Regeneration of monsoon rain forest in northern Australia: the sapling bank

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Abstract. As part of a wider study examining regeneration pathways in monsoon rain forest vegetation in northern Australia, a one-off, dry season census of saplings was undertaken along transects sampled at each of 33 relatively undisturbed sites broadly representative of the range of regional monsoon rain forest vegetation. Four floristic quadrat groups were derived through TWINSPAN classification. Subsequent analyses involved: (1) comparison of mean dry season stockings of juveniles occurring in different rain forest types, and their structural and environmental correlates; (2) comparison of the contributions of different life forms, and the influence of clonal reproduction in the sapling regeneration banks of different forest types; and (3) exploration of relationships between the distributions of saplings of common tree species with respect to seed bank, floristic, structural, and environmental variables. While data presented here require cautious interpretation given that processes of seedling/sapling recruitment and mortality are highly dynamic, sapling banks were found to be most dense on coarse-textured, moist soils, and least dense on coarse-textured, seasonally dry soils. Canopy cover and fire impact were shown to be highly influential on sapling distribution, especially for saplings of tree species and those growing on seasonally dry sites. Sapling densities were little influenced by proximity to rain forest margins, except for shrubs. The potential for clonal reproduction was significantly greater on dry sites, especially for trees. The majority of saplings sampled were derived from relatively few common, non-clonal, canopy tree species. Sapling distributions of 20 out of 23 common tree species were clumped in the vicinity of conspecific adults; for most species the strength of this relationship was greater than that for any other variable. These data support observations in the literature concerning the distribution of sapling banks in moist and dry tropical forests.

Keywords: Clonal reproduction; Northern Territory; Seedling; Tropical rain forest.

Abbreviations: DCA = Detrended Correspondence Analysis.

Nomenclature: Liddle et al. (1994).

Introduction

Considerable attention has been given in recent years to the study of seedling and sapling regeneration in

tropical rain forest systems. Such work has contributed significantly, for example, to the development of explanatory models for the maintenance of species diversity, gap-phase dynamics, and the elucidation of regenerative pathways in tropical forests generally. With respect to disturbance regimes, it is now well documented that regeneration in small canopy gaps occurs primarily through release of established seedlings and advanced regeneration whereas, in large gaps, regeneration of most tree species occurs through soil-stored seed (e.g. Whitmore 1983, 1984; Denslow 1987). Where large-scale disturbance occurs as a result of clearing, burning, and extensive storm damage, regeneration from stem coppice is also of importance (e.g. Stocker 1981; Uhl et al. 1981; Murphy & Lugo 1986; Bowman 1991a; Kauffman 1991; Yih et al. 1991; Rico-Gray & Garcia-Franco 1992). Despite this growing understanding, limited work has been undertaken to date on the dynamics and regeneration pathways of closed forest vegetation in the markedly seasonal tropics (Murphy & Lugo 1986; Gerhardt & Hytteborn 1992).

As part of a wider study examining regeneration pathways in monsoon rain forest vegetation in northern Australia (cf. Russell-Smith & Lucas 1994), this paper reports on a survey of the distribution of saplings undertaken across the spectrum of rain forest types occurring in that region. While it is recognised that data obtained at a single point in time require cautious qualification given that processes of seedling/sapling recruitment and mortality are typically highly dynamic, this paper seeks to: (1) compare mean dry season stockings of juveniles occurring in different rain forest types, and explore their structural and environmental correlates; (2) compare the contributions of different life forms, and the influence of clonal reproduction in the sapling regeneration banks of different forest types; and (3) consider relationships between the distributions of saplings of common tree species with respect to seed bank, floristic, structural, and environmental variables. The significance of these data for our understanding of rain forest regeneration pathways is considered in discussion.

Study region

The study was undertaken in the Northern Territory, Australia. Full description of the study region, including climate, soils, and rain forest vegetation, is given in Russell-Smith (1991). Of particular relevance is the restriction of rainfall to the summer months, principally November through March, associated with the arrival of the monsoon. Rainfall declines steeply over the latitudinal range of rain forest vegetation (12 - 18 °S), from ca. 2000 mm/yr in the northwest to 600 mm/yr in the south. While the amount of rainfall received in any one area is highly variable from year to year, the annual wet season is a highly reliable event (Taylor & Tulloch 1985).

Over this gradient small patches of rain forest, mostly less than 5 ha in extent, occur typically as habitat islands in a sea of *Eucalyptus* or *Melaleuca* open forest or woodland savanna. While boundaries between rain forest and surrounding savanna vegetation types typically are abrupt, floristic and structural transitions (ecotones) are more frequently observed at moist sites and occur over distances mostly less than 50 m (Bowman 1992). Rain forest vegetation occupies a variety of land forms, including small perennial springs; seasonally flooded riparian habitats; and, most typically, excessively-drained substrates such as coastal dunes, deeply weathered lateritic surfaces, igneous outcrops, and actively eroding sandstone escarpments. The regional rain forest flora comprises a total of ca. 650 species (Liddle et al. 1994); mean species richness in 16 floristic vegetation types ranged from 24 to 106 species per patch (Russell-Smith 1991).

Methods

Data collection and compilation

Sapling data were obtained from survey transects located in 33 small rain forest patches broadly representative of the floristic and environmental range of monsoon rain forest vegetation in the Northern Territory, Australia. All sites were sampled in the latter part of the dry season (June-December). Data were obtained over the years 1987-1989 in association with a comprehensive regional floristic survey (Russell-Smith 1991). While transects were of variable length, each comprised a series of contiguous 10 m × 10 m quadrats typically running at right angles from rain forest patch margins into patch interiors. In all instances rain forest patch margins abutted sharply with surrounding savanna vegetation types; transitional/ecotonal vegetation was not sampled in this study. Transects at 21 of the survey sites extended also for variable distances into the surround-

ing savanna. In total, data presented here are derived from 303 rain forest interior quadrats, as well as 81 quadrats external to patch margins. Full site descriptions are available on request.

In each 10 m × 10 m quadrat individuals of all species present, excluding those present as germinants only – i.e. with cotyledons attached, including epigeal, semi-hypogeal, and hypogeal types – (cf. Ng 1978), were inventoried. Saplings were recorded by species in two height classes (≤ 2 m; > 2 m but < 5 cm DBH) in at least six (and at most 10) 1 m × 1 m sub-quadrats systematically located along a central tape. Measurement of DBH, canopy top height, and presence of fire-scars, was undertaken on all stems ≥ 5 cm DBH. Other data recorded from each sub-quadrat included grass cover (%), rock cover (%), and canopy cover (open = 0; partial canopy = 0.5; $> 50\%$ canopy = 1). As well, environmental variables were measured as follows: slope (%), topographic position (six categories), field pH, soil texture class, augured soil depth (max. 1 m), depth of organic staining, and presence/absence of standing free water. Mean annual rainfall estimates for individual sites, and thus constituent quadrats, were calculated using the Australia-wide climatic predictive package BIOCLIM (Busby 1990).

