

Seedling dynamics after different intensities of human disturbance in a tropical dry limestone forest in Jamaica

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Abstract: The Hellshire Hills are an extensive area of tropical dry forest over limestone, located on the south coast of Jamaica. Despite being a protected area, they are subject to encroachment and clearance by charcoal burners, leaving a relatively pristine core within more disturbed areas of forest. Future management requires a consideration of the forest's resilience to such disturbance, and this study reports on seedling dynamics before and after different intensities of disturbance. The study was conducted within twelve 225-m² plots comprising four blocks and three treatments. The treatments were removal of all trees (≥ 2 cm dbh), removal of 50% of stems (> 5 cm) and an uncut control plot. Seedling dynamics were monitored before and 3, 8, 13 and 20 mo after the application of treatments. The study indicates that regeneration by seed was not severely affected by this small-scale disturbance. However, the density of some species was affected by the environmental conditions created by partial and clear cutting, and seasonal effects were more pronounced after disturbance. Biomass recovery by seedlings was negligible in comparison with coppice regrowth which clearly offers considerable resilience to disturbance in this dry forest where successful regeneration by seed is highly susceptible to rainfall seasonality. This will likely affect long-term species diversity if the present rate of clearance continues.

Key Words: disturbance, light intensity, regeneration, seedling mortality, seedling recruitment, tropical dry forest

INTRODUCTION

It is estimated that the extent of tropical or subtropical dry forest accounts for 42% of total global forest cover (Murphy & Lugo 1986). They have been exposed to severe, large-scale changes, through the cutting of valuable trees, creation of pastures, accidental or intentional fires (Gerhardt & Hytteborn 1992) and as a source of fuel wood (Murphy & Lugo 1986). Despite their over-exploitation there have been relatively few studies of tropical dry forest, especially of their recovery following man-made disturbance. They are still being heavily utilized and continue to support a larger human population than do the humid forest areas. In Central America less than 2% of the tropical dry forests have remained in a more or less intact state and less than 0.1% have conservation status (Janzen 1988*a, b*).

Successful establishment of seedlings in the dry tropics is dependent mainly upon moisture availability. The timing and duration of rainfall is crucial as there is a high probability that a given seedling will be left stranded in a drying soil and there is therefore a low probability of

successful regeneration from seeds (Ewel 1977, 1980). The pronounced seasonality affects patterns of seed production, germination, survival and seedling development (Khurana & Singh 2000). Seeds of a majority of dry tropical species mature in the dry season and they are dispersed at the beginning of the rainy season when sufficient moisture is available for germination and seedling growth (Singh & Singh 1992). The favourable growing period is restricted to short rainy seasons when seeds are expected to germinate and seedlings establish. During this period, the canopy of the dry forest recovers to the pre-dry season condition, and seedlings emerging in this season experience reduced intensity and modified quality of light under relatively closed canopies, and those in the open encounter high light intensities (Khurana & Singh 2000) but with adequate moisture. However, the deciduous state of some or most tree species during the dry season allows for an increase in irradiance that, in the absence of moisture, exacerbates desiccation in seedlings and hence higher rates of mortality (e.g. Gerhardt 1996*a*). Thus, seedling emergence, establishment and growth in the dry tropics are subject to very heterogeneous conditions in terms of irradiation, temperature and moisture availability (Khurana & Singh 2000). Microhabitats within these areas may provide a suitable environment for seedling

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establishment. Shaded well-sheltered sites are important in the survival of seedlings during dry periods. As a result seedling density during dry periods or in seasonally dry places tends to be higher under well-shaded sites than in open sites (Gerhardt 1996a, Lieberman & Li 1992, Russell-Smith 1996). Shade demand or shade dependence, rather than shade tolerance, of young tree seedlings may therefore be a more appropriate model for predicting survival in open dry areas (Ray & Brown 1995). The shade demand of a species may be conceptualized as 'an ecological property that integrates drought tolerance and light requirements' (Ray & Brown 1995). A number of studies have shown that high-light environments of disturbed forest sites may favour the germination and early establishment of some species in which growth is high and mortality low (Gerhardt 1993, 1996a, b, 1998; Gerhardt & Fredriksson 1995, Morris *et al.* 2000, Rincon & Huante 1993), but dry-season conditions usually increase mortality rates among individuals (Gerhardt 1993, 1996a, b, 1998; Gerhardt & Fredriksson 1995, Hammond 1995). However, the relative effects of moisture and shade are by no means clear-cut. Smith & Huston (1989) predicted that plants could not simultaneously acclimate to shade and drought because of physiological trade-offs. As a result plants are expected to be less tolerant to shading under drier conditions. However, Holmgren *et al.* (1997) predict that the impact of drought is relatively strong at high irradiance, but weaker in moderate shade because of facilitation, and strong in deep shade; and Sack & Grubb (2002) demonstrated orthogonal impacts of deep shade and drought on seedling biomass and allocation in shade-tolerant woody seedlings. Knowledge of woody seedling growth responses to combined effects of shade and drought is important to explain species differentiation in many forest and scrub systems (Sack & Grubb 2002).

The low success rate of regeneration by seed and the poor re-colonization potential of many forest species, through inefficient dispersal pathways and abnormally high seed/seedling losses upon arrival, combined with a continued expansion of unfavourable secondary habitats, mean that human disturbance in the dry tropics that involve removing stems and roots (thus eliminating regeneration by vegetative means) may in the long run lead to a landscape of permanently deflected secondary successions and dwindling biotic diversity (Hammond 1995). Therefore the knowledge of seed germination and seedling establishment is not only important for understanding the community processes such as plant recruitment and succession, but is also required for the success of conservation and management efforts and for the success of efforts on augmentation, introduction, and re-introduction of species populations in restoration efforts (Khurana & Singh 2000).

Despite the heavy usage, high conversion rate, and low success of regeneration by seeds in the dry tropics, there

has been little research on the different aspects of regenerative ecology (phenology, seed dispersal, seedling establishment and mortality) of individual dry forests, especially in response to human-related disturbances. This was the focus of a study by McLaren (2001) in the forest of the Hellshire Hills, Jamaica. The Hellshire Hills are an extensive area of tropical dry forest over limestone, located on the south coast of Jamaica, just to the west of the capital Kingston. Given the proximity of the Hellshire Hills to the capital they are one of the prime production centres for charcoal (Vogel *et al.* 1995). Unregulated actions of charcoal burners over the last 10–20 y have resulted in a significant reduction of the forest area. The central and most of the western (seaward) sections are covered with little-disturbed, primary tropical dry forest but on the northern side, the charcoal burners have intruded 2–3 km into the forest. The Hellshire Hills now have a protected-area status and there is a need to implement conservation strategies to protect, preserve, and replenish the remaining natural forest cover. This is important as the area is one of the last remaining stands of primary limestone forest in the Caribbean, and the last remaining global habitat for the endangered Jamaican iguana *Cyclura collei*. One conservation strategy being considered is the establishment of an outer buffer zone surrounding the central core of pristine forest, with cutting permitted in the buffer zone. However, nothing is presently known about how the forest regenerates and it is not known to what extent the forest can withstand cutting.

