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Forestry Ecology and Management 99 (1997) 133–152

Forest Ecology
and
Management

The effects of ecological rehabilitation on vegetation recruitment: some observations from the Wet Tropics of North Queensland

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Accepted 9 May 1997

Abstract

The nature of vegetation colonisation in four small rehabilitations and adjacent, protected control sites in tropical north Queensland were studied. Seven-year-old rehabilitation plots contiguous with forest had recruited up to seventy-two plant species across all growth forms and successional phases. Recruitment in 5-year-old plots was less abundant and diverse. Control sites by comparison were dominated by disclimax grasses and diversity of recruitment was reduced to only nineteen species at the upland control site. The effect of isolation on reducing abundance and diversity were demonstrated at one site located over 500 m from intact forest. Soil seed bank analysis was undertaken to examine any cumulative effect. Samples contained large numbers of weeds and grasses and only two native trees were recorded. The majority of species recorded in the plots were fleshy fruited zoochorous taxa, typical of plants in the early and intermediate stages of successional development, although a number of late successional species were also recorded. Fruit size and type suggests birds are responsible for most of the effective dispersal. The ability of ecologically rehabilitated areas to recruit and sustain new life forms is a true measure of their contribution to biodiversity conservation. In the tropics, the process of plant colonisation may be accelerated by establishing combinations of fleshy fruited native plant species from different stages of a normal forest succession, which attract seed dispersing birds and mammals. © 1997 Elsevier Science B.V.

Keywords: Rehabilitation; Rain forest; Recruitment; Dispersal; Frugivory; Seed bank

1. Introduction

Restoring biodiversity across increasingly fragmented ecosystems is a major challenge for all land managers. Rain forests offer particular challenges because of rapid rates of deforestation (World Resources Institute, 1994), inherent species richness (Connell, 1978) and the inability of ecological specialists to cope with fragmentation effects (Laurance, 1991). The need to begin the rehabilitation process has long been recognised (Lovejoy, 1985).

In the Wet Tropics of Far North Queensland, moist tropical forest clearing has resulted in the creation of 190 000 ha of land requiring some form of rehabilitation (Wet Tropics Management Authority, 1995). The effects of this clearing on relict populations of highly endemic plants and animals are increasingly apparent in the remnants of original and regrowth forest forming the landscape mosaic (Goosem and Young, unpubl. data; Laurance, 1991; Crome and Bentrupperbaumer, 1993; Laurance and Laurance, 1996). Larger forest blocks are fragmented by the effects of roads and electricity line clearings (Goosem and Marsh, unpubl. data), the latter accounting for 1316 ha of disclimax grassland within the main

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forest massifs (Wet Tropics Management Authority, unpubl. data).

Ecological rehabilitation assumes a key role in ameliorating fragmentation effects, as a means of creating, directing and accelerating successional processes across degraded areas of the landscape (Brown and Lugo, 1994; Goosem and Tucker, 1995; Lamb et al., in press). Many authors have examined plant succession in old fields and remnants, describing factors implicated in the rate of colonisation. The importance of disturbance history and disturbance per se (Hopkins, 1990), diaspore availability (van Ruremonde and Kalkhoven, 1991; McClanahan, 1986), reserve size (Peterken and Game, 1984), dispersal vectors and vegetation structure (McDonnell and Stiles, 1983; Dzwonko and Loster, 1992; Guevara and Laborde, 1993; Robinson and Handel, 1993; Parrotta, 1995) to the rate and diversity of the succession is well accepted and detailed. All of these factors are also important design considerations if ecological rehabilitation is to be successful (Goosem and Tucker, 1995).

The success of rehabilitation can be measured by many parameters (Ewel, 1987; Noss, 1990; Clusener Godt and Hadley, 1993). Most studies to date have focused on the 'catalytic' effect of rehabilitation on vegetation recruitment. A combination of changes in soil moisture, fertility and temperature, reduced weed competition and provision of wildlife habitat, provides a suitable catalyst for the establishment of new species across many life forms. In some cases the relationship between the catalysing effect on succession and dispersal vectors has been explored (McClanahan and Wolfe, 1993; Parrotta, 1995). Jansen (1997) has demonstrated the catalytic effects of a tropical rehabilitation on the re-establishment of leaf litter invertebrate communities. However, the paucity of data relating to recruitment of other forms of biodiversity reflects the relative infancy of the practice of rehabilitation ecology, and this lack of knowledge and practice is nowhere more apparent than in tropical forests.

The purpose of this study was to evaluate the success of four rehabilitation projects in north Queensland by examining native plant species recruitment. An assessment of the dispersal mode(s), likely origin (whether seed bank or seed rain), life form and successional status and diaspore size of each species was

made, to examine whether these plantings will develop into complex and multi layered forests. One plot isolated from a primary seed source was included within the study to assess the effects of isolation on recruitment.

2. Site descriptions

All rehabilitation sites were established and maintained using the Framework Species Method as described in Goosem and Tucker (1995) and Lamb et al. (1997). This method uses suites of fleshy fruited local species known to be frugivore attractants with good site capture abilities. Framework species are established as a perching resource and a 'bait crop' to entice seed dispersing wildlife from adjacent areas, relying on these dispersers to accelerate the establishment of other species and life forms. All rehabilitation sites were blanket sprayed with a non-residual herbicide prior to planting. All sites have a closed canopy ranging from 6.4 m high at 5 years of age to 8.7 m in the 7-year-old plots, light levels vary depending on crown architecture of the various planted species.

