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Structure, diversity, and regeneration of tropical dry deciduous forest of northern India

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Abstract. This study examined the impact of disturbance on the pattern of diversity, forest structure and regeneration of tree species in the Vindhyan dry tropical forest of India. A total of 1500 quadrats distributed over five, 3-ha permanent plots in five sites, differing in degree of disturbance, were used to enumerate and measure the tree species. A total of 65 species with 136,983 individuals were enumerated in the total 15-ha area for stems ≥ 30 cm height. The number of species and number of stems ranged from 12 to 50 and 8063–65331 per 3-ha area. The number of species and stems for trees ≥10 cm dbh ranged from 3 to 28 species, with a mean value of 16 species ha^{-1}, and from 16 to 477 stems, with a mean value of 256 stems ha^{-1}, respectively. The adult based PCA ordination indicated uniqueness of sites in terms of species composition and habitat characteristics. PCA ordination also showed uniqueness of sites in terms of seedling composition, but the seedling and adult distributions were not spatially associated. The distinct species composition at the different sites and at the two life-cycle stages on the same site is indicative of marked spatio-temporal dynamics of the dry tropical forest. The density–diameter semi-logarithmic curves ranged from a near linear to an overall concave appearance with a limited plateau in the mid-diameter ranges. The α-diversity and its components decreased with increasing disturbance intensity, reflecting enhanced utilization pressure with increasing disturbance. The site-wise and species-wise regression analyses of the number of individuals in different stages of the species revealed that both the level of disturbance and the nature of species strongly affect the regeneration. In conclusion, although the forest is relatively species-poor, the differential species composition on different sites and the temporal dynamics lend a unique level of diversity to the tropical dry deciduous forest.

Introduction

The dry tropical, subtropical and woodlands once covered more than half of the world's tropics (Janzen 1988), but have decreased considerably during the last decennia. On a global basis, 52% of the total forests are tropical (Singh and Singh 1988). In India, tropical forests account for ca. 86% of the total forest land (Singh and Singh 1988). These forests, however, are strongly impacted by anthropogenic activities (Champion and Seth 1968; Singh et al. 1991). Because of high anthropogenic pressures in the past several decades, the dry deciduous forest cover in most parts of central India is being converted into dry deciduous scrub, dry savanna and dry grasslands which are progressively species poor. This situation calls for in-depth study of these forests with respect to species diversity, structure and regeneration.

The density–diameter (d–d) distribution of stems has been used repeatedly to represent the population structure of the forests (UNESCO/UNEP/FAO 1978). The population structure of a species in a forest can convey its regeneration behaviour (Saxena and Singh 1984); these data have also been used by several workers to interpret the successional patterns (Shugart and West 1980). The population structures, characterized by the presence of sufficient population of seedlings, saplings and adults, indicate a successful regeneration of forest species (Saxena and Singh 1984), and the presence of saplings under the canopies of adult trees also indicates the future composition of a community (Austin 1977). According to West et al. (1981), the information on the d–d distribution can be a basis for making inferences about stand history as well as for developing strategies to achieve a desired condition of composition and size classes.

The long-term permanent plot studies can potentially provide information about spatio-temporal forest composition, structure and dynamics (Ayyappan and Parthasarathy 1999). Such large-scale permanent plot studies are important for conservation and management of tropical forests (Field and Vazquezyanes 1993). The large-scale permanent plot studies have drawn increasing attention over the last two decades, and about 11 large scale (≥ 16 ha) permanent inventory plots have been established in the major tropical forest formations of the world (Condit 1995).

There is a lack of information from large-scale permanent inventory plots from dry tropical forests of India although these forests account for 46% of the forest land in India (Singh and Singh 1988). The present study is based on five, 3-ha permanent plots located at five sites in the Sonebhadra district of the Vindhyan region, and documents the diversity patterns, composition and regeneration of the dry tropical forest. The permanent plots were established to facilitate inventory of trees and to provide a basis for long-term study on forest dynamics.

Materials and methods

Study site

The region is undergoing rapid changes in vegetation and is experiencing large-scale anthropogenic forcing in the form of mining, thermal power generation, cement industry, etc. (Jha and Singh 1990). The human population of Sonebhadra district increased from 683,249 in 1981 to 930,953 in 1991 (about 36.25% increase in 10 years). Similarly, the cattle population has also increased from 132,904 in 1988 to 276,586 in 1997 (about 108% increase in a 9-year interval) (Rajya Niyojan Sansthan 2000). This has led to illegal tree felling, widespread lopping and enhanced extraction of non-timber resources. These forests have been traditionally managed by the Uttar Pradesh Forest Department through selection felling, i.e. harvesting of individuals above a certain diameter and leaving a few mother trees for regeneration. The interval and diameter for harvest varied according to species. No tree less than 10 cm diameter was felled. The diameter considered suitable for felling was > 30 cm for *Boswellia serrata*, > 50 cm for *Shorea robusta*, > 70 cm for *Sterculia urens* and > 60 cm for other species. The rotation period for felling was 30 years except for the fast growing *Holarrhena antidysenterica* for which it was 10 years. Leaving 15–40 mother trees per ha, beyond recommended diameter for felling, of *Shorea robusta*, *Terminalia tomentosa*, *Anogeissus latifolia*, *Lagerstroemia parviflora*, *Adina cordifolia*, *Acacia catechu*, *Hardwickia binata*, *Miliusa tomentosa* and *Chloroxylon swietenia*, was the practice (Upadhyay and Srivastava 1980; Harikant and Ghildiyal 1982).

The study was conducted on five sites, viz. Hathinala, Khatabaran, Majhauli, Bhawani Katariya and Kota (24°6′52″–24°26′16 N and 83°1′86″–83°9′60″ E) in the Vindhyan dry tropical forest of India (Sonebhadra district) in the years 1998–2000 (Figure 1). The sites were selected on the basis of satellite images and field observations to represent the entire range of conditions in terms of canopy cover and disturbance regimes. The elevation above mean sea level ranges between 313 and 483 m. The climate is tropical with three seasons in a year, i.e. summer (March–mid-June), rainy (mid-June–September) and winter (October–February). The annual rainfall varies between 850 and 1300 mm, of which about 86% is received from southwest monsoon during June–August. The soils are Ultisols, sandy loam in texture and reddish to dark grey in colour, and are extremely poor in nutrients (Singh et al. 1989). The topography is relatively flat on Kota and Khatabaran sites, gentle at Bhawani Katariya and undulating at Hathinala and Majhauli sites. Physico-chemical characteristics of soils at the sites are reported by Sagar et al. (2003). Sand content ranged from 57.7 to 87.0%, water holding capacity from 30.6 to 53.9%, total soil N from 0.10 to 0.15%, and soil organic C from 1.18 to 2.79%.

The five sites were categorized in a disturbance gradient by estimated relative impact of the composite elements of disturbance (viz. distance from road, agricultural land, inhabitation and market, visual estimate of cutting and lopping intensity, grazing and browsing intensity, soil erosion and rockiness). The total score for disturbance was: 22, Hathinala; 28, Khatabaran; 30, Majhauli; 96, Bhawani Katariya; and 106, Kota (Sagar et al. 2003; Sagar and Singh 2003).

Sampling and data analysis

At each of the five sites, three 1-ha contiguous permanent plots, having same intensity of disturbance, were established. Each plot was divided into 100 quadrats, each 10 × 10 m in size. In each quadrat, dbh (diameter at breast height) of each adult individual (≥9.6 cm dbh) was measured. In the centre of