The hypothesis central to the study by McLaren (2001) was that coppicing is the primary regeneration mechanism of trees in a dry-forest site that have been exposed to different intensities of cutting with stem and roots remaining in place. Regeneration by seed will be less important because of its susceptibility to moisture availability, compounded by the light environment, both of which are accentuated by human disturbance and rainfall seasonality. Coppice regrowth was indeed shown to be very high; the average diameter recovered by species after 14 mo approximating to 29% y^{-1} (McLaren & McDonald, in press). The study reported here explores the latter part of the hypothesis by examining the effects of human disturbance on seedling dynamics and how they are affected by a change in light environment arising either by seasonal effects, the effects of disturbance and/or both. Seedling establishment, mortality and growth rates were assessed to determine the effects of tree removal on the species distribution. The research questions are: is there a lower probability/lower rate of successful regeneration from seeds in cut and uncut sites? If so, then what are the factors (environmental) that cause this limitation? At the species level, it is hypothesized that seedlings will undoubtedly show some difference in their ability to recover in the newly created environments. Are these abil-

ities related to the 'shade demand' of the species as conceptualized by Ray & Brown (1995)?

METHODS

Experimental design

The study was conducted within the Hellshire Hills, a gently rolling range covered with dry forest growing on hard limestone. They are located on the south coast of Jamaica, just to the west of the capital Kingston, forming a peninsula which measures about 10 km in the north-south and 15 km in the east-west direction covering an area of 114 km² (Vogel *et al.* 1995). Weathering of the limestone terrain has produced a coarse reddish soil of the 'terra rossa' type, which is usually found in small volumes in crevices and pockets and in larger volumes in patches downslope. Large areas of the ground are bare rock with most areas covered with a layer of partially decomposing organic matter over bare rock. The site selected for the study was an area within the central region, which Vogel *et al.* (1995) reported as being pristine and undisturbed. Due to the nature of this study (involving tree removal), the deeper pristine central area, which was the iguana habitat, was avoided and the study site was situated in the outer zone of this pristine area where there was evidence of some past, albeit small-scale, disturbance (the remnants of one or two charcoal kilns). However, in our study area only four trees were cut and these were located outside of the plots.

The long-term (30 y) mean annual rainfall at Great Salt Pond, an area within the Hellshire Hills, is 780 mm (1961–1981, Figure 1). The area is subjected to a short rainy season in May to June with the main rainy season starting in September. This is usually followed by a dry period, which is 4–5 mo long, from December to April. The mean annual temperature (1961–1981) was 27 °C and potential evapo-transpiration to precipitation ratio was 2.25 (The Jamaica Meteorological Office).

In August 1997, 12 permanent sample plots measuring

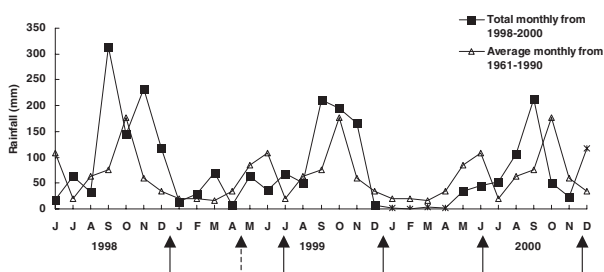


Figure 1. Total monthly rainfall for the study site from June 1998 to December 2000, and the long-term (30 y) average annual rainfall for the Great Salt Pond, an area within the Hellshire Hills (Source: The Jamaica Meteorological Division). Solid arrows indicate the time of sampling while the broken arrow indicates when the treatments were applied.

20 × 20 m were established in the forest in an arrangement of four blocks each with three plots. Within each block, the three plots were randomly allocated to be either clear cut, partially cut or uncut control. An inner assessment plot of 15 × 15 m was assigned, and each entire plot was separated by a buffer of at least 20 m. Each assessment plot was subdivided into 225 1 × 1-m quadrats to assist in the relocation of seedlings and light measurement points in each census. In January 1999 (corresponding with the end of the 1998 rainy season), and before the application of treatments, all seedlings (seedlings here refers to any individual of 0–20 mm root-collar diameter (RCD)) within each plot (for the first enumeration, only one control plot was sampled) were identified, tagged and root-collar diameter (or dbh (diameter at 1.3 m from the ground) for any individuals falling within the specified range but taller than 1.3 m) and height measured. RCD was measured using a Digimatic digital caliper (with a 0.01-mm resolution and an accuracy of ± 0.02 mm) and the diameter was recorded after five successive measurements, by which time successive measurements usually fell within 0.1 mm of the preceding measurement. When this was achieved, two successive RCD measurements which fell within 0.1 mm of each other were recorded and averaged.

Treatment application

In April 1999, the following treatments were applied to one plot within each block:

- (1) Clear cut, where all individuals ≥ 2 cm diameter (dbh) were removed. This approximated to a $96 \pm 3.3\%$ reduction of the total basal area of the plot and will be referred hereafter as 100% basal area removed or 100% BAR.
- (2) Partially cut, by the removal of 50% of the stems ≥ 5 cm in the plot on a size-class basis. That is, all stems ≥ 5 cm were grouped in the size classes 5–10, 10–15, 15–20, 20–30, 30–40, 40–50, > 50 cm and 50% of the stems in each size class was removed. This approximated to a $38 \pm 2.1\%$ basal area reduction and will be referred hereafter as 40% basal area removed or 40% BAR.
- (3) No removal, hereafter referred to as 0% basal area removed or 0% BAR.

The treatments were allocated randomly to a plot within each block and trees were cut at a standard height of 0.5 m. The trees that were removed in the 40% BAR plots were selected randomly irrespective of species and if they were represented by more than two individuals within all plots.