Eubenangee Swamp National Park (145° 20' E, 17° 25' S) is a 1700 ha coastal wetland reserve at 0 m a.s.l. Average annual precipitation is 3641 mm, chiefly during the November to April 'wet' season, mean annual temperatures varying from 27.5°C in January to 19.5°C in July (Tracey, 1982). (The strongly seasonal pattern of rainfall is common to all sites.) The main community under rehabilitation is Tracey's Type 3a (Tracey, 1982), Complex Mesophyll Vine Forest (CMVF) with dominant palms, reflecting seasonally impeded soil drainage and granitic soil parent materials. The park contains other vegetation communities including paperbark (*Melaleuca* spp.) woodlands and extensive swamp grasslands and sedgelands.

Plantings at this site are concentrated along the Alice River where historically (ca. 1930s), timber extraction, clearing for beef production and inappropriate fire regimes have reduced riparian vegetation to a strip varying from 2 to 10 m wide. The area was gazetted National Park in 1968 and since the early 1980s, rehabilitation has focused on the closure of artificial drains, the use of fire and fire breaks to manipulate fire tolerant communities for maintenance

of successional diversity, and revegetation to restore mesophyll vine forest to appropriate areas.

Lake Barrine National Park, gazetted in 1934, (145° 38' E, 17° 15' S), is a 491 ha upland rain forest reserve at 760 m a.s.l. Average annual precipitation is 1428 mm and mean annual temperatures vary from 25°C in January to 15.5°C in July (Tracey, 1982). The community under rehabilitation is CMVF, Type 1b, located on basaltic kraznozems (Tracey, 1982). Plantings are concentrated in degraded areas of former road reserve within the park. All these areas are disclimaxes of molasses grass (*Melinis minutiflora*) and guinea grass (*Panicum maximum*) remaining from roadworks in the late 1950s. Rehabilitation commenced in 1988.

The Mulgrave River section of Wooroonooran National Park (145° 45' E, 17° 08' S) is an area of riparian forest at 40 m a.s.l. Average annual precipitation (Cairns) is 2224 mm, mean annual temperatures varying from 31.5°C in January to a 16.7°C in July (Tracey, 1982). The community under rehabilitation is CMVF Type 1C, commonly associated with greater seasonal dryness, characterised by increased deciduousness and fewer trunk epiphytes (Tracey, 1982).

This community has been seriously degraded by the effects of logging, clearing, wildfires, sugar cane growing (practised since the early 1880s), and invasion by the exotic vine blue thunbergia (*Thunbergia grandiflora*), introduced in the 1930s (P. White, personal communication, 1996). This aggressive species has created large (>1 ha) forest gaps by smothering the crowns of canopy trees which are knocked down during floods, caused by regular, intense rainfall events in the summer cyclone season. Gaps are immediately colonised by *Panicum maximum*. The area was gazetted National Park in 1921 and rehabilitation, involving weed control and revegetation, has been under way since 1984.

Plantings at these forest sites are located on existing forest margins, subject to the same disturbance pressures and with the same floristics as their controls. Plots are sequentially arranged, each yearly planting commencing at the edge of the previous planting. Control sites were located in immediately adjacent areas with known disturbance histories. All controls were dominated by grasses and woody weeds.

The dairy farm (Backshall's) site is located 2 km west of Malanda township (145° 36' E, 17° S), at

762 m a.s.l. Annual precipitation is 1690 mm, mean annual temperatures varying from 28.5°C in January to 10.8°C in June (Tracey, 1982). The area has been cleared and used for dairying since the 1910s, previously supporting CMVF, Tracey's Type 1b (Tracey, 1982), overlapping with Type 5b, where canopy leaf size is generally reduced to notophyll.

Rehabilitation has been under way since 1987 along the eroding banks of gullies flowing into the north Johnstone River which flows through the property. The 1989 planting is located adjacent to the banks of the farm dam and the 1991 site follows a gully to the river. The removal (ca. 1910) of all streambank vegetation has led to serious soil erosion problems and the isolation of many rainforest fragments in the Malanda district. This project aims to provide shade and shelter for stock, arrest soil loss and increase habitat area and diversity. The plots are 600 m from the Malanda Falls Environmental Park, a 19.12 ha reserve containing some relatively intact Type 5b forest, and the nearest source for natural dispersal and recruitment by native flora and fauna.

3. Methods

3.1. Vegetation recruitment

Rehabilitation plantings aged five and seven years, approximately 5000 m² in area, were sampled over a two week period in January 1996 at four sites. Sampling involved delineation of 1500 m² within each restoration plot and control and random placement of eight, 5-m radius, circular plots (78.5 m²). At the Mulgrave River site, 10 plots were needed to adequately record site diversity. At Backshall's dairy farm site only four random plots could be studied. No suitable control could be found for this site. Seedlings located within the 78.5 m² area were recorded, counted and identified to species level. Later assessment of dispersal mode, typical successional stage and growth habit were made by the authors and others based on field experience.