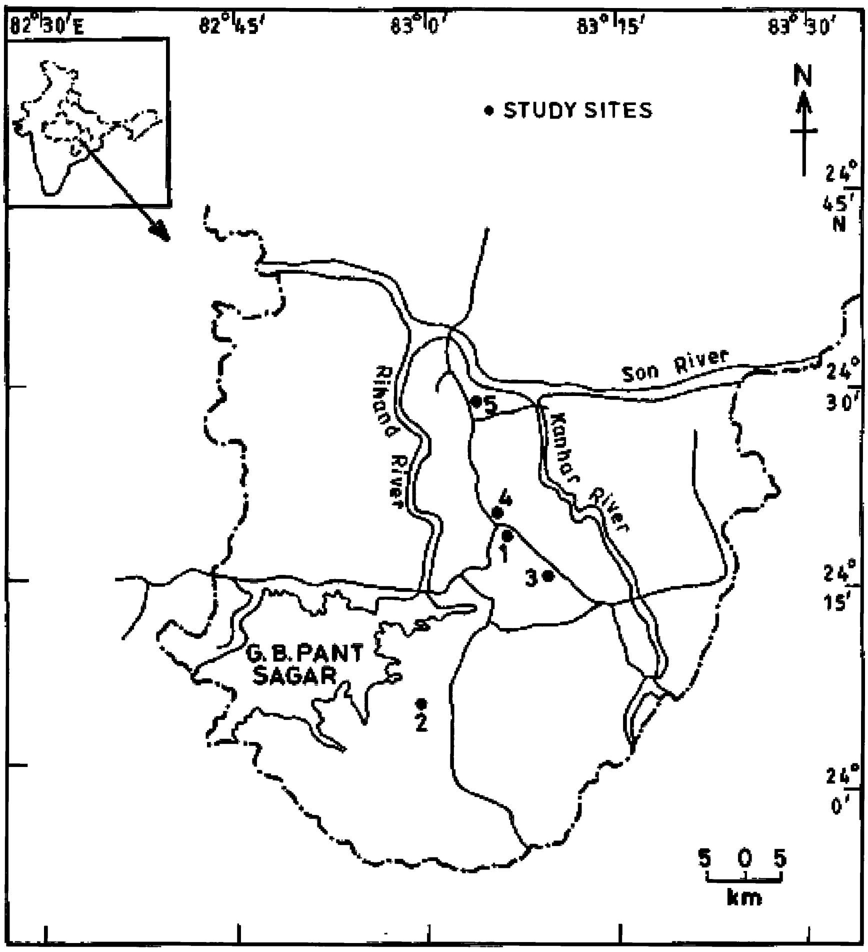


Figure 1. Location of the study area. Numbers 1, 2, 3, 4 and 5, respectively, indicate the approximate locations of the Hathinala, Khatabaran, Majhauli, Bhawani Katariya and Kota sites in the Vindhyan dry tropical forest of India.

each 10 × 10 m quadrat, a 2 × 2 m area was marked for enumeration of saplings (individuals 3.2 to < 9.6 cm dbh) and established seedlings (individuals < 3.2 cm diameter but ≥30 cm height). All the individuals were tagged with sequentially numbered aluminium tags. The seedlings < 30 cm height were considered ephemeral and not counted. Stem diameter of adult and sapling individuals was measured at 1.37 m from the ground and for seedlings it was measured at 10 cm above the ground. Thus, all individuals were enumerated and measured by species.

To estimate the population structure of each tree species, the following dbh classes were distinguished, and the number of individuals in each class was tallied. A, established seedling; B, sapling; *C*, 9.6–19.0 cm; *D*, 19.1–28.5 cm; *E*, 28.6–38.1 cm; *F*, 38.2–47.7 cm; *G*, 47.8–57.2 cm; *H*,≥57.3 cm.

The number of individuals per hectare in a dbh class was plotted against the mid-diameter point of that dbh range to get the d–d curve.

The sites were ordinated using relative density of the species by principal component analysis (PCA) with Biodiversity pro ver (2) software (1997). The relationships of PCA axes with soil nutrients as well as disturbance intensity were determined using SPSS statistical software package (SPSS 1997).

The α-diversity (exp H') and its components, i.e. species richness (Margalef index) and evenness (Whittaker index) were calculated for each 1 ha-plot. β-Diversity was also calculated for each plot to represent the degree of habitat heterogeneity. These diversity indices were calculated using the following equations:

$$\mathrm{SR} = \frac{S-1}{\ln(N)} \quad \text{(Margalef 1958)}$$

$$E_{\mathrm{w}} = \frac{S}{\ln N_i - \ln N_s} \quad \text{(Whittaker 1972)}$$

$N_1 = e^{H'}$ (Hill 1973), where $H' = \sum Si = 1 p_i \ln p_i$ (Shannon and Weaver 1949)

$$\beta_{\mathrm{w}} = \frac{Sc}{\bar{S}} \text{(Whittaker 1972)}$$

In the above equations, SR = Margalef index of species richness, S = number of species, N = total number of individuals, E_w = Whittaker index of evenness, N_i = number of individuals of most abundant species, N_s = number of individuals of least abundant species, p_i is the proportion of individuals belonging to species i, H' = Shannon–Wiener index, ln = natural log (i.e. base 2.718), β_w Whittaker index of β-diversity, Sc = total number of species, $\bar{S}$ = average number of species per sample and N_1 is the number of equally common species which would produce the same diversity as H'. N_1 has been used because the units (number of species) are more clearly understandable (Krebs 1989). Furthermore, the diversity of different sites was compared using a *k*-dominance plot, in which percentage cumulative abundance is plotted against log species rank (Platt et al. 1984).

Data were subjected to ANOVA to see the effect of degree of disturbance on total number of species, evenness, α-diversity and stem density. Relationships between number of individuals of adults versus seedlings, and saplings versus adults and seedlings versus saplings were examined through regression analysis. For these analyses data only for those species were used which were represented in both the concerned life-cycle stages. All statistical analyses were done using the SPSS package (SPSS 1997).

Results

Species composition and forest structure

A total of 65 species (Appendix 1) with 136983 stems (Table 1) was recorded from the five areas, each of 3 ha. The number of species and number of individuals varied from 12 to 50 and 8063–65332 per site (Appendix 1). Table 2 shows the total number of species in different categories (established seedlings, saplings and adults) at the five study sites. The total number of species occurring as adults, saplings and established seedlings were highest at the least disturbed Hathinala site and lowest at the drastically disturbed Kota site. The number of species which occurred only as adults, and only as seedlings was highest for the Khatabaran and Hathinala sites, respectively.

Diospyros melanoxylon was most abundant at the Bhawani Katariya and Khatabaran sites. Among all species, *D. melanoxylon* had the highest number of individuals in the lower diameter class (< 9.6 cm) on the above two sites as well as on the Majhauli site. *H. antidysenterica* was the most abundant species at the Kota site, while *T. tomentosa* was predominant at the Majhauli and Hathinala sites. *H. binata* was the most abundant species in the upper diameter stratum (≥9.6 cm) of the Kota and Bhawani Katariya sites. The upper stratum was dominated by *S. robusta*, *Tectona grandis* and *Acacia catechu* at Majhauli,

Table 1. Summary of stem inventory in different stages from five 3-ha permanent plots in the dry tropical forest of India.

Site	Seedlings	Saplings	Adults	Total
Hathinala	60900	3175	1257	65332
Khatabaran	5975	1250	838	8063
Majhauli	19650	6525	1187	27362
Bhawani Katariya	8500	2125	646	11271
Kota	21125	3725	105	24955
Total	116150	16800	4033	136983

The adults (individuals ≥9.6 cm dbh) were enumerated in 300, 10×10 m quadrats and established seedlings (≥30 cm height but < 3.2 cm diameter) and saplings (≥3.2 to < 9.6 cm dbh) were enumerated in 300, 2×2 m quadrats at each of the five dry tropical forest sites. The established seedling and sapling stems were scaled up in same unit as adults.

Table 2. Total number of species in different life-cycle stages on the five sites.

Category	Hathinala	Khatabaran	Majhauli	Bhawani Katariya	Kota	Total for five sites
Adult (≥9.6 cm)	31	30	23	22	7	49
Sapling	22	8	18	17	6	36
Seedling	47	17	27	19	7	57
Only as adult	3	15	5	4	3	7
Only as sapling	0	0	0	0	1	0
Only as seedling	16	2	9	1	2	14

Khatabaran and Hathinala sites, respectively. *Bridelia retusa* was most abundant in the lower stratum of Hathinala site. Across all sites, 9% of species were common (*A. catechu*, *Anogeissus latifolia*, *D. melanoxylon*, *H. antidysenterica*, *L. parviflora* and *Lannea coromandelica*) (Appendix 1).

The PCA ordination of the five sites on the basis of relative density of species in the adult tree population is illustrated in Figure 2a. The PCA axes 1 and 2 accounted for 39 and 25% variation, respectively. The PCA axis 1 was related with soil nitrogen ($r = -0.881$, $p = 0.049$) and PCA axis 2 represented the disturbance gradient ($r = -0.943$, $p = 0.016$). The PCA ordination for sites using species composition and relative abundance of established seedlings is given in Figure 2b. The PCA axis 1 for seedling communities accounted for 59% variation in species composition while PCA axis 2 accounted for 27% variation.

Figure 3 shows the semi-logarithmic d–d distribution curves for the five sites and for the entire study area. The number of stems decreased rapidly at first and then more slowly with an increase in the diameter class. The general look of the curve was in between rotated sigmoid and concave. The d–d curves for two species (*T. tomentosa* and *D. melanoxylon*) are plotted for each site in Figure 4 to show that the shape of the curve for a species changed on different sites.

