

## Dynamics of pioneer and primary successional stage trees in a logged Trinidadian tropical rainforest and the influence of drought

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**Abstract:** This study tested the hypothesis that pioneer and primary stage tree species responded differently to drought events which are thought to be increasing in importance as an ecological driver in the eastern Caribbean and northern South America. Data were collected and analyzed from trees  $\geq 20$  cm dbh from 18 one ha plots over a 13 year period in a seasonal evergreen rainforest in Trinidad. Total, pioneer and primary species stem density changes were compared between 1983-84 and 1996-97. Stem density changes for individual species were also compared. Stem density changes of the different successional stage species were compared on a shorter timescale of before and after a drought. Mortality and recruitment rates for all stems and for each successional stage were tested for difference between drought and non-drought intervals. Total and primary stem density showed significant increases over 13 yrs but no significant difference at the shorter time scale before and after drought. Two primary and two pioneer stage species increased in stem density over 13 years while one species, a pioneer, decreased in stem density. Mortality and recruitment rates of pioneer and primary stage species were different and both were affected by drought conditions, but none more than the other. The results were discussed in the light of past logging history of the forest and projected climate change for the region.

**Resumen:** En el presente estudio se puso a prueba la hipótesis de que las especies arbóreas pioneras y de etapas primarias responden de manera diferente a eventos de sequía. Se piensa que la importancia de éstos como controladores ecológicos ha aumentado en la parte oriental del Caribe y el norte de Sudamérica. Se obtuvieron y analizaron datos para árboles  $\geq 20$  cm dap en 18 parcelas de 1-ha durante un periodo de 13 años en un bosque siempreverde estacional en Trinidad. Los cambios en la densidad total de tallos y de las densidades de especies pioneras y de primarias fueron comparados entre 1983-84 y 1996-97. También se compararon los cambios en la densidad de tallos de algunas especies. Los cambios en la densidad de tallos de las especies de diferentes etapas sucesionales fueron comparados sobre una base temporal más corta, antes y después de una sequía. Las tasas de mortalidad y reclutamiento para todos los tallos y para los de cada etapa sucesional fueron comparadas entre los periodos de sequía y en los que no la hubo. La densidad total de tallos y las densidades de especies primarias se incrementaron significativamente a lo largo de los 13 años, pero no hubo una diferencia significativa en la escala temporal más corta para comparar antes y después de la sequía. Las densidades de tallos de dos especies primarias y dos pioneras se incrementaron a lo

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largo de los 13 años, mientras que la densidad de tallos de una especie pionera decreció. Las tasas de mortalidad y reclutamiento de especies de etapas pioneras y primarias fueron diferentes y ambas fueron afectadas por las condiciones de sequía, pero no una más que la otra. Los resultados fueron discutidos a la luz de la historia pasada de extracción de madera en el bosque y del cambio climático proyectado para la región.

**Resumo:** Neste estudo testou-se a hipótese de que as espécies arbóreas no estágio pioneiro e primário respondem diferentemente a surtos de seca que se pensa vêm aumentando de importância como uma derivação ecológica nas Caraíbas orientais e norte da América do Sul. Os dados foram colhidos numa floresta de chuvas na Trindade e analisadas árvores com  $DAP \geq 20$  cm em 18 parcelas de 1 ha durante um período de 13 anos. As mudanças na densidade total de espécies, das pioneiras e das primárias, foram comparadas entre 1983-84 e 1996-97. As mudanças na densidade dos troncos para as espécies individuais foram, igualmente, comparadas. As mudanças de densidade das espécies nos diferentes estádios sucessionais foram comparadas numa escala temporal mais curta, antes e depois a seca. As taxas de mortalidade e a recuperação para todos os troncos e para cada estágio sucessionais foram testadas quanto às diferenças entre os intervalos de seca e não-seca. A densidade total e primária de troncos mostrou um aumento significativo ao longo dos 13 anos mas não significativas diferenças numa escala temporal curta antes e depois da seca. A densidade de troncos entre duas espécies primárias e duas pioneiras aumentou ao longo dos 13 anos enquanto uma espécie, uma pioneira, decresceu quanto à densidade dos troncos. As taxas de mortalidade e recuperação de espécies pioneiras e primárias foram diferentes e ambas foram afectadas pelas condições de seca, mas nenhuma mais do que a outra. Os resultados foram discutidos à luz da história de abate da floresta e das mudanças climáticas projectadas para a região.

**Key words:** Climate change, drought, mortality rate, neotropics, pioneer tree, primary tree, recruitment rate, Trinidad and Tobago, tropical rainforest.

## Introduction

Two forests can have much the same standing biomass at equilibrium and yet differ a great deal in the mean turnover rates of their trees. The general pattern emerging from studies of a variety of wet tropical forests is of a high rate of mortality and turnover (Phillips & Gentry 1994; Richards 1996; Sheil *et al.* 2000; Swaine & Lieberman 1987). This has implications for studies of population dynamics, as well as for such practical problems as diversity maintenance and timber production (Phillips & Gentry 1994; Sheil *et al.* 2000; Swaine & Lieberman 1987; Whitmore 1978). Changes in turnover rates arising from long-term climate changes and increases in the frequency and severity of the El Niño-Southern

Oscillation (ENSO) are thus of significance in tropical forest ecology and management.

Our focus is on possible effects due to drought in the eastern Caribbean (Holmgren *et al.* 2001), in particular the continental island of Trinidad. We analyze 13 years of mortality and recruitment data for rainforest canopy trees in southeastern Trinidad, with the purpose of uncovering meaningful differences between species of different stages of succession.