To evaluate dispersal, proportions of the dispersal mechanisms assigned to each species found in a particular plot were calculated by counting the number of species with each dispersal mechanism. These were totalled and divided by the total number of species at

that site. Because many species have mixed dispersal mechanisms, the resulting proportions calculated do not sum to one.

Data were transformed, (\log_{10} abundance + 1) for mean species numbers and (\log_{10} density + 1) for density of individuals. The effects of establishing plantings, on numbers of recruited species, and mean density of recruits were examined by two way Analysis of Variance, to determine differences between sites, and differences between years (1989, 1991, and control). Where significant differences occurred ($P < 0.05$) comparisons between means were performed using Tukey's HSD. Four subplots were randomly selected from each site for the calculation of means and standard deviations.

The Braun-Blanquet Cover Abundance Scale was used to measure ground cover. A visual assessment of the ground cover was performed on a grading scale where $>75\%$ cover = 5, to 5% cover = 1 and a solitary individual/small cover = r . Cover abundance values were converted to a 1–7 scale to allow for grass cover statistical analysis, where $1 = r$ and $7 = 5$. Percentage cover and type were assessed during plot surveys. Spearman Rank Correlation Analysis was used to demonstrate the relationship between the diversity and abundance of woody native species recruitment and grass cover.

3.2. Soil seed bank

Soil seed bank sampling was undertaken using cylindrical brass cores to extract 160 cm² of soil to a depth of 50 mm. Three replicate samples were taken from random points in each of the four sites in January, 1996. Samples were transferred to the nursery, the cores placed on coarse blotting paper to prevent soil loss, and seated inside free draining seed germination trays. Trays were placed in the nursery germination room, and kept moist by daily watering.

All seedlings were counted, identified and removed after 42 days, any unidentifiable individuals were potted into larger tubes to permit later identification. The soil surface was then disturbed to a depth of 15 mm to encourage further germination. The same procedure of identification/growth encouragement was repeated at days 56, 82 and 98. No germination was recorded after this period. Classification of growth form and dispersal mechanism was based on

Kleinschmidt and Johnson (1987) and the author's field experience.

4. Results

4.1. Soil seed bank

Soil seed banks were dominated by forbs (48 of the total of 74 records) and grasses, only two trees were recorded (Fig. 1). Dominance was assumed by Asteraceae and Poaceae, together accounting for 32 of the 66 family records. Wind dispersal was common. The two small seeded, native trees recorded can both be associated with disturbed areas. The other native species are common in open and disturbed areas and all other plants are exotic grasses, old field and roadside weeds. Exotic species comprised 82%, native species 10% and 8% could not be identified. Germinated species from soil samples showed a total number of 547 individuals from 37 species (Appendix A).

4.2. Native plant species recruitment

A total of 13 072 individual seedlings were recorded in the four sites, representing 68 families, 133 genera and 190 species (Appendix B). Eight seedlings could not be identified. The most common families ranked by number of recordings/number of species were; Euphorbiaceae (53:5), Lauraceae (36:6), Sapindaceae (35:5), Moraceae (25:5), Myrtaceae (23:5), Apocynaceae (20:6), Araliaceae (18:4), Rutaceae (13:5), Vitaceae (13:6), Rhamnaceae (11:4),

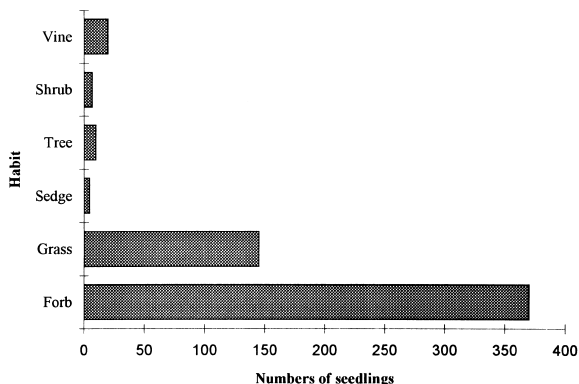


Fig. 1. Habit of soil seed bank species recorded in rehabilitation and control sites at four sites in far North Queensland.

Rubiaceae (11:6), Dilleniaceae (11:3), Fabaceae (11:4), Arecaceae (10:3), Sapotaceae (10:4), Poaceae (10:6). The ten most common species, recorded by plot presence, were; *Omalanthus novo-guineensis* (9), *Cryptocarya triplinervis* (9), *Litsea leefeana* (8), *Polyscias elegans* (8), *P. australiana* (7), *Melicope elleryana* (7), *Tetracera nordiana* (7), *Rhodamnia sessiliflora* (7), *Melodinus australis* (7), *Guioa acutifolia* (7).

The highest diversity of recruitment was recorded at the Mulgrave 7-year-old plot (72 species) and the lowest at the Backshall's 7-year-old plot (23 species). The highest density of recruitment was recorded at the Eubenangee 7-year-old plot (3086 individuals) and the lowest at the Backshall's 5-year-old plot (170).