Other, derived variables calculated from these raw data included basal area and two indices as follows. A canopy closure index (CCI) was calculated for each quadrat by summation of canopy cover values for sampled sub-quadrats, divided by the number of sub-quadrats; values of CCI for each quadrat thus lie between 0 and 1. A fire-scar index (FSI) was calculated for each quadrat as the proportion of stems ≥ 5 cm DBH with evident charring/scarring.

Analysis

In order to derive a rain forest floristic typology as a framework for further analysis, polythetic divisive classification was undertaken with TWINSpan (Hill 1979a) on a data matrix comprising 303 internal patch quadrats × 180 species (presence/absence) occurring in at least 10 quadrats. Classification was truncated at the second division after examination of the resulting groups and complementary ordination by Detrended Correspondence Analysis (DCA: Hill 1979b; Hill & Gauch 1980).

Using these four TWINSpan groups as a framework, a first set of analyses involved: (1) calculation of group means and standard errors for measurement variables (e.g. numbers of rain forest and savanna species seedlings and saplings per quadrat, stem density, basal area, slope, FSI); (2) calculation of group frequencies for nominal (soil moisture status) and ordinal (e.g. position on slope) variables; (3) statistical differences be-

tween TWINSpan group means were tested using Tukey's multiple comparison method, since this method allows for unequal cell sizes; and (4) testing for significant differences between groups for all variables by Kruskal-Wallis non-parametric one-way ANOVA. In this analysis, and others detailed below, the numbers of saplings of rain forest woody species were pooled for both height classes given that stems > 2 m height accounted for only a small proportion of the total (see results). The definition of saplings (RFSPL) as applied here thus encompasses established juveniles which have developed beyond the cotyledon stage, but covering a range of height and stem development up to 5 cm DBH. Trees are defined as individuals with stems ≥ 5 cm DBH.

A second set of analyses examined relationships between RFSPL, and saplings of rain forest tree, shrub, vine and palm species, with vegetation structure and environmental variables, including distance from patch margins. Given marked deviations from normality of dependent variables, these relationships were explored by rank correlation (Spearman's r).

A third analysis compared numbers of rain forest saplings produced by vegetatively reproducing (i.e. clonal), and non-clonal, woody tree (stems typically > 8 m), shrub, vine and palm species. Testing for significant differences between TWINSpan group means was undertaken using Tukey's test, and testing for significant differences between groups by Kruskal-Wallis non-parametric one-way ANOVA.

Given both the ecological significance of the tree layer, and the predominance of tree saplings in sample quadrats (see results), a final set of analyses explored sapling distribution patterning in 23 common rain forest tree species occurring in at least 30 quadrats; that is, a minimum 10% of all quadrats sampled. These analyses comprised: (a) rank correlations (Spearman's r) between sapling densities of individual taxa with environmental and vegetation structural variables (including conspecific basal area and stem density), per TWINSpan group; and (b) simple proportional comparison of the densities of saplings produced by tree species possessing extended seed dormancy, with those exhibiting restricted seed longevity, for each TWINSpan group. Extended seed dormancy is defined here as the capacity to retain seed viability for periods of at least six months; that is, for a minimum period comparable with the annual extent of the dry season (cf. Russell-Smith & Lucas 1994).

All data handling and manipulation was undertaken with the DECODA package (Minchin 1990). All other statistical procedures were performed with SAS Version 5 (Anon. 1985).

Results

Floristic typology

TWINSpan classification and complementary DCA ordination yielded four readily interpreted quadrat groups (Table 1). The first dichotomy distinguished between rain forest vegetation associated with sites of perennial moisture (124 quadrats), and rain forest occupying seasonally dry substrates (179 quadrats). In the second level, the moist sites were split into those occurring on heavy-textured, neutral to basic soils (39 quadrats, Group 1), and those occurring on sandy, acid soils derived typically from sandstone parent materials (85 quadrats, Group 2). The seasonally dry sites were split into those occurring on a range of freely draining landforms other than those derived from sandstone, ranging from coastal dunes to igneous and limestone rocky outcrops (100 quadrats, Group 3), and those occurring on sandy soils derived from sandstone, typically in rugged mountainous terrain (79 quadrats, Group 4).

This classification substantially reproduces upper levels of the floristic typology derived for Northern Territory rain forests (Russell-Smith 1991), with the exception that a distinct inland, very low-rainfall component is not differentiated in this analysis. In sum, the groupings derived here are representative of the groups presented in Russell-Smith (1991) as follows: Group 1 with Groups 1 and 2 in Russell-Smith (ibid.); Group 2 with Groups 3 - 7; Group 3 with Groups 9 - 15; and Group 4 with Group 8. As such, these quadrat data are legitimately considered as being broadly representative of most rain forest vegetation in the study region.

Sapling density

The great majority of saplings counted in this study were less than 2 m in height, with only 7.1 % being taller than 2 m, but less than 5 cm DBH. The proportion of saplings greater than 2 m in each of the four TWINSpan groups ranged from 5.2 % in Group 2, through 5.5 % in Group 4 and 7.0 % in Group 1, to 11.2 % in Group 3. Sapling densities of rain forest species (RFSPL) ranged from a mean of 136/10m² in Group 2 quadrats, to 30/10m² for Group 4 (Table 1). Mean densities of savanna saplings were negligible in all groups save Group 4 (4.4/10m²; Table 1). Other vegetation structure and environmental characteristics of each of the four TWINSpan groups are summarised also in Table 1.

Correlations between RFSPL and vegetation structure and environmental variables are given in Table 2. In total, RFSPL is strongly correlated with a wide range of variables, but particularly canopy height, canopy closure, stem density, deep organic soils, and free water

Table 1. Sapling densities, and vegetation structural and environmental characteristics, in each of four groups derived from TWINSpan classification of 303 quadrats $\times$ 180 species. Values of p for significant differences between groups by Kruskal-Wallis non-parametric one-way ANOVA; for measurement variables different letters denote significantly different means; where given, all values $\pm$ SEM.