Mortality rates of different regeneration guilds in tropical forests have been the subject of several studies. In line with conventional wisdom, Swaine *et al.* (1987) concluded that early successional stage trees have much higher mortality than later stages. Manokaran & Kochummen (1987) confirmed this difference in rainforest trees of at least 10 cm dbh in

Southeast Asia. Slik (2004) found drought increased mortality in a Bornean tropical rainforest, particularly in logged forests, due to an extremely high mortality rate of pioneers in the genus *Macaranga*, but also noted greater recruitment of the same species in the gaps left after mortality due to the drought. He concluded that drought is an ecological driving force for change in tree species composition in tropical forests. However, Condit *et al.* (1995), found differential mortality between regeneration guilds to be true only for size classes below 10 cm dbh at a neotropical locality; in larger size classes they found no difference between early and later successional stage species. One factor that may impede a decisive comparison between studies is the difficulty in assigning species according to different successional stages in what is, in fact, a continuum. In the absence of even an arbitrary standard classification, it is hard to be sure whether the apparently disparate results of Manokaran & Kochummen (1987) and Condit *et al.* (1995), for example, reflect a real difference between forests or simply a methodological artifact.

The responses of tropical forests to climate change have been studied by means of models of expected overall effects in particular areas (Bebber *et al.* 2004; Condit *et al.* 1995; Connell & Green 2000; Delissio & Primack 2003). The main parameters that are likely to affect tropical forests are the amount and seasonality of rainfall, temperature, and CO<sub>2</sub> levels (Sear *et al.* 2001). In the eastern Caribbean, the most recent period of atmospheric warming is associated with an average decrease in rainfall in the early wet season (June-August), an average increase at the end of the wet season (December-February), with a net slight decrease in annual rainfall (New *et al.* 2001; Sear *et al.* 2001). These changes in annual rainfall and seasonality are likely to be overlain by more extreme drought and flooding events associated with more intense ENSO patterns (Holmgren *et al.* 2001). Taken together, recent data suggest that the eastern Caribbean will be subject to more severe seasonal droughts in the coming years.

A number of studies have found the numerical ratio of pioneer to primary-stage

species is decreased by drought because the pioneer species appear to be more susceptible to water stress and show a higher mortality as a result (Condit *et al.* 1995; Swaine & Hall 1983). Other studies, in contrast, predict that pioneer species will survive and grow better than primary-stage species under increased CO<sub>2</sub> levels, another associate of global climate change in the present period (Reekie & Bazzaz 1989; Winter & Lovelock 1999). The relative importance of these and other ecological parameters is a key unsettled question. In an undisturbed forest of the Brazilian Amazon, stem density of pioneers showed no significant change over 18 years (Laurance *et al.* 2004). In the same study, fast-growing old-growth species increased in stem density and/or basal area, while slow-growing species in the same habitat decreased. Laurance *et al.* (2004) suggested that increased primary productivity in old-growth forest due to higher CO<sub>2</sub> levels and insolation were behind this pattern.

In this paper, we examine a 13-year record of mortality and recruitment of canopy trees in a selectively logged rainforest in southeastern Trinidad. Our aims were to determine how mortality and recruitment rates of different regeneration guilds change in response to drought and how these various responses contribute to changes in mortality and recruitment of the canopy as a whole.