4.3. Rate of colonisation by native species

The rate of colonisation, expressed in terms of mean numbers of species/site and density of individuals/site, is shown in Figs. 2 and 3. Differences between sites were not significant ($F_{2,8} = 5.97$, $P = 0.06$, df 2) but differences between years and controls were highly significant ($F_{2,8} = 76.96$, $P = 0.0006$, df 2). The Backshall's site was not included in this analysis. Tukey (HSD) pairwise comparisons of yearly

mean numbers showed rehabilitated plots were not significantly different (means of log values were 1.48 for 7-year-old plots and 1.39 for 5-year-old plots), while control plots had significantly lower numbers of species (mean of log value 0.46).

There was no significant difference between sites in average density of forest species ($F_{2,8} = 1.68$, $P = 0.2951$, df 2), but significant differences between years and controls ($F_{2,8} = 13.37$, $P = 0.0169$, df 2). Tukey (HSD) pairwise comparisons of yearly mean density showed that the rehabilitated plots were not significantly different (means of log values were 0.67 for 7-year-old plots and 0.50 for 5-year-old plots) while control plots had significantly lower numbers of recruited species than the 7-year-old plots (mean of log value was 0.10), but similar numbers to the 5-year-old plots. If the rate of recruitment is reflected in both the number of species and density of seedlings then both the preceding analyses suggest that it is greater in plantations than in controls. There were significant negative correlations between abundance and cover ($r = -0.2447$, $n = 82$, $P < 0.05$) and also between diversity and cover, ($r = -0.2381$, $n = 82$, $P < 0.05$).

Birds were important as dispersal vectors, especially in fragmented landscapes where foraging may

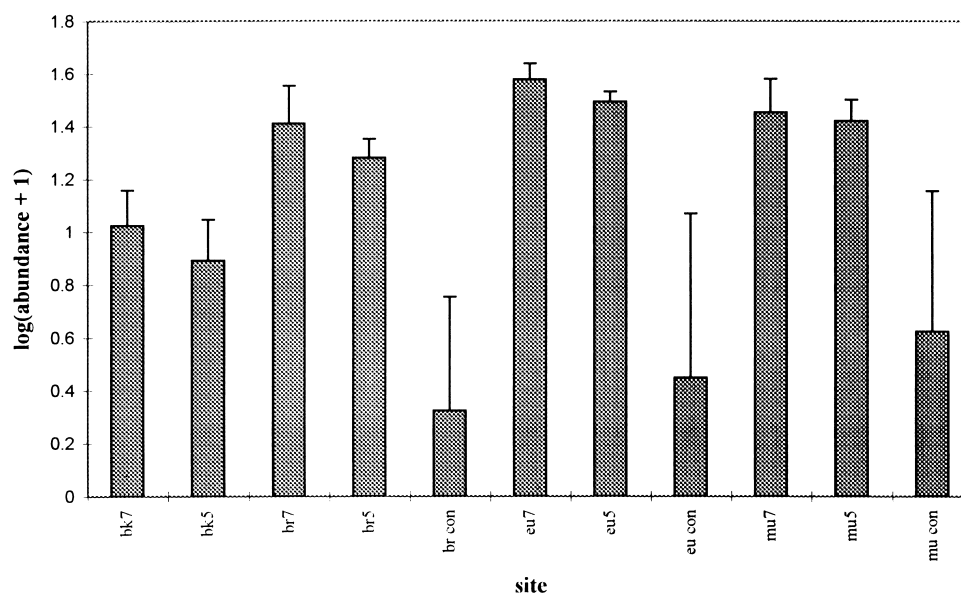


Fig. 2. Mean number of colonising species per site at four location in far North Queensland. Bk, Backshall's; Br, Barrine; Eu, Eubenangee; Mu, Mulgrave; 7, 7-year-old plot; 5, 5-year-old plot.

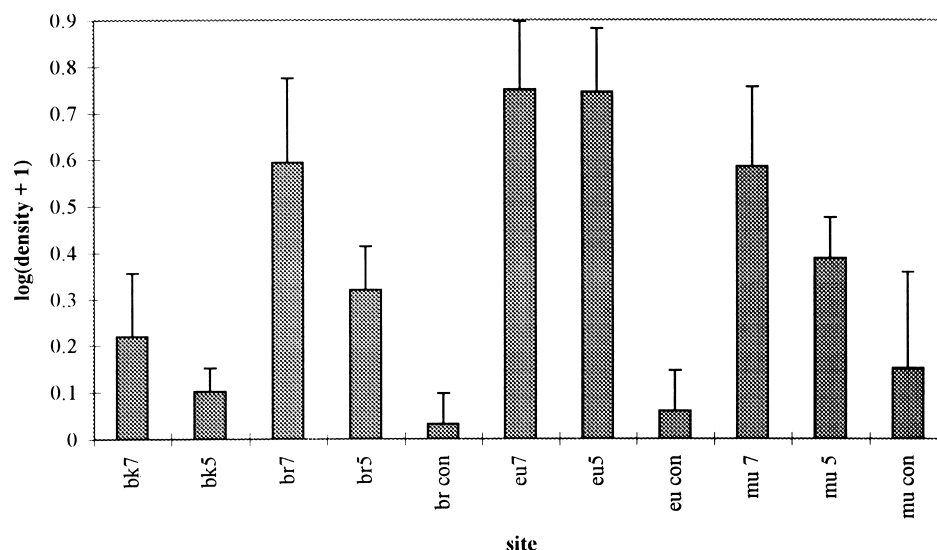


Fig. 3. Mean density of colonising individuals per site at four locations in far North Queensland. Bk, Bakshalls; Br, Barrine; Eu, Eubenangee; Mu, Mulgrave; 7, 7-year-old plot; 5, 5-year-old plot.

be required over larger areas. Higher proportions of water dispersed species were recorded at the riparian sites (Mulgrave, Eubenangee, and Backshall's) (Fig. 4).