Species diversity

ANOVA revealed that differences in the total number of species ($F_{4,10} = 14.62$, $p = 0.000$), evenness ($F_{4,10} = 13.39$, $p = 0.001$), α-diversity ($F_{4,10} = 28.92$, $p = 0.000$) and stem density ($F_{4,10} = 9.54$, $p = 0.002$) due to sites (and disturbance intensity) were significant. The species richness, evenness and α-diversity declined with disturbance intensity, whereas β-diversity, which accounted for changes in species composition within site, did not exhibit any pattern with disturbance, except that it had the maximum value for the highly perturbed Kota site (Figure 5a). Figure 5b shows the k-dominance of species rank plot. The bottom curve (Hathinala site) represented the highest diversity, while the uppermost curve (Kota site) represented the lowest diversity.

Analysis of diversity patterns at different diameter classes showed that Margalef index of species richness and α-diversity were highest for the intermediate diameter class (9.6–19.1 cm dbh) for three out of five sites (Table 3). The least disturbed Hathinala site exhibited maximum diversity for established seedlings. Opposite to this, the highly stressed Kota site exhibited an increasing trend of diversity with increasing diameter class except for species richness. The total number of species declined from lower diameter class to higher diameter class except for Bhawani Katariya site (Table 3). The mean number of stems ha^{-1} also declined with increasing diameter thresholds (Table 4). Evidently, species and individuals which could attain a large size (high diameter) were few in number, indicating a small structure.

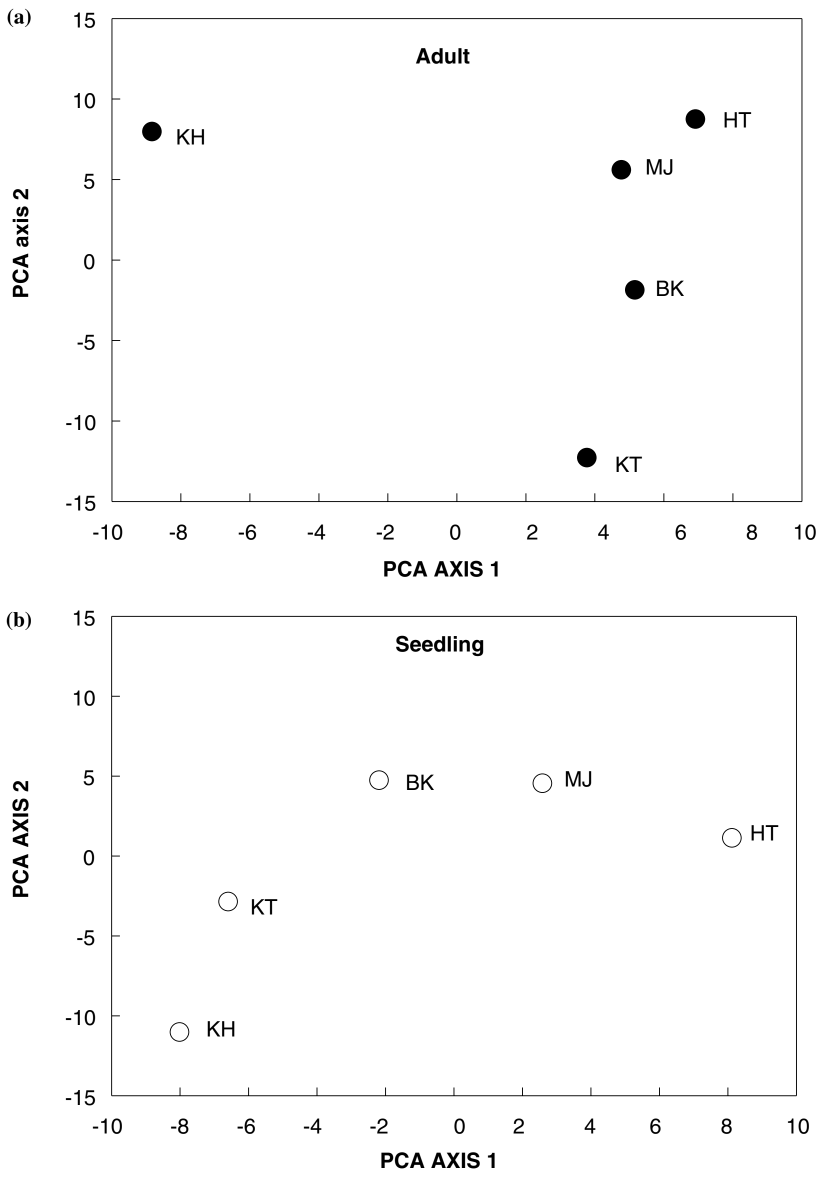


Figure 2. PCA ordination of dry tropical forest sites. (a) Adult-based PCA ordination, PCA axes 1 and 2, respectively, explained 39 and 25% of total variance in adult species composition. (b) Seedling-based PCA ordination. PCA axes 1 and 2, respectively, explained 59 and 27% of total variance in species composition. HT, KH, MJ, BK, and KT, respectively stand for the Hathinala, Khatabaran, Majhauli, Bhawani Katariya, and Kota sites.

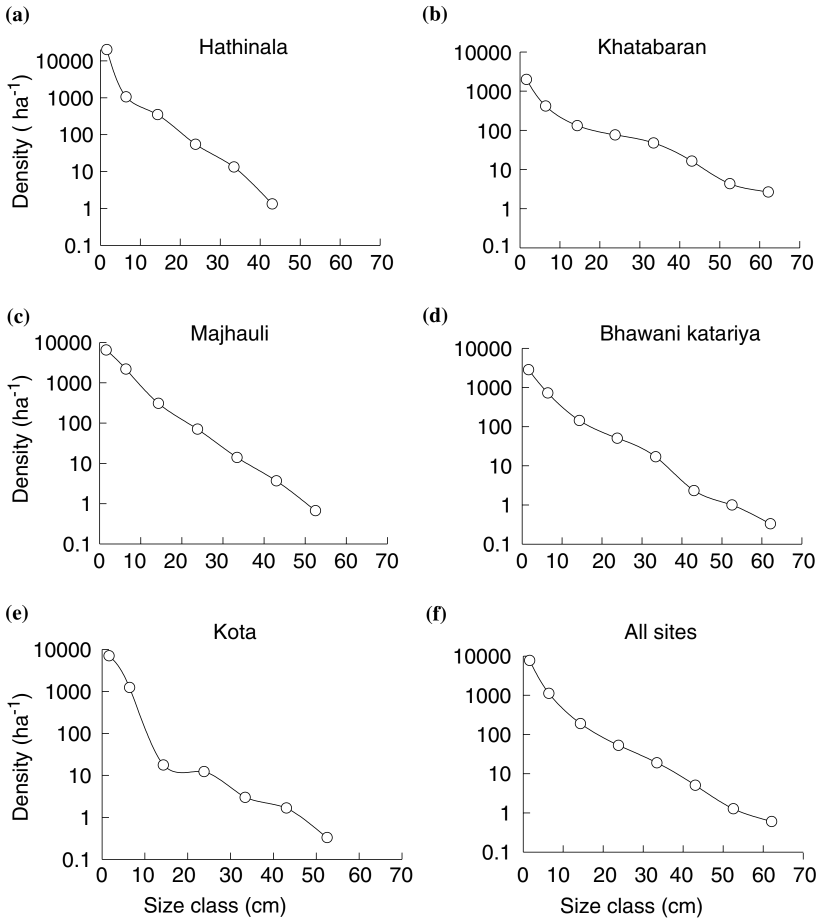


Figure 3. Density–diameter distribution curve for all species within the Vindhyan dry tropical forest of India. (a) Hathinala, (b) Khatabaran, (c) Majhauli, (d) Bhawani Kataria, (e) Kota, (f) all sites.

Regeneration

The number of individuals at the seedling, sapling and adult (≥9.6 cm dbh) stages occurring on different sites were related with each other (Figure 6, Table 5). These relationships were explored also across species, by pooling the data for five sites (15-ha area) (Figure 7, Table 6). Species which did not have individuals at any one of the stages were excluded from these analyses. It was evident that the Kota and Hathinala sites were outliers, as the exclusion of data from these sites resulted in a significant improvement in the r^2 values. Similarly, exclusion of certain species significantly improved the relationships between seedlings and adult, and between adult and saplings.