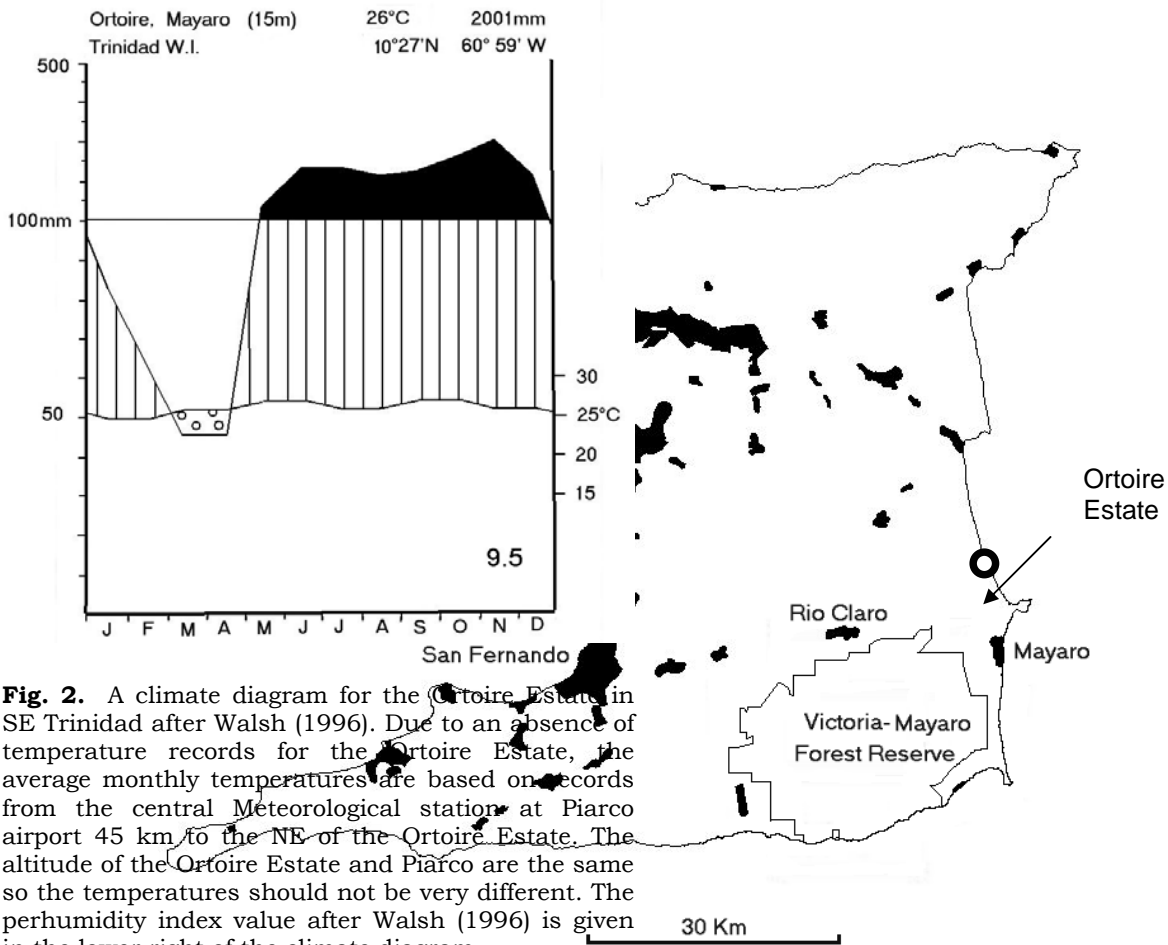
## Materials and methods

### *Site description*

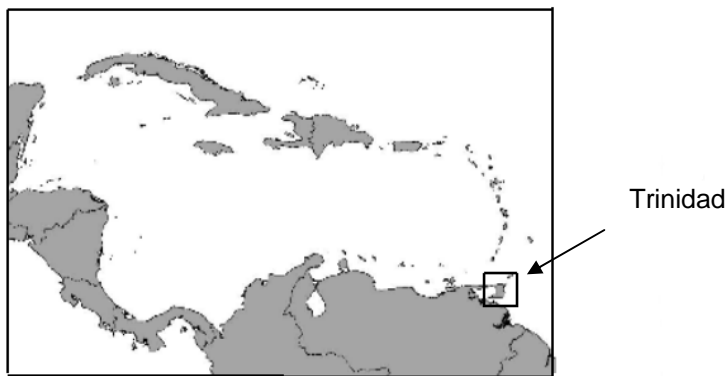
Trinidad is an inshore island approximately 12 km off the coast of northern South America at 10°30'N and 61°10'E (Fig. 1). Trinidad is in the zone of marginal or seasonal rainforest and was probably part of the dry forest zone covering the Caribbean coastal regions of Columbia and Venezuela during glacial periods in the upper Pleistocene (Pennington *et al.* 2000). In the current inter-glacial and prior to the arrival of humans, Trinidad was thought to be mainly covered with lowland tropical rain forest that was very similar in species composition to that found on the South American continent (Beard 1946). Up to 65% of the forest has since been converted to sugar or cocoa plantation but two large blocks of forest

remain. The Victoria-Mayaro Forest Reserve (VMFR) is the second largest and is located in the SE of the island. The VMFR is flat to undulating with small steep hills rising 10 to 15 m. Altitude in the VMFR ranges from 25 m to over 80 m a.s.l. and it is bounded to the south by the Trinity Hills which rise up to 330 m. The rainfall in the VMFR is approximately 2000 mm per annum. There is a distinct dry season from January to May each year, but the monthly average falls below 50 mm for only March and April during this period (Fig. 2) and the forest is evergreen. The perhumidity index (Walsh 1996) for the Ortioire Estate rainfall station (the closest rainfall station to the VMFR) is 9.5,

placing it in the Tropical Wet Seasonal climatic class (Walsh 1996). The Holdridge life zone classification for the VMFR is Tropical Moist Forest (Nelson 2005). The forest was classified by Beard (1946) as mainly evergreen seasonal forest with two main faciatiions: the Crappo-Carat faciation which is a mixed forest in which *Carapa guianensis* Aubl. (Meliaceae) and the Carat Palm *Sabal mauritiformis* (H.Karst.) Griseb. & H.Wendl. are common. The second faciation is the Mora faciation that has the same tree species composition as the Crappo-Carat faciation with the addition of *Mora excelsa* Benth. (Leguminosae) which dominates the canopy.



**Fig. 2.** A climate diagram for the Ortoire Estate in SE Trinidad after Walsh (1996). Due to an absence of temperature records for the Ortoire Estate, the average monthly temperatures are based on records from the central Meteorological station at Piarco airport 45 km to the NE of the Ortoire Estate. The altitude of the Ortoire Estate and Piarco are the same so the temperatures should not be very different. The perhumidex index value after Walsh (1996) is given in the lower right of the climate diagram.



**Fig. 1.** The location of the Victoria-Mayaro Forest Reserve (VMFR) in Trinidad W.I.

Monthly rainfall readings for the Government water authority (WASA) measurement station on the Ortoire Estate approximately 10 km to the north-east of the study area were obtained for the period 1981-1996. A year was classed as a drought year when the number of consecutive months with

rainfall less than 50 mm (drought months) was greater than the average annual consecutive number of drought months calculated for the thirteen years of rainfall measurements.

A greater number of sequential drought months (rainfall < 50 mm) than the ten year average of 2 months occurred at the Ortoire

Estate in 1987, 1988, 1994 and 1995 when there were four drought months in succession (Fig. 3). No other years had runs of drought months above the ten year average during the period of monitoring apart from 1990 in which the months January to April had figures of 47, 30, 29 and 46 mm respectively and so was considered a marginal drought year and not considered as such in the analysis. The drought periods fell in the intervals between census 2 and 3 and between censuses 4, 5 and 6.

*Forest management and permanent sample plots (PSPs)*

The forests of the VMFR in which the sample plots used in this study (permanent sample plots or PSPs) are located are logged according to a periodic block system (Clubbe & Jhilmit 1992). In this system blocks 160-320 hectares in area are opened for harvesting every 30 yrs. Forestry Division personnel select trees for harvesting at a density of approximately 2-4 trees per hectare. Harvesting takes place over 2 yrs at the end of which the block is closed once more for 30 yrs. The network of PSPs was established starting in 1983 to estimate timber yield.