There was a dominance of small-seeded taxa in all plots, but the trend was particularly evident in the control plots and the isolated site, (Fig. 5, cf. Appendix B). Eighty-two percent of the colonising species had small seeds (<10 mm diameter), 17% of species had intermediate size seeds (10–20 mm diameter), and 1% had large seeds (>20 mm).

Growth forms were well represented in the tree and vine categories, with canopy trees being less common in the controls and the isolated site (Table 1). Grasses and herbs were more abundant in the control plots.

5. Discussion

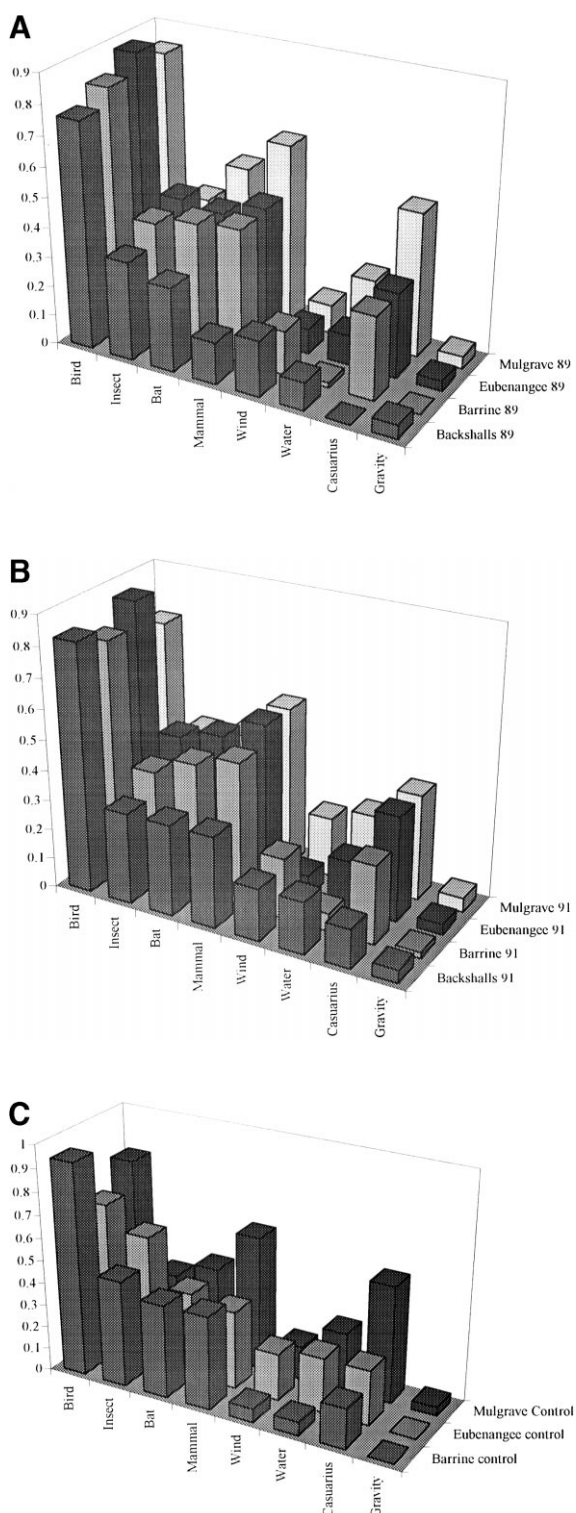
It is clear that the rehabilitation plots have had a significant catalytic effect on recruitment. All plots located adjacent to existing forest have been colonised by a wide range of species from across the successional spectrum, and growth habit is spread across all forms. Lowland sites demonstrated the highest diversity and abundance. Several factors are likely to be implicated including the concentration of biological richness in riparian areas and hence a greater likelihood of successful dispersal.

The planting stock for each site varied because of the difference in forest types. There was no significant statistical difference in mean numbers or density between sites, suggesting species composition has been less important than structure in accelerating succession. More detailed research is needed to discern potential differences between structure alone and structure with early maturing, fleshy fruited species.

Controls demonstrated lower diversity and abundance of recruitment. All controls were dominated by grasses, e.g. *Panicum maximum*, signal grass (*Brachiaria decumbens*), and vines, e.g. *Thunbergia grandiflora* on the lowlands; and glycine (*Neonotonia wrightii*) on the uplands. All control sites are considerably older than the treatments, the Barrine site being the youngest at 30 years since disturbance. This suggests the plantings have created a structure more favourable to natural regeneration of forest species than the natural succession processes, combating the grass and vine structures of the controls.