Census protocol

Following the application of treatments in April 1999, seedling censuses were carried out 3, 8, 13 and 20 mo

after the gaps were created, within all 12 plots, giving a total of four census periods. These times approximated to the late dry season/early rainy season (July–Sept 1999), immediately after the rainy season (Dec 1999–Jan 2000), end of the dry season (May–July 2000) and immediately after the rainy season (Dec 2000–Jan 2001). During the censuses, all plots were resurveyed and all new seedlings were tagged and surviving seedlings noted and their RCD measured (except for Dec 1999).

Light measurements

During the first seedling enumeration, within all plots (except for two of the three control plots that were not assessed) light (PAR) was measured at a randomly located point within each 1 × 1-m quadrat. A coloured stone was placed at each point to allow for the ease of location of points during re-measurement. Three consecutive 1-min readings were taken at the point located within each of the 1 × 1-m quadrats. Measurements under the canopy were taken at ground level between 10h00 and 14h00 initially and this was extended to 10h00 and 15h00, on two differing days. Where possible, if a measurement was taken at a point on the first day between 10h00 and 12h00, on the subsequent day of measurement, it was taken between 12h00 and 15h00. This ensured that the measurements obtained reflected a 'logged' period of 1 d. A reference measurement representing an open area was made using a data logger. The open area chosen was not shaded at any time during the day. The times were synchronized before any measurements were taken within the plots. From this reference measurement relative PAR (rPAR) for each minute of recording was calculated (PAR undercanopy × 100/PAR open). Measurements of rPAR were first averaged over the 3 min they were collected, and then averaged over the 2 d they were collected, and then averaged for each plot. The mean values for each plot were then used in the analysis of variation in seedling size (RCD) distribution with respect to light regime.

A variety of equipment was used to measure light initially and in the final stages of fieldwork. These included three Delta-t PAR sensors (Delta-t Devices, Cambridge, UK), two Didcot PAR sensors (Didcot Instruments, Oxford, UK), four Li-cor PAR sensors (LI 190, LI-COR, Nebraska, USA), one Skye PAR sensor (SKP 215, Skye Instruments, Powys, UK), one Delta-t data logger (DI2e, Delta-t Devices, Cambridge, UK), two Campbell Scientific data loggers (21x, Campbell Scientific, Utah, USA). The calibration of all of the equipment except for the Li-cor and Didcot sensors was checked by their respective manufacturer and the Li-cor and Didcot light sensors were calibrated against a calibrated reference sensor. This reference sensor was used to further calibrate both the calibrated and uncalibrated equipment to ensure that the output of each did not differ significantly. Any data that were

collected before calibration were adjusted with a correction factor given by the manufacturer.

Data analysis

The data analysed include the total number of seedlings found alive, total number of recruited individuals, mortality rates, the number of dead seedlings recorded, growth rates and total number of individuals found alive for each species found in each plot. This analysis was conducted to indicate seasonal effects, and to more carefully assess the treatment effects, the fate of the original populations present before the treatments, and the cohort of new seedlings recruited during the first rainy season after the application of the treatments was assessed. The per cent survival, mortality rates, growth rates (absolute, relative and the percentage of individuals showing a negative growth rate) were analysed.

Overall, mortality rate was calculated as:

$$\frac{\ln(N_0) - \ln(N_t)}{t}$$

(following Condit *et al.* 1995), where N_0 is the number of initial seedlings, N_t the number of seedlings remaining alive at time t (mo) and $\ln(N)$ is the natural logarithm of N . Mortality rates were calculated for the periods Jan–July 1999, July–Dec 1999, Dec 1999–June 2000 and June–Dec 2000. For the recruited cohort the data that were available were for the last two periods. Seedling growth rates were analysed in terms of absolute (mm mo^{-1}) and relative ($\% \text{ mo}^{-1}$) growth rates. Growth rates were calculated from the periods Jan–July 1999, July 1999–June 2000 and June–Dec 2000. The mean absolute and relative growth rates were calculated for each plot for each species and for all species after which the effects of the treatment on growth rates were analysed. The percentage of individuals with negative growth rates at each census was calculated on a plot basis. For calculation of absolute and relative growth rates for all individuals, only seedlings > 5 mm were used. For the calculation of absolute and relative growth rates for the initial population, seedlings were split into two arbitrary groups < 5.0 mm RCD which represented small, recently recruited seedlings and > 5.0 mm RCD which represented larger older seedlings. For the cohort recruited after the treatment application, no growth rates were calculated because, for most plots, there were insufficient individuals remaining at each sample point from which to calculate growth rates. Seedling height was recorded in the first census but is not presented because it was found that height was an inadequate surrogate of the developmental age or status of seedlings, a similar condition reported in the seasonally dry sites in a monsoon rain forest in northern Australia (Russell-Smith 1996). Aerial shoots for most species were killed in response to low moisture availability experienced during the dry season

only to be replaced in the following wet season by resprouts. As a result measurements of seedling height were discontinued from the second census.

All statistical analyses were carried out using the GENSTAT 5 computer package (Lane *et al.* 1987, Payne 1987). All the data collected were first analysed using repeated-measures ANOVA of a randomized block design. Data that had significant changes in their profile over time were analysed using an ante-dependent analysis, which highlighted the time at which significant changes among the treatments occurred and if the treatment effects differed overall. Time periods in which there were significant differences were analysed using an ANOVA of a randomized block design to determine the nature of the effects. Seedlings found alive were analysed for those species adequately represented within all the plots (26 in total). Regression analyses on a plot basis were conducted on the relationship between changes in light climate, the total number of seedlings found alive, the percentage survival, mortality, and absolute, relative and negative growth rates of the initial seedling population versus the recruited cohort.

RESULTS

The rainfall over the experimental period was extremely variable. In 1998, there was a 4-mo rainy season from September to December with most of the rain falling in September and November. There was a severe 5-mo drought from December 1999 to April 2000 and total precipitation during that period was 16.2 mm or 86% lower than the 30-y mean for this period, and 93% lower than the previous year. Jan 2000–Jan 2001 represented a rela-

tively dry year (Figure 1) with total rainfall during this period being 29% lower than the previous year, and 9% lower than the 30-y mean. Total rainfall measured within the study site was 917 mm in 1999 and 650 mm in 2000.

A total of 64 species of seedling was sampled, all of which had adult representatives throughout the plots before the application of treatments. Unidentified species made up on average $1 \pm 0.1\%$ of seedlings recorded. Over the sample period, a total of 15 786 seedlings were recorded, of which 9759 were recruited, and a total of 11 588 seedlings died in all the plots throughout the study period.