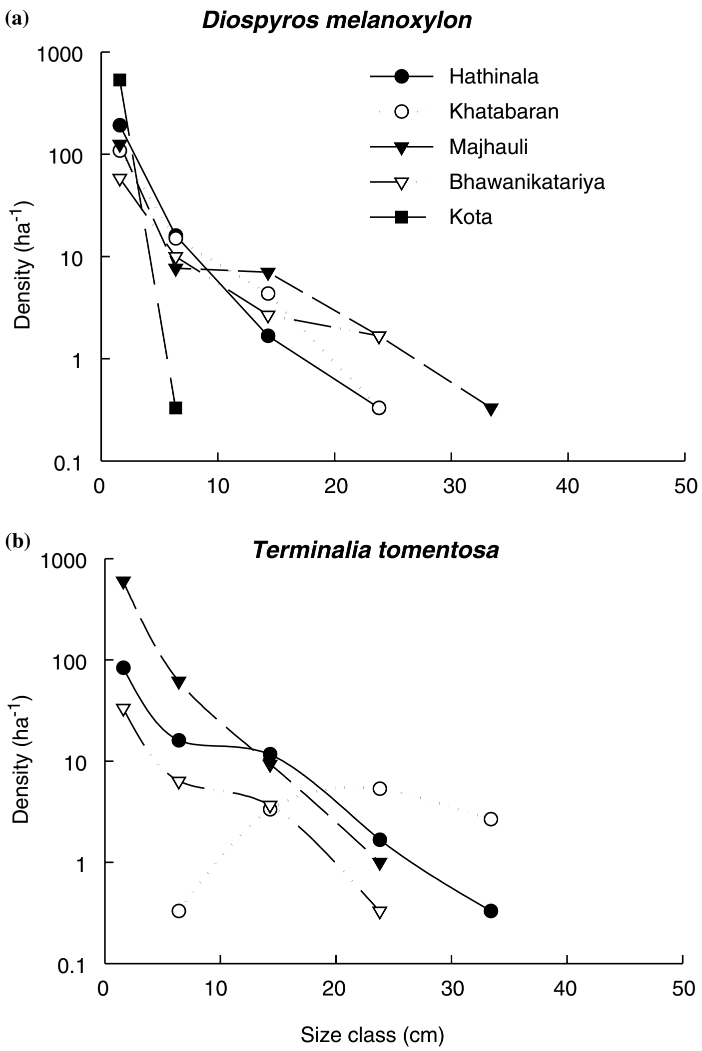


Figure 4. Density–diameter distribution curve of (a) *Diospyros melanoxylon* and (b) *Terminalia tomentosa* at different dry tropical forest sites.

Discussion

Species composition and forest structure

The PCA ordination indicated uniqueness of sites in terms of species composition and habitat characteristics (soil-N and disturbance gradient). Similar differences in species composition related to habitat conditions are reported in several instances (see Webb and Peart 2000; Scheller and Mladenoff 2002).

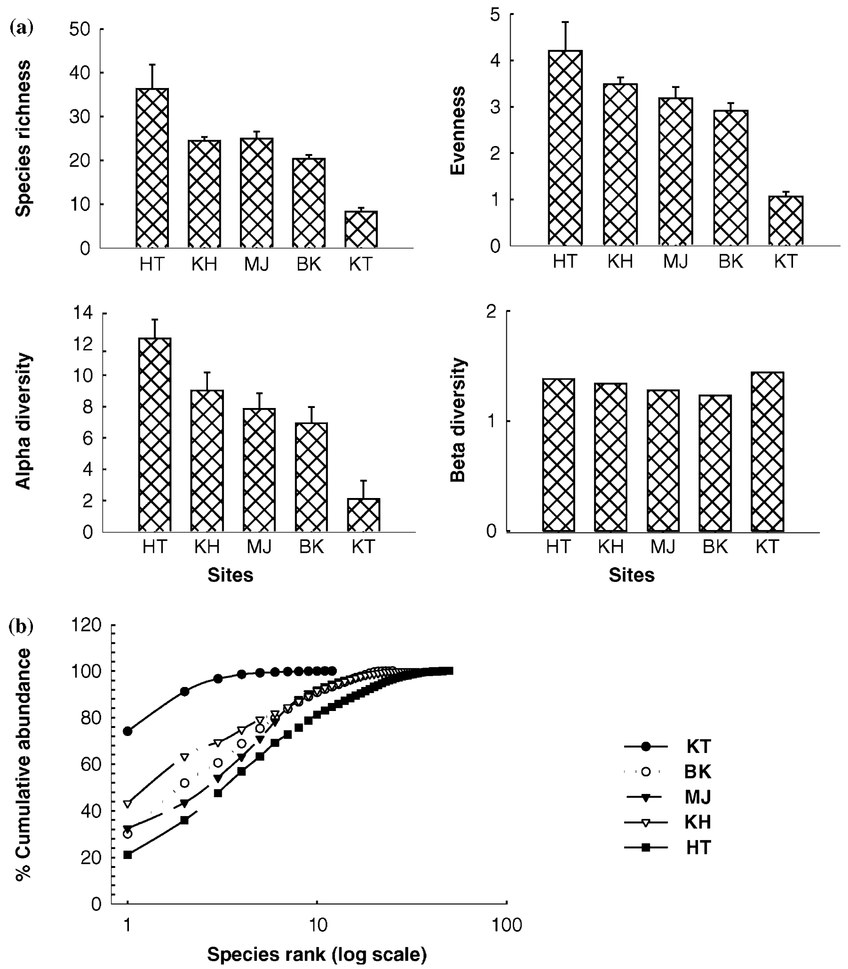


Figure 5. (a) Species richness, evenness, alpha and beta diversity in a gradient of disturbance (from least to highest) in the dry tropical forest region. (b) The *k*-dominance plot in which percentage cumulative abundances is plotted against log of species rank for each site.

PCA ordination also showed uniqueness of sites in terms of seedling composition, but the seedling and adult distributions were not spatially associated. This indicated that seedling community on a site was distinct from the adult tree community. Webb and Peart (2000) argued that such a situation could arise due to high survival of rare recruits to suboptimal habitats and high density-dependent mortality of seedlings in optimal habitats. We suggest that the distinct species composition at the different sites and at the two life-cycle stages (i.e. seedlings and adults) on the same site is indicative of marked spatio-temporal dynamics of the dry tropical forest. For example, on the Hathinala site, as many as 16 species were found only as seedlings. Of these, 10 species did

Table 3. Species richness, evenness and α-diversity in three diameter classes, calculated for 3-ha plots on each site, along the disturbance gradient in dry tropical forest of India.

	Hathinala	Khatabaran	Majhauli	Bhawani Katariya	Kota
Seedling					
Total no. of species	47	17	27	19	7
Margalef index	4.175	1.840	2.632	1.989	0.603
Evenness	7.479	3.527	4.926	3.922	1.074
Exp H'	15.320	5.800	8.840	7.850	1.990
9.6–19.1 cm dbh					
Total no. of species	30	26	20	20	6
Margalef index	4.169	4.183	2.784	3.130	1.259
Evenness	5.459	5.500	3.658	4.352	1.820
Exp H'	13.660	10.940	9.460	9.670	3.470
28.7–38.2 cm dbh					
Total no. of species	16	16	10	7	5
Margalef index	4.066	3.022	2.408	1.520	1.820
Evenness	6.439	4.030	3.607	2.148	3.607
Exp H'	5.240	8.780	6.880	4.230	4.170