Variable	Group 1 (<i>n</i> = 39)		Group 2 (<i>n</i> = 85)		Group 3 (<i>n</i> = 100)		Group 4 (<i>n</i> = 79)		<i>P</i>
<i>Saplings (no./10m²)</i>									
Density rain forest saplings (RFSPL)	66.1	± 7.6 ^a	136.3	± 14.3 ^b	64.7	± 5.0 ^a	30.0	± 3.3 ^a	< 0.0001
Density savanna saplings (SAVSPL)	0 ^a		0.2	± 0.1 ^a	0.2	± 0.1 ^a	4.4	± 0.7 ^b	< 0.0001
Density total saplings (TOTSPL)	66.1	± 7.6 ^a	136.5	± 14.3 ^b	64.8	± 5.0 ^a	34.4	± 3.1 ^a	< 0.0001
<i>Vegetation structure</i>									
No. species (per 0.01 ha)	17.2	± 0.8 ^a	18.3	± 0.7 ^a	21.6	± 0.7 ^b	23.0	± 0.7 ^b	< 0.0001
Basal area (m ² /ha)	46.4	± 5.2 ^a	59.1	± 5.2 ^a	26.7	± 3.5 ^b	31.9	± 3.1 ^{ab}	< 0.0001
Density (stems/0.01 ha)	13.8	± 0.8 ^a	18.6	± 1.3 ^b	15.4	± 0.7 ^a	7.2	± 0.5 ^c	< 0.0001
Canopy height (m)	21.6	± 0.1 ^a	24.9	± 0.08 ^b	12.0	± 0.05 ^c	14.5	± 0.6 ^d	< 0.0001
Canopy Closure Index (CCI)	0.94	± 0.02 ^a	0.92	± 0.02 ^a	0.8	± 0.02 ^b	0.7	± 0.04 ^b	< 0.0001
Fire Scar Index (FSI)	0.02	± 0.01 ^a	0.1	± 0.03 ^a	0.1	± 0.02 ^a	0.7	± 0.04 ^b	< 0.0001
Grass (%)	0.2	± 0.2 ^a	0.9	± 0.4 ^a	0.8	± 0.3 ^a	6.8	± 1.2 ^b	< 0.0001
<i>Environmental variables</i>									
Modal position on slope	footslope		footslope		topslope		topslope		< 0.0001
Modal soil texture	clay loam		sandy loam		sandy loam		sand		< 0.0001
Free water (% quadrats)	66.1		60.0		1.0		1.3		< 0.0001
Slope (%)	2.8 ± 0.6 ^a		13.3 ± 2.1 ^b		18.1 ± 2.3 ^{bc}		25.5 ± 3.0 ^{bc}		< 0.0001
pH	7.5 ± 0.1 ^a		5.4 ± 0.1 ^b		6.6 ± 0.1 ^c		5.7 ± 0.1 ^b		< 0.0001
Soil depth (m)	100.0 ± 0 ^a		81.3 ± 3.8 ^b		69.9 ± 4.3 ^b		41.5 ± 4.5 ^c		< 0.0001
Depth soil organic staining (m)	98.1± 1.5 ^a		39.5 ± 2.5 ^b		14.7 ± 1.3 ^c		10.9 ± 1.2 ^c		< 0.0001
Rock (%)	0 ^a		10.4 ± 2.1 ^a		21.9 ± 3.3 ^b		29.7 ± 3.7 ^b		< 0.0001

Table 2. Correlations between rain forest sapling density (RFSPL) and independent variables, in four TWINSpan groups; r = Spearman's rank correlation coefficient; $\alpha = 0.01$.

Variable	Group 1		Group 2		Group 3		Group 4		Total	
	r	p	r	p	r	p	r	p	r	p
<i>Vegetation structure</i>										
Canopy height (m)	0.46	0.004	0.44	< 0.0001	NS		NS		0.46	< 0.0001
Canopy closure index (CCI)	0.50	0.001	NS		0.54	< 0.0001	0.36	0.001	0.45	< 0.0001
Density (no. stems/0.01 ha)	NS		NS		NS		NS		0.38	< 0.0001
Fire Scar Index (FSI)	NS		NS		NS		NS		-0.36	< 0.0001
Grass (%)	NS		NS		NS		NS		-0.35	< 0.0001
Basal area (m ² /ha)	NS		NS		NS		NS		0.26	< 0.0001
No. species	NS		NS		0.55	< 0.0001	0.29	0.009	NS	
<i>Environmental variables</i>										
Depth soil organic matter (m)	NS		0.36	0.0006	0.47	< 0.0001	0.38	0.0006	0.47	< 0.0001
Soil depth (m)	NS		NS		0.45	< 0.0001	0.39	0.0004	0.44	< 0.0001
Free water	NS		0.47	< 0.0001	NS		NS		0.39	< 0.0001
Rock (%)	NS		NS		-0.45	< 0.0001	-0.33	0.003	-0.37	< 0.0001
Slope (%)	NS		-0.39	0.0002	-0.38	< 0.0001	NS		-0.33	< 0.0001
Position on slope	NS		-0.31	0.004	NS		NS		-0.29	< 0.0001
Latitude	NS		NS		NS		-0.32	0.005	-0.28	< 0.0001
Rainfall (mm)	NS		NS		NS		NS		0.24	< 0.0001
pH	NS		NS		-0.46	< 0.0001	NS		-0.21	0.0002
Soil texture	NS		-0.33	0.002	NS		NS		NS	
Longitude	NS		NS		NS		NS		NS	
Distance to edge (m)	NS		NS		NS		NS		NS	

(an index of soil moisture status). Conversely, rain forest sapling density is shown to be strongly negatively correlated with increasing fire damage, flammable grasses, and increasing rockiness and slope.

Similarly, densities of rain forest tree and palm saplings were strongly associated with better developed forest sites (Table 3). By contrast, saplings of shrub species tended to be located in lower, more open canopy rain forest vegetation exhibiting greater incidence of fire damage. Vine saplings showed no clear habitat preferences other than for non-rocky sites with deeper soils (Table 3). Additionally, with the notable exception of shrub saplings, whose distribution was shown to be strongly correlated with rain forest margins, significant relationships were not demonstrated between RFSPL with increasing distance from rain forest patch margins, both for RFSPL in total or separately for each Group (Table 2), nor for trees, palms or vines (Table 3). However, sapling densities of rain forest species were found to collapse dramatically within metres of the external margin of sampled rain forest patch canopies (Fig. 1).

Saplings and clones

Whilst no attempt was made in the field to distinguish between saplings produced from seeds, or clonal resprouts, a measure of the significance of these two pathways is to consider the number of saplings or clonal

resprouts produced by non-clonal and clonal (e.g. rhizomatous) woody species, respectively. Of 249 woody rain forest species sampled in this study, two thirds (164) are non-clonal species which regenerate from seed only (Table 4). Most of these (100) are trees. A further 76 species are clonal species which potentially may reproduce from seed or clonal resprout; the regenerative status of another seven species is unknown. Sampled clonal species were relatively evenly spread through the tree, shrub and vine life-form categories. All four palms are non-clonal species, although two species (*Hydriastele wendlandiana*, *Ptychosperma bleeseri*) may produce multiple stems from their bases.

Most regeneration sampled in this study was from seed, particularly tree species occurring on moist sites (Groups 1 and 2; Table 4). Saplings produced by non-clonal tree species accounted for 57% of all saplings and possible resprouts combined. While saplings of tree species dominated regeneration across all Groups, on seasonally dry sites (Groups 3 and 4) the potential for tree species regeneration from clonal resprouts markedly increased in proportion; a trend not evident with shrubs and vines. For both shrubs and vines, saplings and potential resprouts occurred in more-or-less similar proportions in any one Group, but always at densities much less than those for tree saplings and clones combined. As with tree saplings, densities of palm saplings were found to be greatest on moister sites (Table 4).

Table 3. Correlations between numbers of rain forest tree, shrub, palm and vine saplings, and independent variables. Note ordering of independent variables follows that in Table 2 (i.e. order of significance of correlation with RFSPL). r = Spearman's rank correlation coefficient; $\alpha = 0.01$.