5.1. Origin of recruitment

Most of the soil seed bank in the plantings consisted of forbs and shrubs. Only two small-seeded, native trees were recorded, on only one site (Mulgrave 1989), compared to the 139 native forest species



found by Hopkins and Graham (1983) beneath intact rain forests in the same area. Tucker and Mair (unpubl. data) also found forbs and grasses dominated the seed bank (99%) between 2 and 20 m from the edge of disturbed forests, suggesting recruited taxa recorded on all sites arrived in the seed rain, either dispersed in or from seeding of planted trees. The prominence of forbs and grasses in the seed bank suggests that in 7-year-old plots, a significant disturbance could encourage the re-establishment and dominance of a grass and forb community.

The importance of birds to seed dispersal was obvious at all sites, strikingly so at the isolated plot. Potential dispersal agents were also recorded and whilst all of these vectors need individual evaluation for 'efficiency', 'quality' or 'legitimacy' (Schupp, 1993), they are all assumed to play some role.

Crome (1990) and Crome et al. (1994) present lists of birds recorded in a remnant and riparian regrowth community on the Atherton Tableland and similar lists have been recorded from various rehabilitation plots including those under study. At a 2 ha, isolated (>500 m) rehabilitation near the Backshall's site, we recorded 25 frugivore species after only 6 years. Jones and Crome (1990) record nine obligate frugivores in a list of 33 North Queensland rain forest birds known to include fruit as a major component in the diet. The other 24 species are common in disturbed areas with territories including areas of intact forest and disturbed margins. None of these birds have sufficient gape width to be considered effective dispersers of intermediate to large fruits (20–60 mm).

Flying foxes (*Pteropus* spp.) are important dispersers of rain forest fruits (Richards, 1990a). Eggert (unpubl. data) recorded 30 plant species in the diet of *P. conspicillatus* in North Queensland, including fifteen *Ficus* spp. and a number of large fruited taxa, i.e. *Faradaya splendida* (ca. 65 × 45 mm, Verbenaceae). Evidence presented by Richards (1990b) implicates *P. conspicillatus* in dispersal of larger fruits;

Fig. 4. (A) Proportion of colonising species utilising dispersal vectors in 7-year-old plantings at four locations in far North Queensland. (B) Proportion of colonising species utilising dispersal vectors in 5-year-old plantings in four locations in far North Queensland. (C) Proportion of colonising species utilising dispersal vectors in control sites at three locations in far North Queensland.

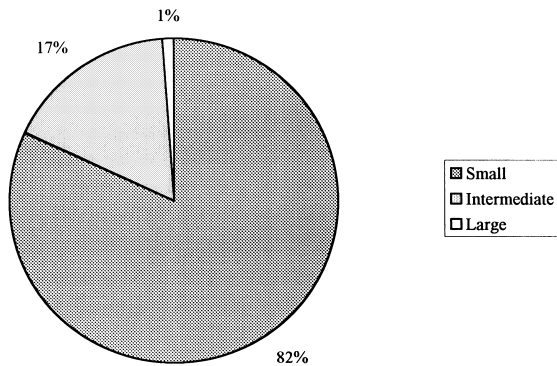


Fig. 5. Proportion of colonising species classified by seed size into small (<10 mm diameter), intermediate (10–20 mm diameter) or large (>20 mm diameter) seed size.

however, seed weight and foraging habits are likely to restrict this dispersal to distances between 30 and 200 m. Smaller seeds may be carried over greater distances due to ingestion.

Other mammals, particularly rodents, may also play significant roles in regulating recruitment in the rehabilitation plots. The rodents undertake significant roles in predation and dispersal of some rain forest seeds in North Queensland, particularly larger taxa with a hard endocarp (Harrington et al., 1997). Sev-

eral local area studies (Laurance, 1991, 1994; Crome et al., 1994; Laurance and Laurance, 1996) have demonstrated presence in remnant and regrowth communities, of species such as the Cape York rat *Rattus leucopus*, bush rat *R. fuscipes*, house mouse *Mus musculus*, grassland melomys *Melomys burtoni*, fawn-footed melomys *M. cervinipes* and the larger white tail rat, *Uromys caudimaculatus*. All these rodents, and the coppery brushtail possum, *Trichosurus vulpecula*, long nosed bandicoot, *Perameles nasuta* and the water rat, *Hydromys chrysogaster*, have been trapped or observed in informal surveys at all the rehabilitation sites, although no *U. caudimaculatus* have been trapped at the isolated Backshall's site. A seed predation trial undertaken in three of the rehabilitation plots under study, showed reduced predation and increased survivorship in the isolated plot (Murphy and Tucker, unpubl. data).