The data analyzed in this paper were collected by personnel of the Forest Research, Inventory and Management (FRIM) section of the Forestry Division, Ministry of Agriculture and Land Resources in Trinidad W.I.. It was extracted from a sub-set of the PSPs set up in the VMFR in 1983-90. Of the 86 PSPs that were established 18 were included in the analysis for this paper. Each of the PSPs that were used was established in 1983-84 and was censused five times. Other PSPs were left out of the analysis because they were established later than 1983-84, were affected by logging or damaged by fire during the period of monitoring or were not

censused five times. Each census took between 12 and 19 months to complete and the time between the censuses ranged from 36 to 45 months (Table 1).

**Table 1.** Periods of census of the permanent sample plots (PSPs) from 1983 to 1997.

	Census 1	Census 2	Census 3	Census 4	Census 5	Census 6
Period of Census	3/83 to 7/84	2/85 to 9/86	4/88 to 6/89	1/92 to 3/93	3/94 to 3/95	3/96 to 3/97
No. of Months	16	19	14	14	12	12
Mid - point of Census	11/83	11/85	11/88	8/92	9/94	9/96

FRIM personnel set up and measured each 1 ha (100 m by 100 m) PSP. Tree identity, dbh and total height of all stems  $\geq 20$  cm dbh in each PSP were measured at the first census. In addition, the dbh of 7 species (*Carapa guianensis*, *Eschweilera subglandulosa* (Steud ex. Berg) Miers, *Guarea guidonia* (L.) Sleumer, *Mora excelsa*, *Spondias mombin* L., *Sterculia pruriens* (Aubl.) K.Schum. and *Terminalia amazonia* (J.F. Gmel.) Excell) that are important for timber production in the VMFR were recorded for stems  $\geq 10$  cm dbh. Stems were individually marked and the same point on the trunk was measured at each subsequent census. Also at each subsequent census, death or recruitment of new stems into the  $\geq 20$  cm size class ( $\geq 10$  cm dbh for the above species) was noted. FRIM personnel identified each stem to common name. The authors then converted these to species level names, where possible and genus level names where several species were lumped under a single common name (e.g. Pois Doux = *Inga* sp).

Species were classified as either primary stage species or pioneer stage species. Primary stage species were characteristic of undisturbed, old growth forest and species that could regenerate in the deep shade found under the closed canopy of these forests. Pioneer species were those species that could not regenerate under a closed canopy but required some level of disturbance to open up gaps in the canopy. They are, therefore, characteristic of disturbed forests. Marshall (1939) classified a large percentage of the native trees of Trinidad and Tobago as shade bearers, moderate shade bearers, moderate pioneers and pioneers. This classification was adopted by this study with shade bearers and

moderate shade bearers taken to mean primary stage species and moderate pioneers and pioneers lumped together as pioneers (Appendix 1). Species not classified by Marshall (1939) but encountered in the PSPs were classified using other material such as Beard (unpublished) and the authors' personal experience.

#### *Data manipulation and statistical analysis*

(a) *Changes in stem density:* Changes in total stem density in plots (stems  $\geq 20$  cm dbh) from 1983 to 1996 were examined using a Wilcoxon matched pairs signed ranks test to get an idea of the overall impact of the relative rates of recruitment and mortality over the 13 year interval. A non-parametric test was selected as it was determined the stem density data for the different intervals were not all normally distributed (using the Kolmogorov-Smirnov statistic, with a Lilliefors significance level for testing normality). The change in stem density of pioneer and primary species guilds between 1983 and 1996 were also tested using a Wilcoxon matched pairs signed ranks test. In addition, the changes in stem densities of species that occurred in at least 9 of the 18 plots considered were also examined using the same statistical test. The opportunity was also taken to include the 10-20 cm dbh data for the seven important timber species and the changes in stem density for these species were compared using stems  $\geq 10$  cm dbh in separate Wilcoxon matched pairs tests.

(b) *Changes in stem density in drought intervals:* Stem densities in plots before and after a drought interval were examined for changes for pioneer and primary species guilds using a non-parametric 2-way ANOVA by ranks (Barnard *et al.* 2001). Changes in stem density

were tested to give an idea of the impact of the drought interval on the forest community composition specifically looking at how the different regeneration guilds responded. Each drought interval was tested individually.

(c) *Changes in mortality and recruitment rates in drought intervals:* Mortality and recruitment rates were calculated for each PSP using the equation proposed by Sheil *et al.* (1995) for mortality and the algebraically equivalent equation proposed by Sheil *et al.* (2000) for recruitment. Mortality and recruitment rates were calculated separately for the two regeneration guilds. The mortality and recruitment rates of intervals in which droughts occurred were compared with non-drought intervals of similar length to minimize the confounding effects of census periods of different length (Sheil & May 1996). The rates for the pioneer and primary species guilds in the drought-affected second interval between censuses were compared to the third interval using a non-parametric 2-way ANOVA by ranks (Barnard *et al.* 2001). The rates for pioneers and primary species guilds were similarly compared between the drought affected second interval between censuses and the fourth interval.

## **Results**

The overall changes in stem density from 1983 to 1996 were not significant when all the stems were considered together ( $Z = -0.644$ ,  $p = 0.519$ ), however, when the different regeneration guilds were considered separately the primary species showed a significant increase in stem density ( $Z = -3.506$ ,  $p < 0.001$ ) and the pioneers showed a significant downward trend ( $Z = -1.967$ ,  $p = 0.049$ ) (Table 2).