Variable	Trees		Shrubs		Palms		Vines	
	R	P	R	P	R	P	R	P
<i>Vegetation structure</i>								
Canopy height (m)	0.54	< 0.0001	-0.47	< 0.0001	0.43	< 0.0001		NS
Canopy closure index (CCI)	0.48	< 0.0001	-0.18	0.001	0.29	< 0.0001		NS
Density (no. stems/0.01 ha)	0.36	< 0.0001		NS	0.25	< 0.0001		NS
Fire Scar Index (FSI)	-0.37	< 0.0001	0.15	0.006	-0.16	0.006		NS
Grass (%)	-0.41	< 0.0001	0.15	0.006	-0.17	0.002		NS
Basal area (m ² /ha)	0.37	< 0.0001	-0.41	< 0.0001	0.33	< 0.0001		NS
No. species		NS	0.23	< 0.0001		NS		NS
<i>Environmental variables</i>								
Depth soil organic matter (m)	0.40	< 0.0001	-0.24	< 0.0001	0.52	< 0.0001		NS
Soil depth (m)	0.39	< 0.0001		NS	0.31	< 0.0001	0.22	< 0.0001
Free water	0.42	< 0.0001	-0.48	< 0.0001	0.36	< 0.0001		NS
Rock (%)	-0.31	< 0.0001		NS	-0.33	< 0.0001	-0.18	0.0009
Slope (%)	-0.27	< 0.0001		NS	-0.21	0.0002		NS
Position on slope	-0.34	< 0.0001	0.37	< 0.0001	-0.40	< 0.0001		NS
Latitude	-0.28	< 0.0001		NS	-0.28	< 0.0001		NS
Rainfall (mm)	0.23	< 0.0001		NS	0.38	< 0.0001		NS
pH	-0.26	< 0.0001		NS		NS		NS
Soil texture		NS		NS		NS		NS
Longitude		NS	0.20	0.0003	-0.25	< 0.0001		NS
Distance to edge (m)		NS	-0.21	0.0002		NS		NS

Fig. 1. Rain forest (RFSPL) and savanna (SAVSPL) sapling densities with respect to distance from rain forest canopy.

Distribution of tree saplings

Relationships between sapling densities and a range of vegetation structure and environmental relationships were explored for each of 23 common tree species sampled from at least 30 of the 303 internal patch quadrats. Saplings of the 19 non-clonal species ac-

counted for 82% of the combined seed-derived tree saplings and possible resprouts sampled over all Groups (range: 67 % for Group 1 to 89 % for Group 2). Combined seed-derived saplings and possible resprouts of four clonal species (*Diospyros calycantha*, *D. maritima*, *Drypetes lasiogyna*, *Strychnos lucida*) accounted for a further 7 %, contributing 0 % to Group 1, 0.6 % to Group

Table 4. Rain forest tree, shrub, vine, and palm sapling densities (no./10m² ± SEM) for clonally and non-clonally reproducing species in each of four TWINSPAN Groups. Values of *p* for significant differences between Groups by Kruskal-Wallis non-parametric one-way ANOVA; for measurement variables different letters denote significantly different means.

Variable	Group 1	Group 2	Group 3	Group 4	<i>P</i>
Trees					
non-clonal species (<i>n</i> = 100)	30.0 ± 5.6 ^a	109.4 ± 13.8 ^b	18.3 ± 2.6 ^a	10.2 ± 2.1 ^a	0.0001
clonal species (<i>n</i> = 31)	1.8 ± 0.6 ^a	4.4 ± 0.9 ^a	13.0 ± 1.7 ^b	3.4 ± 0.5 ^a	0.0001
unknown (<i>n</i> = 1)					
Shrubs					
non-clonal species (<i>n</i> = 27)	2.6 ± 1.0 ^a	0.8 ± 0.3 ^{ac}	10.7 ± 1.6 ^b	5.5 ± 1.3 ^{ad}	0.0001
clonal species (<i>n</i> = 21)	6.8 ± 2.9 ^a	0.7 ± 0.4 ^{ab}	8.7 ± 1.8 ^{ac}	3.0 ± 0.7 ^a	0.0001
unknown (<i>n</i> = 1)					
Vines					
non-clonal species (<i>n</i> = 33)	2.2 ± 0.8 ^a	5.3 ± 1.3 ^{ac}	7.9 ± 1.1 ^b	1.5 ± 0.3 ^{ad}	0.0001
clonal species (<i>n</i> = 24)	4.3 ± 0.7 ^a	4.9 ± 0.8 ^a	4.3 ± 0.7 ^a	3.4 ± 0.5 ^a	NS
unknown (<i>n</i> = 5)					
Palms					
non-clonal species (<i>n</i> = 4)	6.5 ± 2.3 ^a	10.4 ± 1.6 ^{ac}	0.1 ± 0.1 ^b	2.6 ± 0.9 ^{ad}	0.0001
clonal species (<i>n</i> = 0)	-	-	-	-	

2, 3 % to Group 3, and 15 % to Group 4; on the basis of field experience, however, it is probable that most of these were derived from seed also. Sampled seed-derived sapling/resprout densities and basal areas for each of these 23 tree species are presented in App. 1.

Sapling densities of all but three of these 23 tree species were strongly correlated with the distributions of adults of the same species as measured by conspecific basal area or stem density, typically both (Table 5). Further, for most species the strength of the correlation between sapling density and the distribution of conspecific adults was greater than that for any other measured environmental variable. Species not shown to conform to this pattern comprised *Buchanania arborescens*, *Carallia brachiata* and *Pouteria sericea*. Conversely, there was little evidence that sapling distributions of most of these common tree species were significantly influenced by fire disturbance and/or edge effects. However, sapling distributions of five Group 2 species were significantly correlated with distance from patch margins; four positively (*Buchanania arborescens*, *Calophyllum sil*, *C. soulattri*, *Horsfieldia australiana*), and one negatively (*Hydriastele wendlandiana*). As well, for saplings of species occupying mostly seasonally dry substrates, three exhibited clear preferences for shaded situations (*Aglaia brownii*, *Allosyncarpia ternata*, *Diospyros maritima*), and one with low fire impact (*D. calycantha*; Table 5).

Tree saplings and seed dormancy

Of the above 23 tree species 11 are known to possess no capacity for extended seed longevity (see App. 1). Saplings of such species accounted for the great majority of tree saplings sampled from perennially moist sites (TWINSPAN Groups 1 and 2, Table 6). Conversely, saplings of tree species possessing long-lived (dormant) seeds predominated on seasonally dry sites (Groups 3 and 4).

Discussion

Constraints on the data

A number of qualifications apply when interpreting these data. First, this study reports a one-off regional survey of rain forest saplings at each of 33 little-disturbed sample sites. Processes of rain forest seedling/sapling recruitment and mortality are typically highly dynamic even in relatively undisturbed tropical forest types, especially following mast fruiting events (e.g. Fox 1973; Liew & Wong 1973; Hubbell & Foster 1990; Lieberman et al. 1990; Swaine et al. 1990; Turner 1990a,

b; Welden et al. 1991; Lieberman & Li 1992; De Steven 1994). Such dynamism applies particularly to seedlings, with relatively greater population stability exhibited in older (generally taller) size classes (e.g. Lieberman et al. 1990; Swaine et al. 1990; Turner 1990a; DeSteven 1994). Under highly seasonal rainfall conditions, limited available data indicate also that seedling densities are much greater in wet periods; conversely, seedling mortality is greater in dry periods (Lieberman & Li 1992; Russell-Smith unpubl.).