The highest number of individuals recorded was 11 029 seedlings in the 0.27 ha (Dec 1999). The total mean number of seedlings sampled throughout the plots varied corresponding to season (Tables 1 and 2), the highest mean number of seedlings being recorded in Dec 2000 following the period of highest seedling recruitment. The lowest number of seedlings was recorded in June 2000 corresponding to the period of drought. There were higher numbers of seedlings alive over all the censuses in the uncut plots, and of the cut plots, there were more seedlings recorded in 40% BAR than 100% BAR (Tables 1 and 2). Over time, there were fewer seedlings found alive in both 40% and 100% BAR plots relative to the 0% BAR plots and a higher density of individuals were recorded during the dry season in the 40% than 100% BAR although this effect disappeared in the wet season.

The number of seedlings recruited varied over time corresponding to seasonality (Tables 1 and 2) with higher numbers of seedlings being recruited during the wet season. The highest total number of seedlings recruited (5825) was recorded for the period July–Dec 1999.

Table 1. Results of the repeated-measures ANOVA of light, seedling growth and survival measured within treatment plots following cutting in a dry limestone forest in Jamaica. (Cut = 0%, 40% & 100% BAR.) The variance-covariance structure did not exhibit compound symmetry for all of the analyses, therefore the degrees of freedom in the 'Time' and 'Time × Cut' interactions were multiplied by (1) 0.3574, (2) 0.5008, (3) 0.7909, (4) 0.3478, (5) 0.5191, (6) 0.8768, (7) 0.8429, (8) 0.5158, (9) 0.6405, (10) 0.5710 and (11) 0.9031, (12) 0.6312, (13) 0.9641 and (14) 0.4565 respectively before the F values were examined. Residual degree of freedom for 'Cut' is 6.

Parameters	Effects								
	Cut			Time			Time × Cut		
	df	F	P	df	F	P	df	F	P
Seedlings alive	2	12.5	0.007	4 ¹	12.4	0.002	8 ¹	8.94	0.002
Seedlings dead	2	2.09	0.205	4 ²	14.5	0.001	6 ²	9.26	0.002
Seedling mortality rate	2	1.50	0.296	3 ³	32.0	0.001	6 ³	2.96	0.044
Seedlings recruited	2	3.22	0.112	4 ⁴	9.26	0.002	6 ⁴	3.33	0.085
Absolute growth rate	2	11.0	0.010	2 ⁵	2.47	0.156	4 ⁵	0.87	0.460
Relative growth rate	2	1.20	0.364	2 ⁶	3.05	0.086	4 ⁶	0.85	0.505
% negative growth	2	11.6	0.009	2 ⁷	0.10	0.875	4 ⁷	0.93	0.464
Light (rPAR)	2	16.8	0.003	2 ⁹	96.5	0.001	4 ⁹	12.6	0.001
Percentage survival (initial population)	2	57.3	0.001	3 ¹⁰	78.4	0.001	6 ¹⁰	7.49	0.003
Absolute growth rate (initial popn > 5 mm)	2	41.8	0.001	2 ¹¹	4.02	0.066	4 ¹¹	4.31	0.026
Absolute growth rate (initial popn < 5 mm)	2	4.01	0.078	2 ¹²	10.9	0.009	4 ¹²	2.00	0.191
Percentage individuals showing negative growth (initial popn)	2	22.2	0.002	2 ¹³	0.33	0.575	4 ¹³	0.87	0.480
Mortality rate (initial popn)	2	4.27	0.070	3 ¹⁴	60.8	0.001	6 ¹⁴	11.5	0.003
Percentage survival (recruited cohort)	1	2.17	0.195	1	136	0.001	2	13.4	0.002
Mortality rate (recruited cohort)	2	0.90	0.455	1	61.5	0.001	2	3.48	0.076

Table 2. Means and least significant differences of the means (LSD) of cutting treatments (over all the censuses) and time effects (over all the treatments) generated by the repeated-measures ANOVA on light, seedling growth and survival following cutting in a dry limestone forest in Jamaica.

	rPAR (%)	No. alive	No. dead	Mortality rate (% mo ⁻¹)	No. recruited	Ab. growth (mm mo ⁻¹)	Rel. growth (% mo ⁻¹)	Neg. growth (%)
Cut								
0%	20	897	320	9	367	0.015	2.6	30
40%	28	623	235	7	171	0.022	3.4	28
100%	43	341	160	6	61	0.061	4.3	18
LSD	10	272	193	4	299	0.020	2.7	7
Time								
1 (Jan 1999)	13	593						
2 (July 1999)	38	553	218	6	34	0.027	4.9	26
3 (Dec 1999)		927	120	5	494			
4 (June 2000)	43	446	481	15	0	0.022	1.7	24
5 (Dec 2000)		583	134	5	271	0.050	3.7	25
LSD	5	188	135	2	196	0.030	2.8	11

During the period Dec 1999–June 2000 no seedlings were recruited (Table 2). There were no differences in the recruitment of individuals between treatments over all the censuses (Table 1).

Higher numbers of dead seedlings were recorded during the dry seasons (Tables 1 and 2). The highest total number of dead seedlings recorded was 5685 during the period Dec 1999–June 2000 which was also a period of drought. This high number may be attributed to the large numbers of seedlings recruited during the previous rainy season (Table 2). The mean number of dead individuals recorded among the treatments over all the censuses were not significantly different (Tables 1 and 2).

Mortality rates fluctuated over time (Tables 1 and 2) with the highest rate of mortality occurring during the dry period (14.5%) of Dec 1999–June 2000. There were no differences in mortality rates among the treatments over all censuses (Tables 1 and 2).

In terms of absolute, relative and negative growth rates, corresponding to the periods up to July 1999, June 2000 and Dec 2000 censuses, mean absolute growth rates in each period were 0.027, 0.022 and 0.050 mm mo⁻¹ respectively (Table 2), mean relative growth rates were 4.9, 1.7 and 3.7% mo⁻¹ respectively, while negative growth occurred in 26%, 24% and 25% of the total individuals sampled.

Seedlings in 100% BAR had higher absolute growth rates than seedlings in 40% and 0% BAR plots (Tables 1 and 2). However, there were no differences in relative growth rates over time between the treatments (Tables 1 and 2). The only significant treatment effect occurred during the period July 1999–June 2000, when the 100% BAR plots had a higher relative growth rate than both 0% and 40% BAR plots ($P = 0.005$ and $P = 0.034$). For negative growth rates both 0% and 40% BAR plots had a higher percentage of individuals showing negative growth than 100% BAR plots (Tables 1 and 2). The only treatment effect detected occurred during the period July 1999–June 2000 where the percentage of individuals

showing negative growth was higher in 0% than in 100% BAR ($P = 0.002$) and a similar treatment effect was recorded in June–Dec 2000 ($P = 0.046$).