Of the 93 species recorded for the plots considered, 24 occurred in nine or more plots and were included in the analysis of individual species (Table 3). Five of the species showed a significant change in stem density from the first to the last census; four increased and one decreased. The species that increased significantly were two primary stage species, *Mora excelsa* (from 44.67 stems per hectare to 48.39,  $Z = -2.603$ ,  $p = 0.009$ ) and *Sterculia pruriens* (from 3.39 stems per hectare to 4.17,  $Z = -2.032$ ,  $p = 0.042$ ), and two pioneer stage

species *Coccoloba latifolia* Lam. (from 1.22 to 2.00,  $Z = -2.325$ ,  $p = 0.020$ ) and *Spondias mombin* (from 4.94 to 5.61,  $Z = -2.448$ ,  $p = 0.014$ ). The species that decreased significantly was the pioneer species *Cecropia peltata* L. (from 12.22 to 7.56,  $Z = -2.798$ ,  $p = 0.005$ ). When the change in stem densities from the 7 timber species that were recorded to 10 cm dbh was examined using the extra data, 3 species showed a significant fall in stem density (Table 4). All of the 3 species were primary stage species; *Carapa guianensis* (from 33.94 stems

**Table 2.** Stem density changes from 1983-84 to 1996-97 for primary and pioneer stage trees  $\geq 20$  cm DBH.

Guild	Median Stem Density		Wilcoxin Paired Sign Ranks	
	1983-84	1996-97	Z	Sig. (Two Tailed)
All Stems	186.5	194	-0.644	0.519
Primary	159	169	-3.506	< 0.001
Pioneer	28	26	-1.967	0.049

**Table 3.** Changes in stem densities of tree species between 1983 and 1996 in the Victoria-Mayaro Forest Reserve, Trinidad W.I. All stems  $\geq 20$  cm dbh. Species in **bold** changed significantly.

Species	Successional Position	Median Stem Density		Wilcoxin Paired Sign Ranks	
		1983-84	1996-97	Z	Sig. (two tailed)
<i>Carapa guianensis</i>	Primary	16.5	18.0	-1.821	0.069
<i>Casearia decandra</i>	Pioneer	1.0	1.0	-0.347	0.729
<b><i>Cecropia peltata</i></b>	<b>Pioneer</b>	<b>11.5</b>	<b>6.0</b>	<b>-2.798</b>	<b>0.005</b>
<b><i>Coccoloba latifolia</i></b>	<b>Pioneer</b>	<b>0.0</b>	<b>1.0</b>	<b>-2.325</b>	<b>0.020</b>
<i>Cordia panamensis</i>	Pioneer	1.5	2.0	-1.623	0.105
<i>Pterocarpus rohrii</i>	Primary	0.0	0.0	0.000	1.000
<i>Eschweilera subglandulosa</i>	Primary	3.0	3.0	-0.378	0.705
<i>Garcinia humilus</i>	Primary	0.5	0.5	-0.743	0.458
<i>Guarea guidonia</i>	Primary	1.5	1.0	-0.256	0.798
<i>Inga spp</i>	Primary	3.5	4.0	-0.356	0.722
<i>Manilkara bidentata</i>	Primary	0.0	0.0	-1.414	0.157
<b><i>Mora excelsa</i></b>	<b>Primary</b>	<b>32.0</b>	<b>37.5</b>	<b>-2.603</b>	<b>0.009</b>
<i>Mouriri rhizophorifolia</i>	Primary	0.5	1.0	-1.633	0.102
<i>Myrcia/Marlierea ferruginea</i>	Primary	0.0	0.0	-1.807	0.071
<i>Pachira insignis</i>	Primary	6.5	6.5	-0.087	0.931
<i>Pentaclethra macroloba</i>	Primary	48.0	47.0	-1.085	0.278
<i>Pouteria coriacea</i>	Primary	1.0	1.0	-1.342	0.180
<i>Rollinia exsucca</i>	Pioneer	0.5	0.5	-1.134	0.257
<b><i>Spondias mombin</i></b>	<b>Pioneer</b>	<b>4.5</b>	<b>5.0</b>	<b>-2.448</b>	<b>0.014</b>
<b><i>Sterculia pruriens</i></b>	<b>Primary</b>	<b>3.4</b>	<b>4.1</b>	<b>-2.032</b>	<b>0.042</b>
<i>Swartzia pinnata</i>	Primary	0.5	1.0	-0.333	0.739
<i>Terminalia amazonia</i>	Pioneer	0.0	0.5	-1.134	0.257
<i>Trichilia pleeana</i>	Primary	1.5	2.0	-1.026	0.305
<i>Vismia guianensis</i>	Pioneer	1.0	0.5	-1.809	0.070

per hectare to 31.39,  $Z = -2.193$ ,  $p = 0.028$ ); 2.633,  $p = 0.008$ ) and *Mora excelsa* (from 85.44  
*Guarea guidonia* (from 14.06 to 11.89,  $Z = -$  to 80.94,  $Z = -2.807$ ,  $p = 0.005$ ).

**Table 4.** Changes in stem densities of seven important timber tree species between 1983 and 1996 in the Victoria-Mayaro Forest Reserve, Trinidad W.I. All stems  $\geq 10$  cm dbh. Species in **bold** changed significantly.

Species	Successional Position	Median Stem Density		Wilcoxin Paired Sign Ranks	
		1983-84	1996-97	Z	Sig. (two tailed)
<b><i>Carapa guianensis</i></b>	<b>Primary</b>	<b>36.50</b>	<b>31.00</b>	<b>-2.193</b>	<b>0.028</b>
<i>Eschweilera subglandulosa</i>	Primary	7.50	6.50	-1.897	0.058
<b><i>Guarea guidonia</i></b>	<b>Primary</b>	<b>13.50</b>	<b>10.50</b>	<b>-2.633</b>	<b>0.008</b>
<b><i>Mora excelsa</i></b>	<b>Primary</b>	<b>66.50</b>	<b>63.50</b>	<b>-2.807</b>	<b>0.005</b>
<i>Spondias mombin</i>	Pioneer	5.50	6.00	-0.953	0.341
<i>Sterculia pruriens</i>	Primary	6.50	8.00	-1.938	0.053
<i>Terminalia amazonia</i>	Pioneer	2.00	0.50	-1.903	0.057

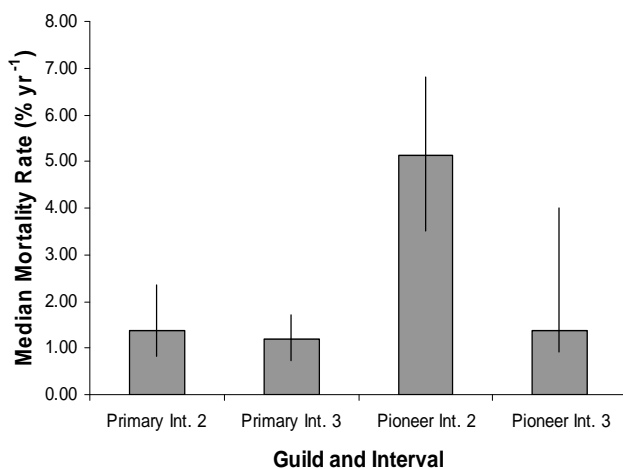
Changes in stem density of the different regeneration guilds in plots after drought intervals were uniformly non-significant across the three drought intervals tested.