Secondly, saplings growing in canopy gaps > 100 m² are not represented here given that such conditions favour a separate suite of principally light-demanding, pioneer species (e.g. Whitmore 1984, 1989; Brokaw 1985; Denslow 1987; Swaine & Whitmore 1988).

And third, it is apparent that the terms *seedling* and *sapling* are variously defined by different authors in the relevant literature. Consider the following definitions: *seedlings* are recently emerged germinants (Ng 1980), recently emerged germinants up to 64 weeks old (Osunkjoya et al. 1993), up to 2 yrs old (Lieberman & Li 1992), < 50 cm (De Steven 1994), < 2 m (Russell-Smith et al. 1993), undefined (Fox 1973; Liew & Wong 1973; Swaine et al. 1990; Turner 1990a); *seedlings and saplings* are individuals < 1m (Martinez-Ramos & Soto-Castro 1993); *saplings* are individuals ≥ 50cm height to 1 cm DBH (DeSteven 1994), > 2 m height to < 5cm DBH (Williams-Linera 1990), ≥ 2 m height to 10 cm DBH (Russell-Smith et al. 1993), 1-4 cm DBH (Welden et al. 1991), 1-8 cm DBH (Hubbell & Foster 1990). Seedlings are strictly germinants still attached to seed tissues (ie. cotyledons). Here, saplings are defined as established juveniles (ie. without cotyledons) covering a range of height and stem development up to an arbitrary 5 cm DBH. Further, height is an inadequate surrogate of the developmental age or status of saplings. This applies particularly to low individuals growing on seasonally dry sites where aerial shoots may have been killed by fire or other periodic disturbance, only to be replaced in the following growing season by resprouts from subterranean lignotuberous tissues (e.g. Lacey & Whelan 1976; Lacey & Johnston 1990).

The distribution of saplings and clones

While floristically simple and comprising typically small, isolated patches, the different rain forest types growing in monsoonal northern Australia describe a subset of more complex and extensive rain forest vegetation growing in lowland, climatically more equable, regions of north-eastern Australia (Webb & Tracey 1981; Russell-Smith 1991). The range of sites surveyed for this study (Table 1) comprise those occurring at sites of perennial moisture availability on fine-textured,

Table 5. Rank correlations (Spearman's r) between numbers of saplings of 23 rain forest tree species recorded from at least 30 10 m $\times$ 10 m quadrats, and vegetation structure and environmental variables (*overleaf*). For each species, correlations are presented for the TWINSpan Group containing the most quadrats in which saplings of respective species were recorded; for four species (indicated by ^a after the species name) with low frequencies of sapling occurrence, correlations are presented over all Groups. Numbers of quadrats in which saplings of respective species were recorded are given for the TWINSpan Group containing most quadrats, and, in parentheses, for total quadrat frequency. Variable names as given in Table 2, with the exceptions that Species BA and Species density refer to the BA and stem density of respective species. * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$.

Species	Seedlings		Vegetation structure				CCI	FSI
	No. quadrats	Species BA	Species density	Total BA	Total density	Canopy height		
Group 1								
<i>Carpentaria acuminata</i>	22 (52)	0.49 ***	0.50 ***					
<i>Melicope elleryana</i> ^a	8 (12)	0.40 ***	0.40 ***					
<i>Syzygium nervosum</i>	8 (8)	0.54 ***	0.57 ***					
<i>Terminalia microcarpa</i> ^a	9 (12)	0.24 ***	0.24 ***					
<i>Vavaea australiana</i>	17 (18)	0.67 ***	0.68 ***					
Group 2								
<i>Buchanania arborescens</i>	16 (21)				− 0.29 *			
<i>Calophyllum sil</i>	28 (32)	0.63 ***	0.60 ***					
<i>Calophyllum soulattri</i>	31 (38)	0.80 ***	0.83 ***					
<i>Carallia brachiata</i>	22 (38)							
<i>Horsfieldia australiana</i> ^a	12 (16)	0.57 ***	0.54 ***	0.15 *		0.23 ***		
<i>Hydriastele wendlandiana</i>	29 (30)	0.53 ***	0.53 ***		0.51 ***			
<i>Myristica insipida</i>	37 (73)	0.48 ***	0.43 ***					
<i>Planchonella</i> DNA 47005	37 (37)	0.71 ***	0.72 ***		0.27 *			
<i>Syzygium minutiflorum</i>	42 (47)	0.91 ***	0.89 ***					
Group 3								
<i>Aglaia brownii</i>	33 (34)	0.59 ***	0.60 ***		0.34 *	0.28 *	0.55 ***	
<i>Celtis philippensis</i>	25 (25)	0.36 **	0.34 **					
<i>Diospyros maritima</i>	37 (38)	0.71 ***	0.71 ***		0.33 *		0.44 ***	
<i>Drypetes lasiogyna</i>	28 (53)	0.32 *	0.31 *					
<i>Strychnos lucida</i>	17 (20)	0.44 ***	0.46 ***					
Group 4								
<i>Allosyncarpia ternata</i>	33 (54)	0.76 ***	0.79 ***			0.32 *	0.42 ***	
<i>Canarium australianum</i> ^a	5 (10)	0.21 ***	0.22 ***					0.19 *
<i>Diospyros calycantha</i>	14 (26)	0.32 *						− 0.43 ***
<i>Pouteria sericea</i>	20 (36)							

neutral to basic soils (Group 1), or coarse-textured, acidic soils (Group 2), to those occupying seasonally dry landforms on a range of typically loamy, neutral soils (Group 3), or coarse-textured, acidic soils (Group 4). The sapling data presented here are thus likely to have wider application to other rain forest formations from the markedly seasonal, to perhumid tropics.

In this study sapling banks were found to be most dense in forest growing on coarse-textured, perennially moist soils, and least dense on coarse-textured, seasonally dry soils; on finer-textured soils sapling banks were intermediate in density, regardless of whether they occurred under ever-moist or perennially dry conditions (Table 1). Analogous comparative data in the literature are scarce, although Liew & Wong (1973) note that, for dipterocarp forests under ever-wet conditions in Sabah, seedling stockings are typically greatest on sandstone ridges and volcanic soils, and, together with Fox (1973), are least dense in swampy forests and riverain situations.

While the distribution of shrub saplings was shown to be preferentially associated with relatively disturbed

open sites, particularly near patch margins (Table 3), no other significant relationships were expressed in these data between rain forest sapling density with increasing distance into patch interiors, for rain forest saplings overall, for different forest types, nor for trees, vines or palms (Tables 2 and 3). Such results are surprising given steep gradients in light and other microclimate conditions prevailing on, or near the margin itself (e.g. Denslow 1987; Williams-Linera 1990; MacDougall & Kellman 1992; Brown 1993), not to mention the impact of recurrent fires. Nevertheless, light availability and fire impact were shown to be highly influential on the distribution of saplings under prevailing monsoonal climatic conditions (Tables 2 and 3).