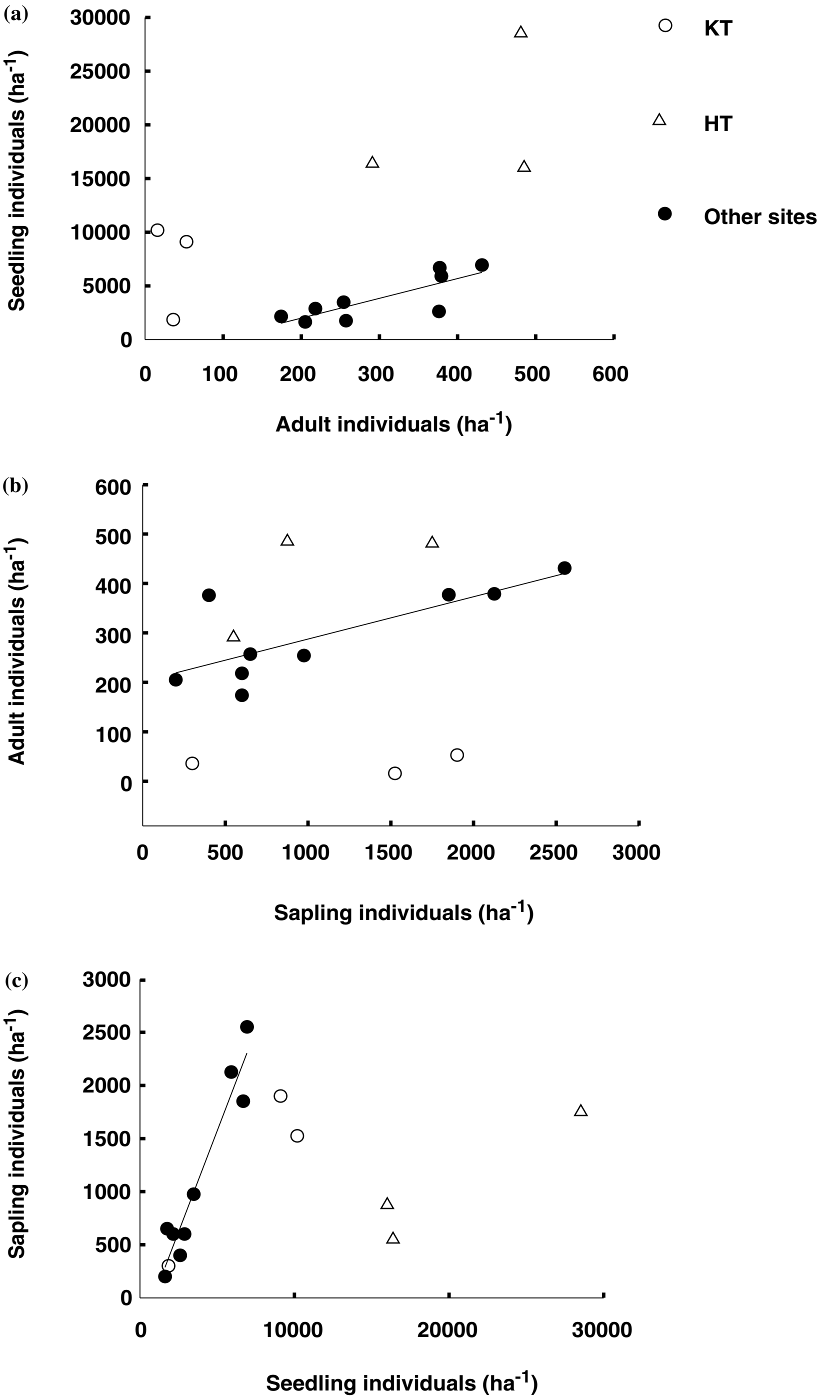
Table 4. Total number of species and stems (ha^{-1}) at different diameter thresholds in the 15-ha permanent plot of Vindhyan dry tropical forest of India.

Minimum diameter threshold (cm)	Total number of species	Stems (ha^{-1})
< 9.6 cm but ≥30 cm height	65	9125.50 (2058.17)
≥9.6	49	268.87 (89.58)
≥19.1	35	78.86 (26.96)
≥28.6	25	25.87 (14.86)
≥38.2	15	6.87 (5.25)
≥47.7	9	1.93 (1.67)
≥57.3	8	0.60 (0.52)
≥66.8	5	0.40 (0.32)

Values in parentheses are ± 1 SE.

▶

Figure 6. (a) Relationship between number of seedlings and number of adult individuals across sites. Number of species having both seedlings as well as adults was 28 at Hathinala, 15 at Khatabaran, 17 at Majhauli, 16 at Bhawani Katariya and 3 at Kota. The relationship was significant (solid curve) ($Y = 1681.90 + 18.39X$, $r^2 = 0.654$, $p = 0.008$) when data for the Kota and Hathinala sites were excluded. (b) Relationship between number of adult individuals and number of saplings. Number of species having both saplings as well as adults was 20 at Hathinala, 8 at Khatabaran, 17 at Majhauli, 15 at Bhawani Katariya and 3 at Kota. The solid curve is fitted by a regression equation ($Y = 202.25 + 0.086X$, $r^2 = 0.594$, $p = 0.015$) after excluding data for the Kota and Hathinala sites. (c) Relationship between saplings and seedlings. Number of species having both seedlings as well as saplings was 22 at Hathinala, 8 at Khatabaran, 17 at Majhauli, 15 at Bhawani Katariya and 4 at Kota. The curve is fitted by a regression equation ($Y = -331.24 + 0.381X$, $r^2 = 0.922$, $p = < 0.0001$) after excluding the Kota and Hathinala sites.



(a)
Seedling individuals (ha-1)
30000
25000
20000
15000
10000
5000
0
0
100
200
300
400
500
600
Adult individuals (ha-1)
KT
HT
Other sites
(b)
Adult individuals (ha-1)
600
500
400
300
200
100
0
0
500
1000
1500
2000
2500
3000
Sapling individuals (ha-1)
(c)
Sapling individuals (ha-1)
3000
2500
2000
1500
1000
500
0
0
10000
20000
30000
Seedling individuals (ha-1)

Table 5. Site-wise relationships ($Y = a + bX$) between tree individuals of different diameter classes in the Vindhyan dry tropical forest of India.

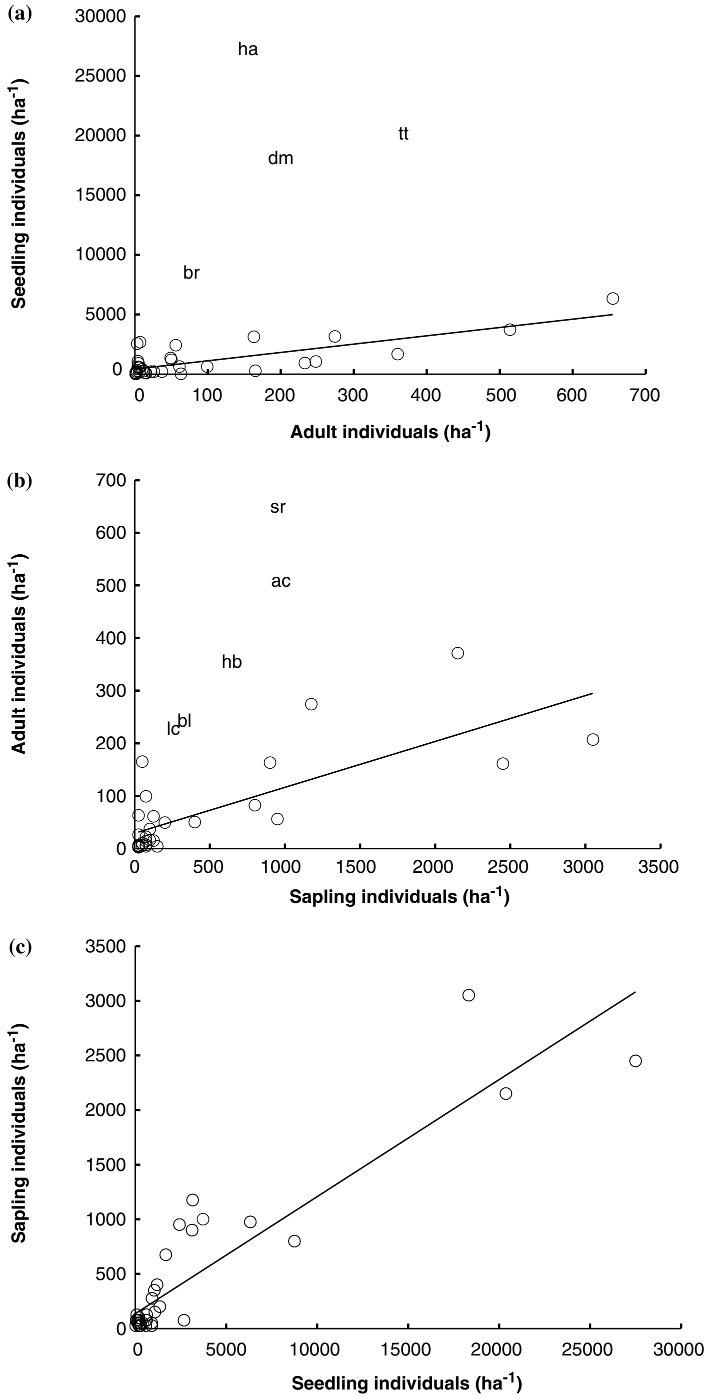
	a	*b*	r^2	*p*	*n*	*df*
Seedling (Y)–Adults (X)						
All sites	1987.70	21.37	0.192	0.102	15	13
Excluding Kota	−8793.80	51.02	0.446	0.018	12	10
Excluding Kota and Hathinala sites	1681.90	18.387	0.654	0.008	9	7
Adult (Y)–Saplings (X)						
All sites	201.87	0.060	0.085	0.293	15	13
Excluding Kota	231.03	0.088	0.392	0.030	12	10
Excluding Kota and Hatihnala sites	202.25	0.086	0.594	0.015	9	7
Sapling (Y)–Seedling (X)						
All sites	856.59	0.035	0.119	0.208	15	13
Excluding Hathinala	143.48	0.217	0.666	0.001	12	10
Excluding Kota and Hathinala sites	−331.24	0.381	0.992	< 0.0001	9	7

not occur on any of the remaining four sites. On the other hand, at the Khatabaran site as many as 15 species occurred only as adult trees. Of these, three species did not occur on any of the other sites. At both the sites, species composition would change in the future perhaps more rapidly at the Hathinala site due to high rate of recruitment of species which were not present on the site in the recent past. Khatabaran forest would decline in species composition because more than 50% of the species currently occurring as adults are not regenerating.