When mortality and recruitment rates were compared between drought and non-drought intervals of similar length, it was found mortality rates were significantly higher overall in interval 2 (drought) compared to interval 3 (non-drought) ( $H = 4.912$ ,  $DF = 1$ ,  $p < 0.05$ ) (Fig. 4) and pioneer mortality rates were significantly higher compared to primary species ( $H = 10.770$ ,  $DF = 1$ ,  $p < 0.01$ ). It did not appear that the drought affected the pioneers more than the primary stage species, as the interaction between the factors was non-significant ( $H = 2.622$ ,  $DF = 1$ ,  $p > 0.05$ ). When mortality rates were compared between interval 4 (drought) and interval 1 (non-

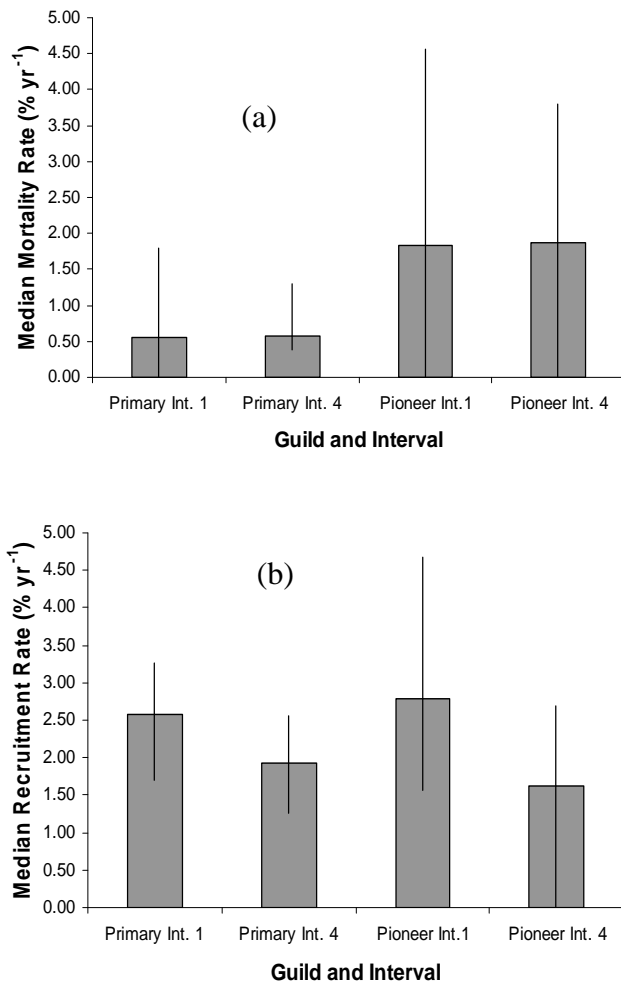
drought) the overall mortality was not significantly higher in the drought interval ( $H = 0.010$ ,  $DF = 1$ ,  $p > 0.05$ ) but the mortality of the pioneers was significantly higher than primary species across both intervals ( $H = 4.009$ ,  $DF = 1$ ,  $p < 0.05$ ) (Fig. 5a). The interaction between the factors in the ANOVA was again non-significant ( $H = 0.117$ ,  $DF = 1$ ,  $p > 0.05$ ).

Between intervals 2 and 3, recruitment rates were not significantly different between regeneration guilds ( $H = 0.493$ ,  $DF = 1$ ,  $p > 0.05$ ) nor between drought intervals and non-drought intervals ( $H = 1.581$ ,  $DF = 1$ ,  $p > 0.05$ ). The interaction between the factors was also non-significant ( $H = 1.573$ ,  $DF = 1$ ,  $p > 0.05$ ). When recruitment rates were compared between intervals 1 (non-drought) and 4 (drought), a significantly higher rate was observed in the non-drought interval ( $H = 5.935$ ,  $DF = 1$ ,  $p < 0.05$ ) (Fig. 5b) but the difference between guilds was non-significant ( $H = 0.001$ ,  $DF = 1$ ,  $p > 0.05$ ) and the drought did not affect one guild to a greater extent over the other ( $H = 0.668$ ,  $DF = 1$ ,  $p > 0.05$ ).

## Discussion



**Fig. 4.** Median mortality rates in primary stage species and pioneer stage species. Bars are the 95% confidence interval. Interval 2 is the drought interval and interval 3 is the non-drought interval.



**Fig. 5.** Median mortality (a) and recruitment rates (b) in primary stage species and pioneer stage species. Bars are the 95% confidence interval. Interval 4 is the drought interval and interval 1 is the non-drought interval.

The overall increase in stem density, particularly by primary stage species, indicates the forest in the VMFR is a recovering secondary forest (Richards 1996). The forest appears to be stage iii as classified by Richards (1996) where biomass is increasing, late secondary species are still present (e.g., *Spondias mombin*) and primary stage individuals are increasing in number (e.g., *Mora excelsa* and *Carapa guianensis*). The disturbance that initiated the secondary succession in this case is probably logging.