Irrespective of location along sample transects, tree sapling densities were shown to be highly dependent on the degree of canopy closure, especially those growing in seasonally dry forests (Groups 3, 4) and in areas exhibiting relatively low fire impact. Lieberman & Li (1992) found seedling density in a tropical dry forest in Ghana also to be greater in shaded situations. In the case

Table 5. (cont.)

Species	Environmental variable								
	Free Water	Soil Texture	Soil Depth	Soil OM	pH	Rock	Slope	POS	Distance to edge
<i>Group 1</i>									
<i>Carpentaria acuminata</i>									
<i>Melicope elleryana</i> ^a	0.29 ***			0.25 ***			– 0.17 *	– 0.18 *	
<i>Syzygium nervosum</i>									
<i>Terminalia microcarpa</i> ^a		0.21 **		0.22 ***					
<i>Vavaea australiana</i>		0.37 *							
<i>Group 2</i>									
<i>Buchanania arborescens</i>					0.31 *				0.38 **
<i>Calophyllum sil</i>		– 0.48 ***	– 0.34 *	0.37 *	0.39 **			– 0.33 *	0.49 ***
<i>Calophyllum soulattri</i>	0.36 **	– 0.31 *	0.40 ***	0.56 ***	– 0.45 ***	– 0.29 *			0.29 *
<i>Carallia brachiata</i>									
<i>Horsfieldia australiana</i> ^a	0.27 ***			0.17 *			– 0.15 *	– 0.27 ***	0.23 ***
<i>Hydriastele wendlandiana</i>			0.38 **	0.40	– 0.31 *	– 0.40 ***			– 0.59 ***
<i>Myristica insipida</i>									
<i>Planchonella</i> DNA 47005								– 0.35 *	– 0.29 *
<i>Syzygium minutuliflorum</i>									
<i>Group 3</i>									
<i>Aglaia brownii</i>			0.45 ***	0.43 ***	– 0.51 ***	– 0.43 ***	– 0.36 **	– 0.26 *	
<i>Celtis philippensis</i>									
<i>Diospyros maritima</i>			0.46 ***			– 0.43 ***	– 0.27 *		
<i>Drypetes lasiogyne</i>			0.35 **			– 0.33 **		– 0.28 *	
<i>Strychnos lucida</i>									
<i>Group 4</i>									
<i>Allosyncarpia ternata</i>			0.34 **						
<i>Canarium australianum</i> ^a									
<i>Diospyros calycantha</i>								– 0.40 **	
<i>Pouteria sericea</i>									

of *Allosyncarpia ternata*, the major canopy dominant of harsh, seasonally dry sandstone habitats, shaded sites are physiologically essential for the establishment of juveniles (e.g. Bowman 1991b), as well as affording safer haven from fires given reduced grassy fuels (Russell-Smith et al. 1993).

Overall, the data express greater potential for clonal reproduction on seasonally dry sites, especially for trees (Table 4). Similar observations have been made by Ewel (1977) and Lieberman & Li (1992) concerning regeneration of dry forest in other tropical regions. Such generalisation, however, masks considerable variability between different lifeforms; for example, larger proportions of shrub and vine species are clonal than are tree species.

Tree saplings

The majority of saplings sampled in this study were derived from a relatively few common tree species. On

perennially moist sites (Groups 1, 2) a significant majority of tree saplings were derived from just 10 non-clonal canopy dominants (ie. common tree species with basal area values > 2 m² ha^{–1} in either Group; App. 1); eight of these species possess non-dormant seeds.

On seasonally dry sites (Groups 3, 4) two distinctive patterns are expressed in the tree sapling data. In semi-deciduous forest and thicket vegetation (*sensu* Webb 1968; Group 3), where saplings of common tree species account for only a small proportion of the whole, there is increased capacity for clonal reproduction and species with dormant seeds dominate the sapling bank. Evergreen forest and woodland vegetation (Group 4) provides a special case given that it is dominated by just one species, *Allosyncarpia*. As for Group 3, however, but with the notable exception of *Allosyncarpia* itself, there is generally increased capacity for clonal reproduction, and species with dormant seeds dominate the sapling bank.

Table 6. Proportions of tree saplings produced by species with dormant and non-dormant seeds, in each of four groups derived from TWINSpan classification of 303 quadrats × 180 species. All data derived from App. 1.

Trees	Group 1	Group 2	Group 3	Group 4
Species with non-dormant seeds (<i>n</i> = 11)	78.4	86.8	47.7	37.0
Species with dormant seeds (<i>n</i> = 12)	21.6	13.2	52.3	63.0

Common to all forest types is the high degree of clumping of saplings of common tree species in the near vicinity of conspecific adults (Table 5), including species exhibiting highly contrasting vagilities (cf. Russell-Smith & Lee 1992). Similar observations have been made for clumping of juveniles growing in seasonal (Hubbell & Foster 1990), and markedly seasonal (Hubbell 1979) rain forest in central America. While the sapling distributions of three common tree species were not correlated with that of conspecific adults, it is equally possible that the sampling design itself was inadequate; thus, narrow transects of 10 m width may not have been sufficient to capture both saplings and nearby conspecific adult stems, especially those with wide canopies.

Sapling bank and patch regeneration

This paper follows an earlier study of dormant soil seed banks sampled from relatively undisturbed situations over a range of monsoon rain forest sites in northern Australia (Russell-Smith & Lucas 1994). That study highlighted the occurrence of a variety of pioneer species, especially trees and shrubs, in regional rain forest seed banks. The present study, also conducted in relatively undisturbed situations over a range of regional rain forest sites, focuses on the pool of juveniles established on the forest floor. Regeneration in small canopy gaps is conventionally considered to derive from this pool (e.g. Denslow 1987; Uhl et al. 1988), with relatively little contribution from the soil seed bank (Hopkins & Graham 1984).

It is instructive to contrast the composition of the sapling and dormant seed bank pools. On perennially moist sites dormant seed banks are dominated by figs and a range of other pioneers, trees in particular. Such species are virtually absent from sapling banks in relatively undisturbed monsoon rain forest. By contrast, sapling banks are dominated by a small number of non-clonal canopy tree species, typically possessing no seed longevity. On seasonally dry sites dormant seed banks are dominated by shrubs and graminoids. By contrast, sapling banks are dominated by trees, but with significantly greater proportions of shrubs and vines, and clonal regeneration, than on moist sites.