The fate of the original population and the first recruited cohort

For the original population, the overall percentage survival was greater in both the 0% and 40% BAR plots than the 100% BAR plots (Tables 1 and 3). The percentage survival of all individuals irrespective of treatments, decreased significantly with time (Tables 1 and 3) and seasonality reduced the per cent survival of the original population in the 100% plots relative to the 0% and 40% BAR plots (Table 1).

Mortality rates were highest during the period when the treatments were applied, after which they fluctuated corresponding to the seasons (Tables 1 and 3). Overall, mortality rates were not found to differ significantly between the treatments. However, the effects of the treatments did change over time ($P = 0.003$). Initially the effects of the treatments resulted in higher mortality rates occurring in 100% BAR than 0% and 40% BAR plots. This changed during the wet season that followed with 0% BAR plots recording a higher mortality rate than 100% BAR plots. Subsequently, no significant differences were detected between treatments.

To determine growth rates, individuals of the original population were split into two size classes (individuals > 5 mm and < 5 mm RCD) except for analysis of the per cent of individuals showing negative growth. For the smaller seedlings, overall growth rates were significantly different (Tables 1 and 3), with 100% BAR plots recording higher growth rates than both 0% and 40% BAR plots. Although absolute growth rate increased over time, the increase was not significant (Tables 1 and 3). The change in seasons had a positive effect on individuals in the 100% BAR plot where over time it significantly increased the absolute growth rates recorded relative to the other treat-

Table 3. Means and least significant differences of the means (LSD) of cutting treatments (over all the censuses) and time effects (over all the treatments) measured within treatment plots of light, seedling growth and survival of the initial population and the cohort recruited following cutting in a dry limestone forest in Jamaica. The values presented were generated by the repeated measures ANOVA.

	Survival (%)	Mortality rate (% mo ⁻¹)	Absolute growth (mm mo ⁻¹) (> 5 mm)	Relative growth (% mo ⁻¹) (> 5mm)	Absolute growth (mm mo ⁻¹) (< 5 mm)	Relative growth (% mo ⁻¹) (< 5mm)	Negative growth (%)	Survival (%) (recruited cohort)	Mortality rate (% mo ⁻¹) (recruited cohort)
Cut									
0%	56	5.3	0.105	4.2	0.105	1.1	32	13	26
40%	46	4.7	0.136	4.2	0.136	1.4	31	21	20
100%	26	6.1	0.168	4.4	0.168	1.5	19	11	25
LSD	7	1.2	0.015	1.3	0.539	0.9	5	12	11
Time									
1 (Jan 1999)									
2 (July 1999)	54	11.0	0.104	6.2	0.104	1.0	28		
3 (Dec 1999)	49	1.8							
4 (June 2000)	38	5.6	0.129	3.4	0.129	1.7	25	20	38
5 (Dec 2000)	31	2.9	0.175	3.1	0.175	1.4	29	10	9
LSD	4	1.6	0.013	1.0	0.035	0.6	11	2	8

ments. For larger seedlings the only significant result was that, irrespective of treatments, over time absolute growth increased. Smaller individuals showed similar relative trends, where the relative growth rate of small seedlings increased over time while for larger seedlings there were no significant results.

For the cohort recruited during the period July–Dec 2000, there were no significant differences between treatments but survival was significantly reduced between censuses (Tables 1 and 3). Initially the percentage survival in the 40% BAR plots was higher than in the 100% BAR plots ($P = 0.025$) but a change in seasons reduced this difference and significantly reduced the per cent survival of all the individuals irrespective of treatments. There was a significant reduction in the mortality rate of this cohort over the 1-y period (from 38% after 6 mo to 9.3% after 1 y), but there were no significant differences between the treatments.

Species level

Of the 26 species whose densities were analysed using the repeated-measures ANOVA, 13 returned significant results (Table 4). For *Capparis cynophallophora*, *C. ferruginea* and *Bursera simaruba*, there were higher numbers of seedlings recorded in the uncut plots. The average number of seedlings sampled of these species within all plots varied significantly between censuses (Tables 4 and 5).

For *Bumelia rotundifolia*, the density of individuals changed significantly over time (Tables 4 and 5) in that there was a greater increase in the numbers of individuals being recorded alive in 0% BAR plots than in 40% and 100% BAR plots (Table 4).

The number of seedlings sampled alive for *Comocladia velutina* fluctuated significantly between censuses (Tables 4 and 5), and over time there was an increase in the

number of individuals recorded in the uncut plots corresponding to the seasons (Table 4).

Six species (*Bauhinia divaricata*, *Capparis flexuosa*, *Diospyros tetrasperma*, *Drypetes lateriflora*, *Metopium brownii* and *Ziziphus sarcomphalus*) all showed overall treatment effects and/or differences between treatments at one or more censuses (except for *B. divaricata* where the number of individuals only fluctuated with a change in seasons). In general, the density of these species was higher in the 0% and 40% BAR plots than 100% plots and this higher density was maintained over one, two or three censuses. For *D. tetrasperma*, this occurred due to a difference between treatments in mortality and recruitment of individuals. For the other species, there were higher rates of recruitment and mortality in the 0% and 40% BAR plots than the 100% BAR plots except *Bunchoisia media*, which had no recruitment throughout the study period. One species, *Krugiodendron ferreum* (Vahl) Urb., although there were no overall treatment effects, had higher numbers of seedlings in 0% BAR than 40% and 100% in December 2000 ($P = 0.045$ and $P = 0.018$ respectively).

The light environment

Relative light levels (rPAR) were higher in the 100% BAR plots than in the 0% and 40% plots ($P = 0.003$; Table 1 and 2). Relative light levels increased over time ($P < 0.001$; Table 1 and 2) and over time the treatments increased light levels in the 100% and 40% BAR plots (with rPAR levels in 40% being higher than 100%) relative to 0% plots. The ante-dependence analysis confirmed that the overall rPAR levels differed among the treatments ($P = 0.001$) and that the first treatment effect occurred in the second measurement after the treatments were applied ($P = 0.001$), after which this difference remained until the final measurement.

Table 4. Results of the repeated-measures ANOVA carried out on the number of individuals of 26 species found at each census within the treatment plots (Cut = 0%, 40% and 100% BAR) which returned significant results. For all the species analysed, the variance-covariance structure did not exhibit compound symmetry for all of the analyses, therefore the degrees of freedom in the 'Time' and 'Time × Cut' effects were multiplied by their appropriate correction factors (Table 1).