The changes in individual species stem densities are also consistent with a return to a more mature forest. It is interesting to note the

reduction in the primary stage species stems in the 10 to 20 cm dbh size class while the density of stems in the size classes above 20 cm dbh increased. It is likely high numbers of smaller stems characteristic of earlier successional stages are giving way to larger stems at lower densities as the smaller stems grow larger and monopolize the resources.

There appears to be a bias against large gap species such as *C. peltata* that are declining even in the larger size classes. It is more difficult to separate the small gap pioneers (the species that persist in the canopy until later succession stages) from primary stage species as representatives from both groups appeared to have an increasing density of stems  $\geq 20$  cm dbh over the 13 year period. However, when the 10 to 20 cm dbh size class is added to the data set it appears that slow growing, deep shade primary stage species show a trend of decreasing stem density but faster growing, persistent pioneer species such as *Spondias mombin* are increasing in stem density. It is not possible to discern whether the most important driving force in the changes taking place in the forest is either the recovery of forest from logging disturbance or a more deterministic, slow change from changes in climate as suggested by Laurance *et al.* (2004) for an undisturbed central Amazonian forest. Both processes may be operating as it would appear the small gap or persistent pioneers are increasing in density even though the plots used have not been disturbed by logging for close to 30 years and these species should be decreasing in density by now Richards (1996). Laurance *et al.* (2004) found it was species with this type of life history strategy that were increasing in stem density in their "undisturbed" forest. They speculated that the increase in stem density was due to the ability of these species to better utilize the increase in resources (insolation- due to more cloud free days and CO<sub>2</sub>) associated with global climate changes.

The lack of stem density changes before and after a drought interval for either primary stage species or pioneer species indicates that individual droughts in this forest are not favouring primary stage species over pioneer species enough to change the stem densities

significantly in this time scale. Higher mortality rates are found in pioneer species compared to primary stage species in general, and mortality rates in both primary and pioneer species appear to be exacerbated by drought but the difference in mortality rates between the guilds do not appear to be significantly changed by drought. Other studies have found mortality rates are promoted by drought conditions (Condit *et al.* 1992, 1995; Hubbell & Foster 1990) and some have found that pioneer species are more affected than primary stage species (Manokaran & Kochummen 1987 Swaine *et al.* 1987). A greater difference in the pioneer stem mortality rates may have failed to show in this study due to the lumping of early pioneer stage or large gap species (e.g., *Cecropia peltata*) with pioneer stage species that persist in the canopy into the primary stage (e.g., *Spondias mombin*). The differing responses of these two pioneers may have cancelled each other out in terms of a significant change in mortality with drought. The classification system proposed by Marshall (1939) could be modified in future analyses to better reflect the differences between life-cycle lengths of the pioneer species.

The overall stem density change over the longer scale of thirteen years indicates the forest is returning to a more primary-stage species dominated forest, but the change does not show up on a shorter time scale and droughts do not appear to influence the rate at which the process is continuing. There may be time lag in mortality and recruitment after a drought event so that large trees will only succumb months or years after the drought event blurring the mortality signature of a drought. Unfortunately it is not possible to test this phenomenon with these data. More detailed mortality records taken at shorter time intervals may shed more light on this process that may be contributing to a Type II error.

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**Appendix 1.** Classification of tree species of Trinidad and Tobago into Pioneer and Shade-Bearer (Primary) species according to Marshall (1936). Species included in Marshall (1936) but not classified have been omitted.

Shade Bearers and Moderate Shade Bearers (Primary Species)	Pioneers and Moderate Pioneers
Anacardiaceae	Acanthaceae
<i>Tapirira guianensis</i>	<i>Bravaisia integerrima</i>
Annonaceae	Anacardiaceae
<i>Duguetia lucida</i>	<i>Spondias mombin</i>
<i>Rollinia mucosa</i>	Annonaceae
Apocynaceae	<i>Rollinia exsucca</i>
<i>Tabernaemontana undulata</i>	Araliaceae
Bignoniaceae	<i>Schefflera morototoni</i>
<i>Tabebuia stenocalyx</i>	Avicenniaceae
Bombacaceae	<i>Avicennia germinans</i>
<i>Pachira insignis</i>	<i>Avicennia schaueriana</i>
Burseraceae	Bignoniaceae
<i>Protium guianense</i>	<i>Crescentia cujete</i>
Capparaceae	<i>Tabebuia chrysantha</i>
<i>Morisonia americana</i>	<i>Tabebuia serratifolia</i>

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## Appendix 1. continued.