The d–d distribution curves for different forests differ in their slope (Rollet 1974). The semi-logarithmic d–d curves for all species at different sites ranged from near linear to overall concave appearance. The d–d curve plotted from pooled data for all sites also had a generally concave shape. However, all the curves had a less- to well-developed plateau near the mid-diameter range. The plateau resulted into a rotation from a concave form at the left to a convex form at the middle part of the curve. The steeper part at the left end of these curves shows under-representation of saplings/small dbh individuals, indicating slow growth of seedlings into saplings or a marked mortality of saplings due to canopy-understorey competition. It is also less labour-intensive and easy to harvest saplings/small trees illegally for fuel wood. The appearance of

►

Figure 7. (a) Relationship between number of seedlings and number of adult individuals across the species. The curve is fitted by a regression equation ($Y = 423.12 + 6.974X$, $r^2 = 0.599$, $p = < 0.0001$) when the data for *H. antidysenterica, D. melanoxylon, B. retusa* and *T. tomentosa* were excluded. (b) Relationship between number of adult individuals and number of saplings. The curve is fitted by a regression equation ($Y = 29.063 + 0.087X$, $r^2 = 0.579$, $p = < 0.0001$) after excluding data for *S. robusta, A. catechu, H. binata, L. coromandelica* and *B. lanzan*. (c) Relationship between saplings (Y) and seedlings (X) individuals according to $Y = 139.06 + 0.107X$, $r^2 = 0.827$, $p = < 0.0001$.


(a)
ha
tt
dm
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Seedling individuals (ha-1)
Adult individuals (ha-1)
(b)
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hb
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Adult individuals (ha-1)
Sapling individuals (ha-1)
(c)
Sapling individuals (ha-1)
Seedling individuals (ha-1)

Table 6. Species-wise relationships ($Y = a + bX$) between tree individuals of different diameter classes in the dry tropical forest of India.

	a	*b*	r^2	*p*	*n*	*df*
Seedling (Y)–Adult (X)						
All species	1213.30	15.757	0.166	0.0083	41	39
Successive removal of:						
H. antidysenterica	781.51	14.07	0.241	0.0013	40	38
D. melanoxylon	578.26	12.224	0.280	0.005	39	37
B. retusa	381.11	12.315	0.317	0.0002	38	36
T. tomentosa	423.12	6.974	0.599	< 0.0001	37	35
Adult (Y)–Sapling (X)						
All species	65.049	0.111	0.270	0.002	33	31
Successive removal of:						
S. robusta	56.36	0.098	0.322	0.0007	32	30
A. catechu	49.817	0.087	0.372	0.0003	31	29
H. binata	42.823	0.084	0.437	< 0.0001	30	28
L. coromandelica	36.178	0.086	0.497	< 0.0001	29	27
B. lanzan	29.063	0.087	0.579	< 0.0001	28	26
Sapling (Y)–Seedling (X)						
All species	139.06	0.107	0.827	< 0.0001	35	33

concavity beyond intermediate dbh classes is evidently because of decreasing removal rate across successively larger dbh classes as argued by West et al. (1981). According to West et al. (1981), the plateau in the d–d curve is produced by increased growth rate or an actual decrease in mortality rate in the intermediate diameter classes. Such a rotated sigmoid curve with an over all concave appearance seems to be typical of deciduous forests (Leak 1973) particularly for small stands, free from gaps or pockets of even-aged trees (Goff and West 1975; Ranney 1978). The relatively straight-line d–d curve for the Majhauli site, as also for Hathinala and Kota sites, would indicate a preponderance of populations containing small mean tree diameters. The paucity of old trees indicates heavy removal of mature trees in the past.

In this study, population structure of individual species varied across sites. For example, the d–d curve for *D. melanoxylon* was concave at Hathinala and Bhawani Katariya sites, sigmoid at Khatabaran and Majhauli sites and linear at Kota site. The d–d curve of *T. tomentosa* was sigmoid at Bhawani Katariya and Hathinala sites, and linear and convex for Majhauli and Khatabaran sites, respectively. The shape of the curves for individual species has been interpreted as indicating their shade tolerance–intolerance abilities (West et al. 1981; Saxena et al. 1984). According to West et al. (1981), the curves for shade-intolerant trees were convex or relatively straight, and for shade-tolerant species it would be concave. The present study indicates that the shape of the curve is not associated with shade-tolerance behaviour of a species, as the same species showed different shapes at different sites, but may be due to different levels of anthropogenic disturbance and species composition at different sites.

Species diversity

Tropical forests are structurally complex plant communities (Phillips and Gentry 1994; Condit et al. 1996). One of the characteristic features of these forests is their high species richness (Ayyappan and Parthasarathy 1999). We enumerated 49 species in the Vindhyan dry tropical forest from the 15-ha area distributed over five sites. The values reported from large scale permanent plot inventories in wet tropical forests (for trees ≥10 cm dbh) were 996 species in a 52 ha plot of Lambir National Park, Malaysia (Condit et al. 2000); 660 species in a 50 ha plot of Pasoh forest reserve, Malaysia (Kochummen et al. 1990), 229 species in a 50 ha Barro Colorado Island, Panama (Condit et al. 1996); 153 species in a 30 ha plot at Varagalaiar, Anamalais, Western Ghat, India (Ayyappan and Parthasarathy 2001), 164 species in a 25 ha plot of Sinharaja Biosphere reserve, Sri Lanka (Condit et al. 2000).

The species richness of individual sample plots (1 ha) in the present study for trees ≥10 cm dbh ranged from 3 to 28 species, with a mean value of 16 species ha^{-1} . This is low when compared with the range across the tropics, 20 species ha^{-1} in Varzea forest of Rio Xingu, Brazil (Campbell et al. 1992) to as high as 307 species ha^{-1} in Amazonian Ecuador (Valencia et al. 1994).

A total of 4033 stems were recorded in the 15 ha area with a mean value of 268.9 stems ha^{-1} ; on hectare basis this number ranged from 16 to 485. The tree density (ha^{-1}) in some large scale permanent plot studies were: 537.6 tree in Costa Rica (Lieberman et al. 1996), 530 in Malaysia (Manokaran and LaFrankie 1990), 424.8 in BCI Panama and from 300 to 635 trees in the Western Ghats, India (Condit et al. 1996; Pascal and Pelissier 1996; Ghate et al. 1998; Ayyappan and Parthasarathy 1999, 2001).

The decreasing trend of α-diversity and its components along the perturbation intensity, as noted in this study, reflects enhanced utilization pressure (Bhat et al. 2000). Increasing disturbance can also lead to decreased resource availability (Brokaw 1985). The *k*-dominance measures intrinsic diversity (Lambshead et al. 1983). Platt et al. (1984) opined that diversity can only be unambiguously assessed when the *k*-dominance curves from the communities to be compared do not overlap. In this situation the lowest curve will represent the most diverse community. Thus in the present study, diversity was maximum for the least disturbed Hathinala site and minimum for the highly disturbed Kota site. The curves for Khatabaran, Majhauli and Bhawani Katariya showed intermediate diversity in consonance with intermediate level of disturbance; however, according to Platt et al. (1984), these sites cannot be discriminated among themselves, because their curves intersect each other.