The 2-m tall flightless ratite, the southern cassowary, *Casuaris casuaris*, musky rat-kangaroo, *Hypsiprymnodon moschatus*, water or gravity, are the only other local dispersal vectors for large fruits. Crome (1976), Stocker and Irvine (1983), and Crome and Moore (1988) have recorded several hundred plant species in the cassowary diet, including many large fruited taxa. Decline in cassowary populations in the

Table 1

Proportion of colonising species classified by growth habit within 5- and 7-year-old rehabilitation plantings and control plots in far North Queensland

Site/Age	Habit							
	CT	GT	UT	V	SH	G	H	F
Blackshalls 7	7	4	5	2	1	0	0	1
Backshalls 5	6	5	4	4	2	0	0	2
Barrine 7	21	3	18	16	1	0	0	0
Barrine 5	15	4	15	12	0	2	2	0
Control	1	2	4	6	0	3	3	0
Eubenangee 7	12	7	19	16	2	0	0	2
Eubenangee 5	14	5	17	14	2	0	0	3
Control	3	4	8	6	2	2	2	3
Mulgrave 7	25	8	17	15	1	1	1	2
Mulgrave 5	16	8	13	14	4	1	1	6
Control	8	3	9	4	0	1	1	1

CT, canopy tree; UT, understorey tree; SH, shrub; H, herb; GT, gap tree; V, vine; G, grass; F, fern. 7, 7-year-old plot; 5, 5-year-old plot.

Wet Tropics of North Queensland has been noted by Crome and Bentrupperbaumer (1993). Cassowaries have been sighted in both the Lake Barrine and Mulgrave rehabilitation plots (personal observation). Dennis (personal communication, 1996) describes *H. moschatus* as the most important disperser of large fruits where the species occurs, being predominately a flesh eater and only consuming a few seeds.

5.2. Nature of recruitment

Forbs with wind dispersed seeds dominate the soil seed bank. The appearance of many small seeded pioneers in the seed rain and their absence in soil seed banks, suggests ground floor conditions are more suitable for immediate germination rather than incorporation into the seed bank to await germination at a more favourable time. This may be partially due to the high light conditions created by the thin crowned pioneer component of the planted stock.

Small wind dispersed taxa are represented by plumed seeds, i.e. *Alstonia muelleriana*. Large winged species are represented by *Flindersia spp.*. Wind dispersed species are almost totally absent from the coastal plots, represented by only three vines, three trees and two ferns, though dispersal via water was probably more likely for the ferns.

Seed rain shows a clear bias toward small to intermediate sized diaspores. The majority of all fleshy diaspore sizes occurred between 3 and 10 mm and the largest drupes are *Gmelina fasciculiflora*, globular fruit around 20 mm diameter, *Palaquium galactoxylum*, oval fruits 25 × 35 mm and *Litsea leefeana*, oval shaped fruit around 25 × 15 mm. Of a similar size, the arillate *Myristica insipida*, only germinates in well shaded and protected sites, has a more specialised coterie of dispersers and its presence indicates the perching/cover value of the vegetation and/or the suitability of forest floor conditions. *Castanospermum australe* is the largest (ca. 50 × 30 mm diameter) diaspore found germinating in any plot (Mulgrave 1989), and its dispersal was most likely attributable to water, although it is also dispersed by rodents.

There were smaller numbers of intermediate (10–20 mm) diaspores though these seeds are larger and heavier and more difficult for the disperser to carry, and hence arrive in lower numbers and more infrequently than small seeded species. Large (>20 mm)

fruits require specialist dispersers such as cassowaries and the musky rat-kangaroo, and until plantings reach reproductive maturity these dispersers are unlikely to be frequent or regular visitors or users of the plantings.

5.3. Successional diversity and species dominance

The importance of successional diversity to maintenance of biodiversity is just as important as the size and habitat complexity of the reserve (Gilbert, 1980; Howe, 1984). Most sites have recruited many new species and life forms from all successional stages. The recruitment of life forms such as vines is critical to the creation of a tropical rain forest structure. Abundance and diversity of late successional species was higher at the Mulgrave and to a lesser extent Eubenangee sites, most likely because of their riparian nature.

Varying degrees of dominance by a single individual or small coterie of recruited species is noted in the recruitment at all sites, to a lesser extent at Mulgrave plots. Dominance may be a reflection of predation, site conditions, seasonal and yearly fluctuations in patterns of fruit production, intensity of frugivory, and seed rain (Martinez-Ramos and Soto-Castro, 1993). Many North Queensland taxa, especially late successional species, produce fruit crops biennially, triennially or erratically, and patterns of recruitment are linked to this phenomenon. The dominance (31% of total recruitment) of *Beilschmiedia obtusifolia* in the 1991 plot at Eubenangee is a reflection of this phenomenon.

The pattern of recruitment exerts a strong influence on the nature and structure of the maturing community although predicting the direction of the succession is difficult (Brown and Lugo, 1994). Dominance by a single species, life form or successional group lowers habitat heterogeneity, and increases the chances of a deflected or arrested succession (Hopkins, 1990). Whilst diversity of recruitment is evidenced on all sites studied, trends toward dominance and likely effects on long term plot structure are unknown, and the degree of dominance may ultimately become simply a more frequent presence in a diverse, mature forest. Only monitoring will report how long any perceived trend continues, or when density dependant stressors exert a stronger influence.

5.4. Isolation

The isolated farm plot demonstrated reduced recruitment and increased numbers of seedlings contributed by planted stems, underlining the effects of plot size, distance to seed source and the apparent lack of dispersal vectors. Guevara et al. (1992) and McClanahan (1986) reported a similar negative correlation between distance of seed source and successful dispersal under isolated trees in man made pastures. Whilst Guevara and Laborde (1993) showed successful dispersal and establishment of many rain forest taxa under isolated *Ficus* spp. in Mexico, this may be due to the keystone resource qualities of *Ficus* spp. (Terborgh, 1986), or differences in vegetation structure and composition, and disturbance history.