Species	Effects					
	Cut		Time		Time × Cut	
	F	P	F	P	F	P
<i>Bauhinia divaricata</i> L.	0.17	0.848	7.77	0.005	1.00	0.386
<i>Bumelia rotundifolia</i> Sw.	5.09	0.051	8.48	0.010	4.07	0.038
<i>Bunchosia media</i> (Ait.f.) DC.	2.02	0.213	5.40	0.043	0.38	0.711
<i>Bursera simaruba</i> (L.) Sarg.	6.13	0.035	14.0	0.005	2.72	0.122
<i>Capparis cynophallophora</i> L.	7.06	0.027	11.6	0.002	6.60	0.006
<i>Capparis ferruginea</i> L.	5.26	0.048	12.2	0.007	5.05	0.034
<i>Capparis flexuosa</i> (L.) L.	2.88	0.133	7.68	0.005	0.88	0.493
<i>Comocladia velutina</i> Britton	0.44	0.663	9.39	0.004	8.52	0.002
<i>Diospyros tetrasperma</i> Sw.	2.72	0.144	21.8	0.034	3.09	0.108
<i>Drypetes lateriflora</i> (Sw.) Krug & Urb.	4.12	0.070	4.10	0.001	2.22	0.085
<i>Metopium brownii</i> (Jacq.) Urb.	2.29	0.182	9.16	0.010	2.32	0.141
<i>Thrinax parviflora</i> Sw.	0.45	0.658	7.98	0.012	2.95	0.083
<i>Ziziphus sarcomphalus</i> (L.) M. C. Johnston	4.52	0.063	5.69	0.021	1.58	0.241

Table 5. Means and least significant differences of the means (LSD) of cut and time effects on the density of individuals of 13 species that showed significant treatment and/or time effects. Values were generated by the repeated-measures ANOVA. Species codes are as follows: *Bauhinia divaricata* (BDI), *Bunchosia media* (BME), *Bumelia rotundifolia* (BRO), *Bursera simaruba* (BSI), *Capparis cynophallophora* (CCY), *Capparis ferruginea* (CFE), *Capparis flexuosa* (CFL), *Comocladia velutina* (CVE), *Drypetes lateriflora* (DLA), *Diospyros tetrasperma* (DTE), *Metopium brownii* (MBR), *Thrinax parviflora* (TPA) and *Ziziphus sarcomphalus* (ZSA).

	BDI	BME	BRO	BSI	CCY	CFE	CFL	CVE	DLA	DTE	MBR	TPA	ZSA
Cut													
0%	27	14	14	18	11	49	9	127	28	133	65	80	13
40%	31	9	3	21	5	42	11	71	11	131	33	59	6
100%	24	4	2	4	2	17	3	22	4	69	23	57	5
LSD	32	12	10	11	6	24	7	277	22	76	49	66	7
Time													
1 (Jan 1999)	30	11	6	6	3	29	10	68	15	151	86	79	10
2 (July 1999)	25	10	5	7	4	25	7	83	12	105	32	56	6
3 (Dec 1999)	34	10	11	30	11	58	8	155	21	127	61	90	10
4 (June 2000)	22	8	6	16	6	38	7	23	13	89	7	56	6
5 (Dec 2000)	24	7	4	14	6	32	6	173	9	83	16	46	6
LSD	6	2	2	9	2	12	2	104	6	20	33	20	2

The effects of the light climate

When per cent survival was regressed against light, there was only a significant negative relationship for rPAR measured in July 1999 and the percentage survival of individuals from Jan 1999 to July 1999 (Table 6; Figure 2a). Mortality rates were related to light levels at the end of both periods (Table 6). For the first period (Jan–July 1999), there was a significant positive relationship with rPAR when measured in July 1999 (Figure 2b); this changed to a negative relationship for the period Dec 1999–June 2000 and rPAR recorded in June 2000 (Figure 2c).

For absolute growth rates of the smaller seedlings, during the period July 1999–June 2000 when regressed against rPAR measured at June 2000 there was a significant positive relationship ($P = 0.001$; Figure 2d). The larger seedlings did not show any relationships with

Table 6. Summary of the regression analysis of average light level (rPAR) measured in July 1999 and June 2000 over each plot against the per cent seedling survival at each of the time light was measured, and mortality rates (for the periods Jan–July 1999 and Dec 1999–June 2000), absolute growth rates and per cent of seedlings exhibiting negative growth rates (for the periods Jan 1999–July 1999, and July 1999–June 2000) for the initial population of seedlings. '% Var' is the percentage variance accounted for by the model.

Regression	Relative PAR	
	P	% Var
July 1999		
Light × Seedling survival	0.021	36.9
Light × Seedling mortality rate	0.013	42.3
Light × Absolute growth	0.069	31.0
Light × % Negative growth	0.313	1.2
June 2000		
Light × Seedling survival	0.136	12.9
Light × Seedling mortality rate	0.040	67.3
Light × Absolute growth	0.001	61.8
Light × % Negative growth	0.005	52.0