Regeneration

In nature, species diversity is maintained through regeneration of component species. We assumed that the adult individuals on a site or of a species constitute the reproductive pool. Therefore, under normal conditions in a forest one would expect a significant relationship between number of adult individuals and number of seedlings. This study indicated that the relationship between the number of seedlings and adult individuals attained statistical significance only when data for the Kota site was removed. With further exclusion of the Hathinala site, there was a significant increase in the r^2 value. On both these sites, particularly on the Hathinala site, the number of seedlings were disproportionally higher compared to the adult individuals, indicating massive seed production and/or high seedling establishment, which could lead to higher recruitment of adults if anthropogenic pressure is controlled.

It is further assumed that the saplings on a site or of a species is the immediate source of the adult individuals. Therefore, under normal conditions there should be a significant relationship between number of saplings and number of adult individuals. This study showed that the relationship between number of saplings and adult individuals was significant, only when data for the Kota site was removed. With further removal of the Hathinala site there was a significant increase in the r^2 value. While on the Kota site, saplings were not successfully converting into adult trees, presumably due to biotic removal, on the Hathinala site the success of saplings was much greater compared to other sites due to minimum anthropogenic pressure.

Under normal conditions one would expect a significant relationship between saplings and seedlings, as the latter constitute a source of the former. This study showed that the relationship between number of saplings and seedlings was significant only when data for the Hathinala site were removed. With further exclusion of Kota site, there was a significant increase in the r^2 value. Apparently on these sites, the success of seedling conversion to sapling has relatively been lower. Illegal harvest of saplings and density-dependent mortality of seedlings could be possible reasons for low recruitment of saplings. The above analyses indicate that both the least disturbed as well as the most disturbed sites did not fall within the pattern exhibited by the sites with intermediate level of disturbance. Perhaps both these situations (i.e. least and heavy disturbance) are unusual for the dry deciduous forest, which has had a long evolutionary history of moderate human pressure (Murphy and Lugo 1986).

On the species basis, pooling of data for all the five sites, the study indicated that the relationship between the number of seedlings and adult individuals was significant, although the r^2 value was low when all species having both adults and seedlings were used. With the removal of *H. antidysenterica*, *D. melanoxylon*, *B. retusa* and *T. tomentosa* there was a significant increase in the r^2 value. Of these species, *D. melanoxylon* and *H. antidysenterica* are excellent coppicers, *B. retusa* and *T. tomentosa* are conserved for seed production (Upadhyay and Srivastava 1980; Harikant and Ghildiyal 1982). These species were particularly preponderant in the seedling population at Hathinala or Kota sites. The study further indicated that the relationship between number of saplings and adult individuals was significant when data for all species were used, but with low r^2 value. With the exclusion of *S. robusta*, *A. catechu*, *H. binata*, *Lannea coromandelica* and *Buchanania lanzan*, there was a significant increase in the r^2 value. These species are economically valuable and enjoy relatively greater protection. In these species greater number of saplings successfully progressed to adult stage, compared to the other species. It is also interesting to note that species which were highly prolific in seedling production were different from species which showed disproportionately higher sapling success. It is also evident that although the number of saplings was a direct function of the number of seedlings across all species, there was considerable mortality of seedlings.

Thus, the study indicates that both the level of disturbance and the nature of species strongly affect regeneration. Although the forest is relatively species-poor, the differential species combinations on different sites and the temporal dynamics lend a unique level of diversity to the tropical dry deciduous forest. It is also evident that large areas need be maintained for conservation of the spatio-dynamic nature of the dry deciduous forest.

Conservation needs

The study points out an urgent need for the conservation of biodiversity of the northern dry tropical forest of India. The marked spatio-temporal dynamics and demographic instability both at site and species levels indicate that fragmentation will likely to enhance the loss of species diversity. Strict measures, therefore, are needed to curb fragmentation, and the existing fragments need to be connected through afforestation of indigenous species. The free-range grazing in the forest needs to be banned. Thus stronger protection and regulatory measures are required. It has been argued that dry forests have the potential to recover to a mature state more quickly than do wet forests, and hence are more resilient (Ewel 1977; Murphy and Lugo 1986). However, such measures will fail unless fuel and fodder requirements of the local inhabitants are met. Singh and Singh (1989, 1992) estimated that the wood extracted from these forests meets 81–100% energy needs of the local populations, and as much as 38% of the total wood extracted is marketed for buying food grain and other requirements (Singh and Singh 1992). These forests support 80–95% of the fodder needs (Singh and Singh 1992). Systematic fuel-wood plantations of fast growing trees on the village commons and setting aside selected forest compartments for raising high density short rotation energy plantations, and developing village pastures with a mixture of grasses and legumes with scattered native fodder trees (such as *H. binata, Dalbergia sissoo* and *Holoptelia integrifolia)*, could be a viable strategy for easing the anthropogenic pressure on these forests. In addition, the existing vegetation on various sites may be enriched by seeding and planting of field-collected or nursery-raised seedlings of desired native species through aggressive forestry. Further, there is a need to integrate the livelihood of local human populations with conservation measures through participatory forest management such that the local inhabitants are able to appropriate a large share of benefits from conservation of these forests.

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Appendix 1

Number of stems for different species in different diameter classes at each of the five dry deciduous forest sites. The * represents unique species of the site; ** represents species common to all sites (for diameter class C–H refer to text).

	Diameter class								
	Seedling	Sapling	C	D	E	F	G	H	Total
Hathinala site									
*Acacia catechu***	3200	350	234	6	–	–	–	–	3790
Adina cordifolia	350	–	–	–	–	–	–	–	350
Aegle marmelos	50	–	–	–	–	–	–	–	50
*Albizia odoratissima**	25	–	1	–	–	–	–	–	26
*Anogeissus latifolia***	1500	125	43	2	1	–	–	–	1671
*Antidesma ghaesembilla**	150	–	–	–	–	–	–	–	150
Bauhinia racemosa	875	25	4	–	–	–	–	–	904
Bombax ceiba	25	–	–	–	–	–	–	–	25
Boswellia serrata	25	25	30	4	7	1	–	–	92
Bridelia retusa	8750	800	72	8	–	–	–	–	9630
Buchanania lanzan	250	25	66	13	–	–	–	–	354
Cassia fistula	–	–	1	–	–	–	–	–	1
Cassine glauca	125	–	–	1	–	–	–	–	126
Chloroxylon swietenia	25	–	–	–	–	–	–	–	25
*Cochlospermum religiosum**	275	–	–	–	–	–	–	–	275
*Diospyros melanoxylon***	5400	575	48	5	1	–	–	–	6029
*Eriolaena hookeriana**	75	–	–	–	–	–	–	–	75
Eriolaena quinqueolocularis	1075	100	3	–	–	–	–	–	1178
Flacourtia indica	1900	–	3	–	–	–	–	–	1903
Gardenia latifolia	150	25	1	–	–	–	–	–	176
Gardenia turgida	375	50	2	–	–	–	–	–	427
Grewia serrulata	2300	–	3	–	–	–	–	–	2303
Hardwickia binata	25	50	73	19	12	1	–	–	180
*Holarrhena antidysenterica***	7550	–	3	–	–	–	–	–	7553
Hymenodictyon excelsum	500	–	–	–	–	–	–	–	500
*Lagerstroemia parviflora***	1900	–	41	2	–	–	–	–	1943
*Lannea coromandelica***	750	50	98	15	–	–	–	–	913
Miliusa tomentosa	575	100	7	2	–	–	–	–	684

Appendix 1. (Continued)

