina, N., Ross, M.S., Heinen, J.T., 2007. A community analysis of Sal (*Shorea robusta*) forests in the western Terai of Nepal. Forest Ecol. Manage. 241, 223–234.

Vandermeer, J., Cerda, I.G., Boucher, D., Perfecto, I., Ruiz, J., 2000. Hurricane disturbance and tropical tree species diversity. Science 290, 788–791.

Vetaas, O.R., 1997. The effect of canopy disturbance on species richness in a central Himalayan Oak forest. Plant Ecol. 132, 29–38.

Webb, E.L., Sah, R.N., 2003. Structure and diversity of natural and managed Sal (*Shorea robusta* Gaertn.f.) forest in the Terai of Nepal. Forest Ecol. Manage. 176, 337–353.

Zar, J.H., 1999. Biostatistical Analysis, 4th ed. Prentice-Hall, Upper Saddle River, New Jersey, p. 663.

Zhu, J.J., Mao, Z.H., Hu, L., Zhang, J.X., 2007. Plant diversity of secondary forests in response to anthropogenic disturbance levels in montane regions of north-eastern China. J. For. Res. 12, 403–416.