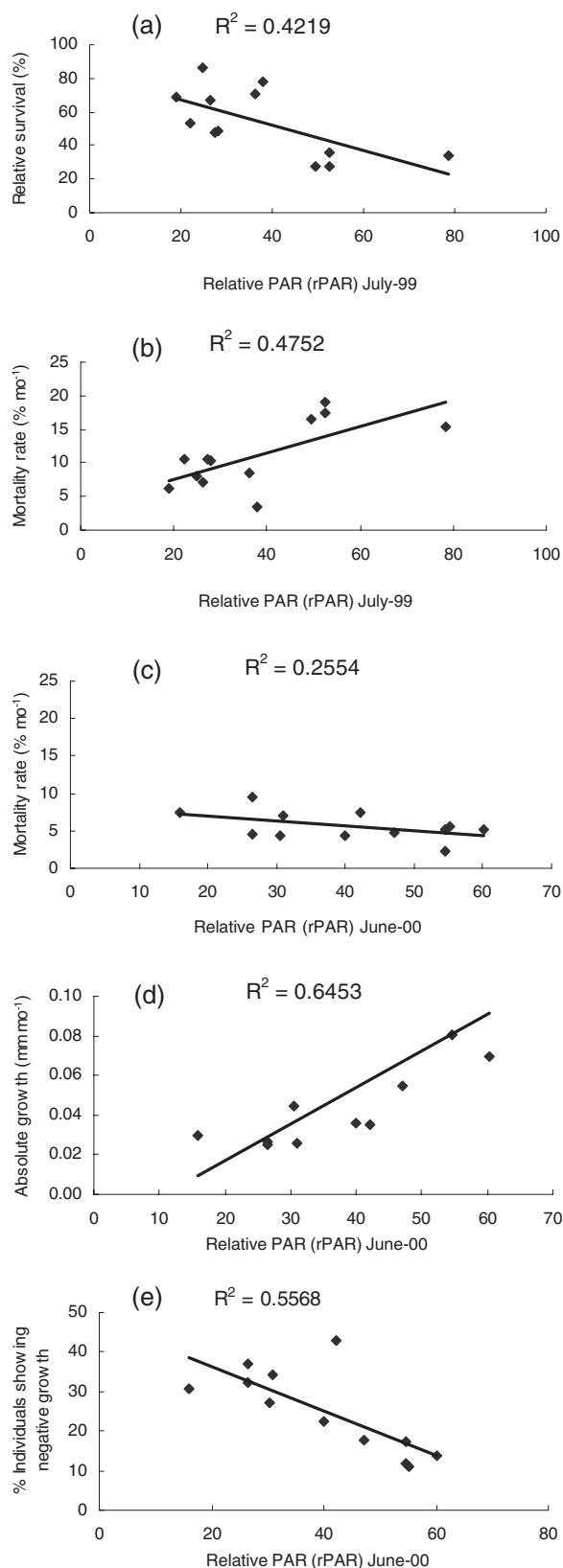


Figure 2. Regression analysis of relative PAR on (a) seedling survival (%) Jan–July 1999 (b) seedling mortality rates (%) Jan–July 1999 (c) seedling mortality rates (%) Dec 1999–June 2000 (d) absolute growth rates (mm mo⁻¹) Dec 1999–June 2000 and (e) percentage of seedlings showing negative growth July 1999–June 2000.

rPAR. For individuals showing negative growth rates regressed against light measured in June 2000, there was a negative relationship obtained for the July 1999–June 2000 period (Table 6; Figure 2e).

Species–light relationships

Regression of rPAR on the number of seedlings showed a significant effect for only six species (Table 7). In July 1999 there was a significant negative relationship for *Capparis cynophallophora* (Table 7). At this time rPAR accounted for 35% of the variation in the number of individuals of this species recorded alive among the plots. In the following dry season (Dec 1999–June 2000) all six species showed a significant negative relationship for number of seedlings alive regressed against rPAR with *C. cynophallophora* having the highest explained variation in the number of seedlings recorded alive (74%; Table 7).

DISCUSSION

The higher seedling density and higher per cent survival in uncut and partially cut plots (even though initial effects were partly a factor of disturbance due to the imposition of the treatments), and strong association with light levels is in keeping with other studies in tropical dry forest. Gerhardt (1996a) investigating the effects of root competition and canopy openness on the survival and growth of seedlings in a secondary dry forest in Costa Rica, found that dry-season survival of seedlings of two dry-forest species was higher in lower light levels. In an African dry tropical forest, Lieberman & Li (1992) found that sheltered well-shaded sites had consistently higher densities of seedlings than exposed, open sites, while Ray & Brown (1995) reported that seedling survivorship was significantly higher in shaded than unshaded plots in a secondary dry forest in the US Virgin Islands. Russell-Smith (1996) working in the monsoon rain forests in northern Australia found that the saplings of species occupying mostly seasonal dry substrates exhibited a clear preference for shaded situations. Gerhardt (1996a) found that seedling responses in dry forest ecosystems were related to drought tolerance rather than shade tolerance and favourable water conditions. Shading improved dry-season survival while competition for moisture had significant effects on seedling performance compared with tree seedlings in the humid tropics.

In this study, seedling numbers were higher in the uncut and partially cut plots but this is not due to a higher seed input. McLaren (2001) showed that disturbance did not affect the weight and number of seeds in the seed rain although the species richness was affected (due to higher numbers of *Bursera simaruba* seeds being dispersed in the cleared plots, and lower numbers of *Canella winterana* (L.) Gaertn.). Also, the levels of disturbance tested

Table 7. Summary of the regression analysis of average light (PAR) measured over each plot against number of seedlings alive of six species that showed significant relationships. Results of the regression analysis are for censuses taken before the application of treatments (Jan 1999), 3 mo after the treatment application (July 1999) and the following dry season (June 2000).

Species	Jan 1999		July 1999		June 2000	
	P	% Var	P	% Var	P	% Var
<i>Bumelia rotundifolia</i>	0.599	–	0.122	14.5	0.002	59.4
<i>Bursera simaruba</i>	0.122	20.7	0.195	7.8	0.012	43.6
<i>Capparis cynophallophora</i>	0.191	8.1	0.024	35.3	0.001	74.2
<i>Capparis ferruginea</i>	0.654	–	0.278	2.8	0.003	56.4
<i>Thrinax parviflora</i>	0.163	10.3	0.427	–	0.001	69.0
<i>Ziziphus sarcomphalus</i>	0.809	–	0.109	–	0.008	47.9

did not significantly alter the rates of recruitment in open plots. However, survival was higher in the uncut plots. Gerhardt (1996a) found that for a dry forest in Costa Rica, the thinning of trees, whilst improving growth during the wet season, had a negative impact on survival during the dry season by exacerbating desiccation of seedlings.

Overall, seedling mortality was higher in the dry season, irrespective of treatment and this was also reflected in both the initial population and the cohort recruited after the treatment. Similar seasonal patterns of mortality were reported for both natural dry forests (Lieberman & Li 1992, Swaine *et al.* 1990) and in experimentally created conditions (Blain & Kellman 1991, Gerhardt 1993, 1996a, b; Hammond 1995, Ray & Brown 1995) where the highest mortality occurred during the dry season. Typical dry-season mortality rates reported in the natural forests include 33% y^{-1} for Pinkwae, Ghana (Lieberman & Li 1992) and 11.0% y^{-1} for the Shai Hills, Ghana (Swaine *et al.* 1990) which are similar to means recorded in the uncut plots in this study. Wet-season mortality was very low: 4% of seedlings in dry forest in Ghana (Lieberman & Li 1992), 2–5% of seedlings in a seasonal dry forest in Costa Rica (Gerhardt 1996a), < 10% for *Swietenia macrophylla* seedlings in Costa Rica (Gerhardt 1996b) as seen in the study (5% for July–Dec 1999 and June–Dec 2000 respectively). However, when seedlings were recruited in high densities in the uncut plots during the wet periods, these high densities were short-lived, as mortality eliminated most of the cohorts within days or weeks of germination (pers. obs.), a similar pattern to that reported by Lieberman & Li (1992).