Chrysobalanaceae	Bombacaceae
<i>Hirtella racemosa</i>	<i>Ceiba pentandra</i>
<i>Hirtella silicea</i>	<i>Ochroma pyramidale</i>
<i>Hirtella triandra</i>	Boraginaceae
<i>Licania heteromorpha</i>	<i>Cordia alliodora</i>
<i>Licania membranacea</i>	<i>Cordia bicolor</i>
Combretaceae	<i>Cordia collococca</i>
<i>Terminalia dichotoma</i>	<i>Cordia curassavica</i>
Ebenaceae	<i>Cordia panamensis</i>
<i>Diospyros ierensis</i>	<i>Cordia sericicalyx</i>
<i>Diospyros inconstans</i>	Burseraceae
Euphorbiaceae	<i>Protium sagotianum</i>
<i>Sapium glandulosum</i>	Capparaceae
Flacourtiaceae	<i>Crateva tapia</i>
<i>Casearia guianensis</i>	Chrysobalanaceae
<i>Laetia procera</i>	<i>Hirtella paniculata</i>
<i>Ryania speciosa</i>	Combretaceae
Guttiferae	<i>Buchenavia tetraphylla</i>
<i>Calophyllum lucidum</i>	<i>Terminalia amazonia</i>
<i>Clusia palmicida</i>	Euphorbiaceae
<i>Garcinia humilis</i>	<i>Alchornea triplinervia</i>
<i>Garcinia macrophylla</i>	<i>Croton gossypifolius</i>
<i>Marila grandiflora</i>	<i>Hippomane mancinella</i>
<i>Rheedia acuminata</i>	<i>Hura crepitans</i>
<i>Symphonia globulifera</i>	<i>Hyeronima laxiflora</i>
<i>Tovomita eggertii</i>	<i>Marpounea guianensis</i>
Lauraceae	Guttiferae
<i>Aniba citrifolia</i>	<i>Vismia cayennensis</i>
<i>Aniba firmula</i>	<i>Vismia guianensis</i>
<i>Nectandra martinicensis</i>	<i>Vismia laxiflora</i>
<i>Ocotea canaliculata</i>	Hernandiaceae
<i>Ocotea leucoxylon</i>	<i>Hernandia sonora</i>
Lecythidaceae	Humiriaceae
<i>Eschweilera subglandulosa</i>	<i>Sacoglottis amazonica</i>
Leguminosae	Lauraceae
<i>Abarema jupunba</i>	<i>Nectandra kaburiensis</i>
<i>Andira inermis</i>	<i>Ocotea wachenheimii</i>
<i>Brownea latifolia</i>	Leguminosae
<i>Calliandra guildingii</i>	<i>Albizia niopoides</i>
<i>Clathrotropis brachypetala</i>	<i>Copaifera officinalis</i>
<i>Erythrina pallida</i>	<i>Hymenaea courbaril</i>
<i>Inga acuminata</i>	<i>Machaerium robinifolium</i>
<i>Inga fastuosa</i>	<i>Platymiscium trinitatis</i>
<i>Inga heterophylla</i>	Malpighiaceae
<i>Inga laurina</i>	<i>Byrsonima spicata</i>
<i>Inga oerstediana</i>	Malvaceae
<i>Inga pilosula</i>	<i>Hibiscus pernambucensis</i>
<i>Inga pilosula</i>	Meliaceae
<i>Inga thibaudiana</i>	<i>Cedrela odorata</i>
<i>Lonchocarpus punctatus</i>	Moraceae
<i>Mora excelsa</i>	<i>Cecropia peltata</i>
<i>Ormosia monosperma</i>	<i>Cecropia schreberiana</i>
<i>Peltogyne floribunda</i>	<i>Maclura tinctoria</i>
<i>Pentaclethra macroloba</i>	Myrtaceae
<i>Pterocarpus rohrii</i>	<i>Myrcia splendens</i>
<i>Swartzia pinnata</i>	Nyctaginaceae
<i>Swartzia simplex</i>	<i>Pisonia eggertiana</i>

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## Appendix 1. continued.

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Melastomaceae	<i>Pisonia salicifolia</i>
<i>Mouriri marshallii</i>	Palmae
<i>Mouriri rhizophorifolia</i>	<i>Acrocomia aculeate</i>
Meliaceae	Polygonaceae
<i>Carapa guianensis</i>	<i>Coccoloba latifolia</i>
<i>Guarea glabra</i>	<i>Coccoloba uvifera</i>
<i>Guarea guidonia</i>	Rubiaceae
<i>Trichilia pallida</i>	<i>Genipa americana</i>
<i>Trichilia pleeana</i>	<i>Isertia parviflora</i>
Moraceae	Rutaceae
<i>Brosimum alicastrum</i>	<i>Zanthoxylum martinicense</i>
<i>Brosimum guianense</i>	<i>Zanthoxylum microcarpum</i>
<i>Ficus yoponensis</i>	<i>Zanthoxylum trinitense</i>
Myristicaceae	Sapinaceae
<i>Virola surinamensis</i>	<i>Cupania americana</i>
Myrtaceae	<i>Cupania rubiginosa</i>
<i>Calycolpus glaber</i>	<i>Melicoccus bijugatus</i>
<i>Eugenia confusa</i>	<i>Sapindus saponaria</i>
<i>Eugenia domingensis</i>	Sapotaceae
<i>Eugenia monticola</i>	<i>Sideroxylon foetidissimum</i>
<i>Eugenia procera</i>	Solanaceae
<i>Eugenia trinervia</i>	<i>Acnistus arborescens</i>
<i>Marlierea ferruginea</i>	Sterculiaceae
<i>Marlierea guildingiana</i>	<i>Guazuma ulmifolia</i>
<i>Myrcia deflexa</i>	Verbenaceae
<i>Myrcia stenocarpa</i>	<i>Aegiphila integrifolia</i>
<i>Pimenta racemosa</i>	<i>Citharexylum fruticosum</i>
Palmae	<i>Tectona grandis</i>
<i>Attalea maripa</i>	<i>Vitex capitata</i>
<i>Bactris major</i>	<i>Vitex divaricata</i>
<i>Euterpe oleracea</i>	
<i>Geonoma interrupta</i>	
Podocarpaceae	
<i>Podocarpus coriaceus</i>	
Polygonaceae	
<i>Coccoloba fallax</i>	
<i>Coccoloba venosa</i>	
Rhizophoraceae	
<i>Cassipourea guianensis</i>	
<i>Rhizophora harrisonii</i>	
<i>Rhizophora mangle</i>	
Rubiaceae	
<i>Amaioua corymbosa</i>	
<i>Rudgea hostmanniana</i> Benth. subsp. <i>freemanii</i>	
<i>Warszewiczia coccinea</i>	
Rutaceae	
<i>Esenbeckia attenuata</i>	
<i>Esenbeckia pilocarpoides</i>	
Sapotaceae	
<i>Chrysophyllum</i> sp.	
<i>Manilkara bidentata</i>	
<i>Pouteria coriacea</i>	
<i>Pouteria guianensis</i>	
<i>Sideroxylon persimile</i>	
Simaroubaceae	
<i>Quassia amara</i>	
Sterculiaceae	
<i>Sterculia pruriens</i>	

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