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References

- Anon. 1985. *SAS User's Guide: Statistics, Version 5 Edition*. SAS Institute Corp., Cary, NC.
- Bowman, D.M.J.S. 1991a. Recovery of some northern Australian monsoon forest tree species following fire. *Proc. R. Soc. Queensl.* 101: 21-25.
- Bowman, D.M.J.S. 1991b. Environmental determinants of *Allosyncarpia ternata* forests that are endemic to western Arnhem Land, northern Australia. *Aust. J. Bot.* 39: 575-589.
- Bowman, D.M.J.S. 1992. Monsoon forests in north-western Australia. II. Forest-savanna transitions. *Aust. J. Bot.* 40: 89-102.
- Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and gap dynamics*, pp. 53-69. Academic Press, New York, NY.
- Brown, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *J. Trop. Ecol.* 9: 153-168.
- Busby, J. 1990. BIOCLIM— A bioclimate analysis and prediction system. In: Margules, C.R. & Austin, M.P. (eds.) *Nature conservation: cost effective biological surveys and data analysis*. CSIRO, Canberra.
- Denslow, J.S. 1987. Tropical rain forest gaps and tree species diversity. *Annu. Rev. Ecol. & Syst.* 18: 432-451.
- De Steven, D. 1994. Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. *J. Trop. Ecol.* 10: 369-383.
- Ewel, J.J. 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop* 1: 103-117.
- Fensham, R.J. 1996. The floristics and structure of dry rain forest at Forty Mile Scrub National Park, North Queensland. *Cunninghamia* 43: 483-495.
- Fox, T.E.D. 1973. Dipterocarp seedling behaviour in Sabah. *Malay. Forester* 36: 205-213.
- Gerhardt, K. & Hytteborn, H. 1992. Natural dynamics and regeneration methods in tropical dry forests - an introduction. *J. Veg. Sci.* 3: 361-364.
- Hill, M.O. 1979a. *TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Dept. Ecology and Systematics, Cornell University, Ithaca, NY.
- Hill, M.O. 1979b. *DECORANA - A FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging*. Dept. Ecology and Systematics, Cornell University, Ithaca, NY.
- Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.
- Hopkins, M.S. & Graham, A.W. 1984. The role of soil seed banks in canopy gaps in Australian tropical lowland rain-forest - preliminary field experiments. *Malay. For.* 47: 146-158.
- Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299-1309.
- Hubbell, S.P. & Foster R.B. 1990. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical diversity. In: Bawa, K.S. & Hadley, M.

- (eds.) *Reproductive ecology of tropical forest plants*, pp. 317-341. UNESCO & Parthenon, Paris.
- Kauffman, J.B. 1991. Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica* 23: 219-224.
- Lacey, C.J. & Johnston, R.D. 1990. Woody clumps and clumpwoods. *Aust. J. Bot.* 38: 299-334.
- Lacey, C.J. & Whelan, P.K. 1976. Observations on the ecological significance of vegetative reproduction in the Katherine-Darwin region of the Northern Territory. *Aust. For.* 39: 131-139.
- Liddle, D.T., Russell-Smith, J., Brock, J., Leach, G.J. & Connors, G.T. 1994. *Atlas of vascular rain forest plants in the Northern Territory, Australia. Flora of Australia, Supplementary Series No.3*. Australian Government Publishing Service, Canberra.
- Lieberman, D. & Li, M. 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. *J. Veg. Sci.* 3: 375-382.
- Lieberman, D., Hartshorn, G.S., Lieberman, M. & Peralta, R. 1990. Forest dynamics at La Selva Biological Station, 1969-1985. In: Gentry, A.H. (ed.) *Four neotropical rain forests*, pp. 509-521. Yale University Press, New Haven, CT.
- Liew, T.C. & Wong, F.O. 1973. Density, recruitment, mortality and growth of Dipterocarp seedlings in virgin and logged-over forests in Sabah. *Malay. For.* 36: 3-15.
- MacDougall, A. & Kellman, M. 1992. The understorey light regime and patterns of tree seedlings in tropical riparian forest patches. *J. Biogeogr.* 19: 667-675.
- Martinez-Ramos, M. & Soto-Castro, A. 1993. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* 107/108: 299-318.
- Minchin, P.R. 1990. *DECODA user's manual*. Research School of Pacific Studies, Australian National University, Canberra.
- Murphy, P.G. & Lugo, A.E. 1986. Ecology of tropical dry forest. *Annu. Rev. Ecol. & Syst.* 17: 67-88.
- Ng, F.S.P. 1978. Strategies of establishment in Malayan forest trees. In: Tomlinson, P.B. & Zimmermann, M.H. (eds.) *Tropical trees as living systems*, pp. 129-162. University Press, Cambridge.
- Ng, F.S.P. 1980. Germination ecology of Malaysian woody plants. *Malay. For.* 44: 406-437.
- Osunkoya, O.O., Ash, J.E., Graham, A.W., & Hopkins, M.S. 1993. Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *J. Trop. Ecol.* 9: 1-18.
- Rico-Gray, V. & Garcia-Franco, J.G. 1992. Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *J. Veg. Sci.* 3: 617-624.
- Russell-Smith, J. 1991. Classification, species richness, and environmental relations of monsoon rain forest in northern Australia. *J. Veg. Sci.* 2: 259-278.
- Russell-Smith, J. & Lee, A.H. 1992. Plant populations and monsoon rain forest in the Northern Territory, Australia. *Biotropica* 24: 471-487.
- Russell-Smith, J. & Lucas, D.E. 1994. Regeneration of monsoon rain forest in northern Australia: the dormant seed bank. *J. Veg. Sci.* 5: 161-168.
- Russell-Smith, J., Lucas, D.E., Brock, J. & Bowman, D.M.J.S. 1993. *Allosyncarpia*-dominated rain forest in monsoonal northern Australia. *J. Veg. Sci.* 4: 67-82.
- Stocker, G.C. 1981. Regeneration of a North Queensland rain forest following felling and burning. *Biotropica* 13: 86-92.
- Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.
- Swaine, M.D., Lieberman, D. & Hall, J.B. 1990. Structure and dynamics in a tropical dry forest in Ghana. *Vegetatio* 88: 31-51.
- Taylor, J. & Tulloch, D. 1985. Rainfall in the wet-dry tropics: extreme events at Darwin and similarities between years during the period 1870-1973. *Aust. J. Ecol.* 10: 281-295.
- Turner, I.M. 1990a. Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* 22: 146-154.
- Turner, I.M. 1990b. The seedling survivorship and growth of three *Shorea* species in a Malaysian rain forest. *J. Trop. Ecol.* 6: 469-478.
- Uhl, C., Clark, K., Clark, H. & Murphy, P. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon Basin. *J. Ecol.* 69: 631-649.
- Uhl, C., Clark, K., Dezzeo, N. & Maquirino, P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751-763.
- Webb, L.J. 1968. Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* 49: 296-311.
- Webb, L.J. & Tracey, J.G. 1981. Australian rainforests: patterns and change. In: Keast, A. (ed.) *Ecological biogeography of Australia*, pp. 607-694. Junk, The Hague.
- Weber, W.A. 1982. Mnemonic three-letter acronyms for the families of vascular plants: a device for more effective herbarium curation. *Taxon* 31: 74-88.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a Neotropical forest. *Ecology* 72: 35-50.
- Whitmore, T.C. 1983. Secondary succession from seed in tropical rain forests. *For. Abstr.* 44: 767-779.
- Whitmore, T.C. 1984. *Tropical rain forests of the Far East*. 2nd ed. Clarendon Press, Oxford.
- Whitmore, T.C. 1989. Canopy gaps and two major groups of forest trees. *Ecology* 70: 536-538.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78: 356-373.
- Yih, K., Boucher, D.H., Vandermeer, J.H. & Zamora, N. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by hurricane Joan. *Biotropica* 23: 106-113.