An indication of high moisture stress is exemplified by the significantly higher occurrence of negative growth rates or diameter shrinkage in the uncut plots, a process known to be a result of moisture stress in tropical dry forest trees (Borchert 1994, Reich & Borchert 1982, Swaine *et al.* 1990) sometimes leading to mortality in seedlings (Gerhardt 1996a). Overall, negative growth rates or diameter shrinkage was more common in uncut and partially cut plots than in clear-cut plots and a similar result was obtained for the initial cohort. The regression showed that the high light/low moisture condition experienced during the dry season also resulted in higher

negative growth/moisture stress under shaded trees than in the open. This may be as a result of a very thin and patchy soil cover (soil only covered *c.* 4% of the area of any of the plots) and the limestone substrate, which is known to cause rapid drainage that increases soil water deficits (Asprey & Loveless 1958, Beard 1955, Kelly *et al.* 1988). Also there may have been higher moisture stress in the more shaded plots due to higher evapotranspiration losses and a higher competition for moisture as a result of a greater number of individuals present. Holmgren *et al.* (1997) observed that an increase in growth or survival under ‘nurse shade’ seems to be a rather general phenomenon in harsh conditions. Facilitative effects are stronger in drier sites and drier years. It would appear that the facilitative effects of the canopy are stronger in drier times, and that alleviation of the moisture stress switches the effect of the interaction from facilitative to competitive.

The recruitment of seedlings showed a strong seasonal pattern being highest during the wet season. Similar seasonal patterns of recruitment were reported for natural dry forests in Ghana (Lieberman & Li 1992, Swaine *et al.* 1990) where for 1 y seedling recruitment increased progressively during the major wet season, reaching a peak at the end of the rainy period at which time approximately 40% of the germination for that year was recorded. Ray & Brown (1995) also found recruitment of individuals not to be significantly different between uncut and cut plots.

Absolute growth was found to be highest in the clear cut plots and showed a positive relationship with increasing light levels. Rincon & Huante (1993) reported that tree seedlings from a Mexican deciduous dry forest showed increased growth rates with increasing light. Gerhardt (1993) investigating tree seedling development in a dry abandoned pasture and forest in Costa Rica found that the highest growth rates were in pasture. Gerhardt & Fredriksson (1995) also found that biomass of roots and shoots of *Swietenia macrophylla* was higher in thinned than unthinned treatments in the forest after just 5 mo of growth, and was higher in a pasture than in the forest suggesting that seedlings of this species are favoured initially by increasing light levels. The trend therefore seems to be that high light levels increase growth, especially

during the wet season, which was the period of highest absolute and relative growth in this study.

The species examined showed different abilities to recover in the newly created environments with the distribution of all seeming to favour uncut and partially cut plots. The shade demand of three species can be assessed by comparison with the results obtained by Ray (1993) and Ray & Brown (1995) reporting on the seedling shade demand and ecological attributes of 10 dry forest tree species in the US Virgin Islands. They determined that for *Capparis cynophallophora* survival was poor without medium shade. Given that the medium shading in their experiment was 20% of full sunlight and in this study the mean per cent of full sunlight (rPAR) in the uncut plots was also 20%, the trend seen for seedling density for this species may indeed be its true ecological character. *Capparis ferruginea* individuals were able to survive and recruit very well in uncut and partially cut plots as opposed to cut plots. *Bursera simaruba*, at the other end of the spectrum, seemed to benefit from disturbance. It was one of two species whose seed dispersal was significantly affected by the treatments (McLaren 2001). Seedling density was significantly higher in partially cut plots than clear-cut plots, higher on average (but not significantly so) in partially cut than uncut plots. Recruitment overall was not significantly affected by the treatments but during the period of highest recruitment (July–Dec 1999), it recruited significantly more seedlings in partially cut plots than clear-cut plots. Its distribution was strongly related to light levels, with light accounting for a high per cent of the variation in the density of individuals. Ray (1993) and Ray & Brown (1995) determined that for *B. simaruba*, survival characteristics were; good survival without shade but survival was enhanced by medium shading. Khurana & Singh (2000) reviewing the ecology of seeds and seedlings in tropical dry forests described the shade demand of *B. simaruba* as facultative, rather than absolute. Overall *B. simaruba* showed good survival characteristics irrespective of treatments. This in part explains the occurrence of emergents of *B. simaruba* in disturbed dry forest throughout Central America (pers. obs.); good dispersal and survival after disturbance, plus the fact that it is not a preferred species for charcoal burners, results in the species being well represented in secondary forests.

Our study indicates that regeneration by seed was not severely affected by this small-scale disturbance. Dry seasons reduced the success rate of regeneration by seed and increased mortality rates. The density of some species was affected by the environmental conditions created by partial and clear cutting, as seasonal effects were more pronounced after disturbance. The only positive effect the treatments had was on growth rates which were highest in the clear-cut plots. Therefore regeneration by seed has to be considered a less important pathway of regeneration than coppice regrowth in response to cutting (McLaren &

McDonald, in press). After the imposition of the treatments, initial coppice regrowth was high with the average diameter recovered after 14 mo approximating to 29% y^{-1} (McLaren & McDonald, in press). This is *c.* 95% more growth increment than measured in seedlings following cutting. It is unlikely that the growth rates of coppice shoots will be maintained over a long period of time but after 14 months this small-scale disturbance did not seem to affect the ability of these species to replace themselves *in situ*.

Some species benefited from the disturbance, and the disturbance-sensitive species may be limited at the establishment phase of the regeneration cycle. It would appear that the facilitative effects of the canopy are stronger in drier times, and that alleviation of the moisture stress switches the effect of the interaction from facilitative to competitive. Most species have some degree of shade demand and the absence of any pioneers suggests that the gap dynamics of regeneration observed in humid forests do not apply in this dry forest. Larger gaps may have brought about a more substantial change in species composition, but the relative contribution of regrowth from coppicing compared with regeneration from seed renders this unlikely. Furthermore, the gap size in our study was of a comparable size to studies in moist forests which did show regeneration by pioneer species (e.g. Brokaw & Scheiner 1989, van der Meer *et al.* 1998). In this forest, with its sparse crowns, lack of seed bank and unfavourable conditions for seedling establishment, coppicing is the main mechanism of regeneration. This will result in a decline in genetic diversity over time, which has important implications for the future management of these forests if the current rate of clearance continues.

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