	Diameter class								
	Seedling	Sapling	C	D	E	F	G	H	Total
*Mimosa himalayana**	225	25	2	–	–	–	–	–	252
*Mitragyna parvifolia**	25	–	–	–	–	–	–	–	25
Nyctanthes arbortristis	200	–	11	–	–	–	–	–	211
Ougenia oojeinsis	125	50	6	–	–	–	–	–	181
Phyllanthus emblica	500	25	35	8	–	–	–	–	568
Pterocarpus marsupium	125	–	1	2	1	–	–	–	129
*Randia uliginosa**	25	–	–	–	–	–	–	–	25
Scherebera swietenoides	25	–	–	–	–	–	–	–	25
*Schleichera oleosa**	25	–	–	–	–	–	–	–	25
Semecarpus anacardium	575	25	–	–	–	–	–	–	600
Shorea robusta	3850	150	138	37	12	1	–	–	4188
Soymida febrifuga	500	125	26	5	1	–	–	–	657
*Sterculia urens**	625	–	–	–	–	–	–	–	625
*Stereospermum suaveolens**	700	–	–	–	–	–	–	–	700
Terminalia bellirica	50	–	–	–	–	–	–	–	50
Terminalia chebula	–	–	1	–	–	–	–	–	1
Terminalia tomentosa	13400	250	48	35	5	1	–	–	13739
Zizyphus glaberrima	700	175	47	–	–	–	–	–	922
Zizyphus nummularia	875	50	–	–	–	–	–	–	925
Unidentified									
Hariari*	25	–	–	–	–	–	–	–	25
Muraila*	125	–	–	–	–	–	–	–	125
Papara*	–	–	1	–	–	–	–	–	1
Total	60900	3175	1049	164	40	4	–	–	65332
Khatabaran site									
*Acacia catechu***	–	–	42	25	5	–	–	–	72
Adina cordifolia	–	–	1	1	2	3	1	1	9
Aegle marmelos	–	–	1	1	–	–	–	–	2
*Anogeissus latifolia***	–	–	4	22	19	12	5	1	63
Bauhinia racemosa	25	–	–	–	–	–	–	–	25
Bombax ceiba	–	–	–	–	1	–	–	–	1
Buchanania lanzan	–	–	49	19	2	3	–	–	73
Butea monosperma	175	–	16	4	3	1	–	–	199
*Carissa spinarum**	75	125	9	4	2	–	–	–	215
Casearia elliptica	100	75	12	2	–	–	–	–	189
Cassia fistula	175	–	5	–	–	–	–	–	180
Cassine glauca	50	–	2	1	4	–	1	–	58
Chloroxylon swietenia	75	–	–	–	–	1	–	–	76
*Diospyros melanoxylon***	3100	325	45	13	1	–	–	–	3484
*Ficus benghalensis**	–	–	1	–	–	–	–	–	1
Gardenia turgida	75	25	1	–	–	–	–	–	101
*Holarrhena antidysenterica***	1000	500	113	11	1	–	–	–	1625
*Holoptelia integrifolia**	–	–	–	–	2	–	–	–	2
Hymenodictyon excelsum	–	–	–	2	2	1	–	1	6
*Lagerstroemia parviflora***	300	100	17	10	7	–	2	1	437
*Lannea coromandelica***	–	–	22	14	6	2	–	1	45
Nyctanthes arbortristis	–	–	1	–	–	–	–	–	1
Phyllanthus emblica	–	–	8	7	3	1	–	–	19
*Randia dumetorum**	25	–	1	–	–	–	–	–	26

Appendix 1. (Continued)

	Diameter class								
	Seedling	Sapling	C	D	E	F	G	H	Total
Scherebera swietenoides	25	–	1	–	–	–	–	–	26
Semecarpus anacordium	–	–	3	3	–	–	–	–	6
Shorea robusta	–	–	8	16	14	3	2	2	45
*Syzygium heyneanum**	–	–	1	–	–	–	–	–	1
*Tectona grandis**	275	50	31	64	53	14	2	1	490
Terminalia tomentosa	175	–	1	10	16	8	–	–	210
Zizyphus glaberrima	300	50	1	–	–	–	–	–	351
Zizyphus nummularia	25	–	–	–	–	–	–	–	25
Total	5975	1250	396	229	143	49	13	8	8063
Majhauli site									
*Acacia catechu***	275	250	84	16	5	–	–	–	630
Adina cordifolia	50	50	–	1	–	–	–	–	101
*Anogeissus latifolia***	1150	725	19	6	2	–	–	–	1902
Bauhinia racemosa	–	–	–	1	–	–	–	–	1
Boswellia serrat	–	–	3	5	2	1	–	–	11
Bridelia retusa	–	–	2	–	–	–	–	–	2
Buchanania lanzan	525	300	51	–	–	–	–	–	876
Butea monosperma	25	–	–	–	–	–	–	–	25
Casearia elliptica	25	–	–	–	–	–	–	–	25
Cassia fistula	25	75	29	2	–	–	–	–	131
Cassine glauca	25	25	1	3	2	1	–	–	57
*Diospyros melanoxylon***	4000	375	23	21	5	1	–	–	4425
Eriolaena quinqueolocularis	–	50	1	–	–	–	–	–	51
Flacourtia indica	350	50	–	–	–	–	–	–	400
Gardenia latifolia	50	–	–	–	–	–	–	–	50
Gardenia turgida	100	–	–	–	–	–	–	–	100
Grewia serrulata	250	–	–	–	–	–	–	–	250
*Holarrhena antidysenterica***	1850	350	23	4	1	–	–	–	2228
Hymenodictyon excelsum	25	–	–	–	–	–	–	–	25
*Lagerstroemia parviflora***	725	600	117	41	5	4	1	–	1493
*Lannea coromandelica***	100	200	64	7	–	–	–	–	371
Miliusa tomentosa	1850	800	33	4	1	–	–	–	2688
Nyctanthes arbortristis	50	–	–	–	–	–	–	–	50
Ougenia oojeinensis	25	–	–	–	–	–	–	–	25
Phyllanthus emblica	125	25	29	7	–	–	–	–	186
Pterocarpus marsupium	75	75	12	4	–	–	–	–	166
Shorea robusta	1750	675	237	59	16	4	1	–	2742
Soymida febrifuga	75	–	1	–	–	–	–	–	76
Terminalia bellerica	25	–	–	–	–	–	–	–	25
Terminalia chebula	–	–	5	2	–	–	–	–	7
Terminalia tomentosa	6000	1800	185	28	3	–	–	–	8016
Zizyphus glaberrima	125	100	1	–	–	–	–	–	226
Unidentified									
Rij*	–	–	–	1	–	–	–	–	1
Total	19650	6525	920	212	42	11	2	–	27362
Bhawani Katariya site									
*Acacia catechu***	250	400	77	4	–	–	–	–	731
*Anogeissus latifolia***	425	50	11	4	–	–	–	–	490

Appendix 1. (*Continued*)

	Diameter class								
	Seedling	Sapling	C	D	E	F	G	H	Total
Boswellia serrata	–	–	2	4	4	–	–	–	10
Buchanania lanzan	275	25	42	3	–	–	–	–	345
*Cassia siamea**	–	100	13	3	–	–	–	–	116
Cassine glauca	–	–	1	4	4	1	–	–	10
Chloroxylon swietenia	25	50	–	–	–	–	–	–	75
*Diospyros melanoxylon***	3175	175	30	8	5	–	–	–	3393
Flacourtia indica	425	25	4	–	–	–	–	–	454
Gardenia latifolia	100	–	–	2	–	–	–	–	102
Gardenia turgida	50	–	1	–	–	–	–	–	51
Hardwickia binata	1650	600	99	78	26	2	1	1	2457
*Holarrhena antidysenterica***	150	50	5	–	–	–	–	–	205
*Lagerstroemia parviflora***	75	150	26	–	–	–	–	–	251
*Lannea coromandelica***	75	25	3	–	–	–	–	–	103
*Madhuca longifolia**	50	75	–	–	–	–	–	–	125
Miliusa tomentosa	50	50	7	1	1	–	–	–	109
Phyllanthus emblica	–	25	1	–	–	–	–	–	26
Pterocarpus marsupium	–	–	–	2	–	–	–	–	2
Shorea robusta	725	150	76	13	10	4	2	–	980
Soymida febrifuga	50	–	24	4	–	–	–	–	78
*Terminalia arjuna**	75	–	–	–	–	–	–	–	75
Terminalia chebula	–	–	1	–	–	–	–	–	1
Terminalia tomentosa	800	100	19	11	1	–	–	–	931
Zizyphus glaberrima	75	75	1	–	–	–	–	–	151
Total	8500	2125	443	141	51	7	3	1	11271
Kota site									
*Acacia catechu***	–	–	7	8	1	–	–	–	16
*Anogeissus latifolia***	150	–	2	2	2	5	1	–	162
*Azadirachta indica**	50	–	–	–	–	–	–	–	50
Butea monosperma	1150	200	15	9	1	–	–	–	1375
Cassia fistula	–	25	–	–	–	–	–	–	25
*Dalbergia sissoo**	–	–	–	1	1	–	–	–	2
*Diospyros melanoxylon***	2650	1600	1	–	–	–	–	–	4251
*Eucalyptus citriodora**	25	–	–	–	–	–	–	–	25
Hardwickia binata	–	25	27	17	4	–	–	–	73
*Holarrhena antidysenterica***	16950	1550	–	–	–	–	–	–	18500
*Lagerstroemia parviflora***	150	325	–	–	–	–	–	–	475
*Lannea coromandelica***	–	–	1	–	–	–	–	–	1
Total	21125	3725	53	37	9	5	1	–	24955

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