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For App. 1, see next page.

App. 1. Mean sapling density (no./10 m²), and basal area (m²/ha), of 23 tree species occurring in ≥ 30 quadrats, in each of four TWINSPAN groups; means $\pm$ SEM. Family acronyms after species names follow Weber (1982). Species with extended seed dormancy annotated by d; clonal species by c. *Hydriastele wendlandiana*, though a clumping palm, is regarded here as non-clonal.

Species	Group 1		Group 2		Group 3		Group 4	
<i>Aglaia brownii</i> (MEL)								
Sapling density	0		0.04 $\pm$ 0.04		8.8 $\pm$ 2.1		0	
Basal area	0		0		0.5 $\pm$ 0.1		0	
<i>Allosyncarpia ternata</i> (MRT)								
Sapling density	0		3.5 $\pm$ 1.1		0		3.0 $\pm$ 0.5	
Basal area	0		8.9 $\pm$ 2.5		0		26.4 $\pm$ 3.2	
<i>Buchanania arborescens</i> (ANA)								
Sapling density	0.2 $\pm$ 0.2		0.6 $\pm$ 0.1		0.03 $\pm$ 0.03		0.09 $\pm$ 0.06	
Basal area	0.1 $\pm$ 0.01		0.3 $\pm$ 0.1		0.6 $\pm$ 0.3		0.2 $\pm$ 0.01	
<i>Calophyllum sil</i> (CLU)								
Sapling density	0		19.0 $\pm$ 4.3		0		0.2 $\pm$ 0.1	
Basal area	0		2.3 $\pm$ 0.1		0		0.1 $\pm$ 0.01	
<i>Calophyllum soulattri</i> (CLU)								
Sapling density	1.4 $\pm$ 0.7		20.3 $\pm$ 5.2		0.03 $\pm$ 0.03		0	
Basal area	0.2 $\pm$ 0.01		4.2 $\pm$ 0.9		0		0	
<i>Canarium australianum</i> (BRS) d								
Sapling density	0		0.04 $\pm$ 0.04		0.2 $\pm$ 0.1		0.2 $\pm$ 0.1	
Basal area	0		0.13 $\pm$ 0.01		1.2 $\pm$ 0.05		0.2 $\pm$ 0.1	
<i>Carallia brachiata</i> (RHZ) d								
Sapling density	1.6 $\pm$ 0.7		2.1 $\pm$ 0.7		0		0.1 $\pm$ 0.05	
Basal area	0.9 $\pm$ 0.04		0.6 $\pm$ 0.2		0		0	
<i>Carpentaria acuminata</i> (ARE) d								
Sapling density	1.4 $\pm$ 0.3		3.6 $\pm$ 1.1		0.07 $\pm$ 0.07		2.5 $\pm$ 0.9	
Basal area	2.1 $\pm$ 0.7		0.6 $\pm$ 0.18		0.05 $\pm$ 0.01		0.8 $\pm$ 0.2	
<i>Celtis philippensis</i> (ULM) d								
Sapling density	0		0		1.4 $\pm$ 0.3		0	
Basal area	0		0		0.8 $\pm$ 0.2		0	
<i>Diospyros calycantha</i> (EBN) c,d								
Sapling density	0.1 $\pm$ 0.09		0.4 $\pm$ 0.1		0.1 $\pm$ 0.1		0.8 $\pm$ 0.2	
Basal area	0		0.04 $\pm$ 0.03		0.07 $\pm$ 0.04		0.01 $\pm$ 0.01	
<i>Diospyros maritima</i> (EBN) c,d								
Sapling density	0		0.08 $\pm$ 0.08		5.5 $\pm$ 1.3		0	
Basal area	0		0		0.7 $\pm$ 0.2		0	
<i>Drypetes lasiogyne</i> (EUP) c,d								
Sapling density	0		0.1 $\pm$ 0.09		2.5 $\pm$ 0.9		1.2 $\pm$ 0.3	
Basal area	0		0		1.2 $\pm$ 0.2		0.06 $\pm$ 0.04	
<i>Horsfieldia australiana</i> (MYS)								
Sapling density	0.4 $\pm$ 0.3		4.2 $\pm$ 1.5		0		0	
Basal area	1.7 $\pm$ 0.8		2.9 $\pm$ 0.9		0		0	
<i>Hydriastele wendlandiana</i> (ARE)d								
Sapling density	0		6.7 $\pm$ 1.5		0		0	
Basal area	0		0.8 $\pm$ 0.2		0		0	
<i>Melicope elleryana</i> (RUT) d								
Sapling density	0.8 $\pm$ 0.3		0.3 $\pm$ 0.2		0		0	
Basal area	0.5 $\pm$ 0.2		0.9 $\pm$ 0.4		0		0	
<i>Myristica insipida</i> (MYS)								
Sapling density	7.2 $\pm$ 2.7		3.1 $\pm$ 0.5		2.2 $\pm$ 0.8		0.3 $\pm$ 0.2	
Basal area	3.0 $\pm$ 0.6		1.7 $\pm$ 0.3		0.8 $\pm$ 0.4		0.03 $\pm$ 0.02	
<i>Planchonella</i> DNA 47005 (SPT)								
Sapling density	0		10.5 $\pm$ 3.1		0		0	
Basal area	0		1.9 $\pm$ 0.6		0		0	
<i>Pouteria sericea</i> (SPT) d								
Sapling density	0		0.04 $\pm$ 0.04		0.6 $\pm$ 0.2		1.2 $\pm$ 0.3	
Basal area	0		0.01 $\pm$ 0.01		0.8 $\pm$ 0.2		0.2 $\pm$ 0.1	
<i>Strychnos lucida</i> (LOG) c,d								
Sapling density	0.03 $\pm$ 0.03		0		1.7 $\pm$ 0.6		0.1 $\pm$ 0.1	
Basal area	0		0		0.2 $\pm$ 0.05		0.01 $\pm$ 0.01	
<i>Syzygium minutiflorum</i> (MRT)								
Sapling density	0.6 $\pm$ 0.3		26.9 $\pm$ 6.2		0		0	
Basal area	3.3 $\pm$ 1.8		8.8 $\pm$ 2.0		0		0	
<i>Syzygium nervosum</i> (MRT)								
Sapling density	3.0 $\pm$ 1.2		0		0		0	
Basal area	5.5 $\pm$ 2.0		0		0		0	
<i>Terminalia microcarpa</i> (CMB) d								
Sapling density	0.7 $\pm$ 0.2		0.04 $\pm$ 0.04		0.06 $\pm$ 0.04		0	
Basal area	2.6 $\pm$ 0.7		0.14 $\pm$ 0.1		0.5 $\pm$ 0.3		0	
<i>Vavaea australiana</i> (MEL)								
Sapling density	3.9 $\pm$ 1.0		0		0.03 $\pm$ 0.03		0	
Basal area	4.5 $\pm$ 1.4		0.05 $\pm$ 0.02		0		0	