Locally, exotic grasses effectively arrest the natural regeneration of closed forests through their flammability, the unfavourable germination niche created by the body of the grass, competitive effects on soil moisture and nutrient availability, and possible allelopathic effects on the root systems of other plants. The invasiveness of pasture grasses, broad leafed woody weeds, and exotic trees compounds isolation effects (Nepstad et al., 1991). We have noted similar trends in several local rehabilitation plots isolated from a primary seed source by at least 500 m. Plots up to 10 years of age and two hectares in area, with complex structure and composition, have not yet attracted large seeded plants or rare species, despite regular recordings of fruit pigeons such as the wompoo, *Ptilinopus magnificus*, considered closed forest specialists (Crome, 1990), and the more mobile spectacled flying fox, *Pteropus conspicillatus*. Aggressive pasture weeds commonly colonise the margins of isolated plots, the introduced leguminous vines *Neonotonia wrightii* and *Desmodium* spp. are especially invasive on the uplands.

6. Conclusions

Early successional vegetation produced by ecological rehabilitation can be utilised by many species and provides a suitable framework for rebuilding biodiversity. These processes may be accelerated by using fleshy fruited early successional taxa and favoured diet species for key dispersers such as fruit

pigeons, flying foxes, cassowaries and specialist dispersers such as white-tailed rats and musky rat-kangaroos. Where extant forest provides a source of dispersers and diaspores, management should focus on planting a mixture of Framework species to minimise management inputs and maximise the value of succession. Plantings do not necessarily need to be large if they are strategically located, with an appropriate species composition.

Despite the relative paucity of recruitment at the isolated rehabilitation site, negative cultural perceptions regarding the value of small extant remnants and regrowth on agricultural lands deserve review. Estrada et al. (1993) and Crome et al. (1994) have described very well the biological richness displayed in mixed agricultural areas in Los Tuxtlas, Mexico and in north Queensland. These areas, especially riparian remnants, provide ideal focal points for nucleation (Yarranton and Morrison, 1974), and should be the priority areas for rehabilitation. The most degraded sites should only be targeted if the task is driven by landowner commitment or provides important linear habitat/habitat islands between remnants.

The value of new commercial woodlots and forest plantations to wildlife could be greatly enhanced by the selective use of commercial species in appropriate sites. Valuable timber species such as *Terminalia sericocarpa* (Combretaceae), *Cryptocarya hypospodia*, *Beilschmiedia obtusifolia*, *Litsea lefeana* (Lauraceae), *Dysoxylum muelleri* (Meliaceae), and various Elaeocarpaceae, are all prominent in frugivore diets. In large plantations it would also be desirable to establish these and other suitable species in mixed species, high density plantings which reduce grass competition and promote structural development and recruitment diversity. Location of these plantings should be primarily based on landscape heterogeneity, focusing on riparian zones and other key landscape features. After the surrounding plantation is harvested, the mixed species blocks can continue to contribute to maintaining and restoring biodiversity.

Large-seeded taxa typical of late successional vegetation have not recruited into the planted or control sites and intervention may be required to ensure establishment. Hand spreading into isolated rehabilitations offers promise in the early stages (e.g. 1–2 years) of plot establishment because of reduced predation,

however in rehabilitation projects closer to standing forest these taxa could be included in the initial planting stock. This has the dual effect of ensuring establishment and providing a foci for specialised dispersers as and when plants reach reproductive maturity.

Insufficient data exists on the favoured diet species of *Pteropus* spp. More comprehensive observations are required to maximise the value of rehabilitations to these important dispersers and pollinators. In the meantime the inclusion of many *Ficus* spp. in rehabilitations can be expected to benefit all frugivores, including *Pteropus* spp.

Assessments of long-term stability and productivity will be more reliable if long-term monitoring of key indicators is undertaken. The true value of a rehabilitation is its usefulness to other natural community components. Sampling of indicator groups such as leaf litter invertebrates, ants, reptiles and small mammals should be used more widely to assess community dynamics, processes and the validity of the approach.

These recommendations and observations need to be seen in the context of the large time scales involving forest dynamics. It is still too early to extrapolate from studies in comparatively young plots. Given the scale of the task and the complexity of the ecosystem, the optimisation of resources for rehabilitation is crucial. A strategic approach, combining accelerated succession with manipulated site conditions seems to be the most appropriate form of rehabilitation management.

Acknowledgements

We wish to thank Rigel Jensen and Stephen McKenna for assistance with field identification and surveys, Dan Murphy for his mammal work, Trina Simpson for assistance with plot surveys and soil seed bank work, Alethea Cardwell, Amy Jansen, Mark Botha and Anthony Mair for assistance with statistical analyses and data presentation and Nick Stevens and Michael Corley for assistance with plot surveys. Thanks to Alan and Anna Backshall for their assistance and permission to use the farm study site. Thanks to Dr. Steve Goosem, Dr. John Parrotta, A.K. Irvine and two anonymous reviewers for reviewing an earlier draft of the manuscript. Thanks to A.K. Irvine

for assisting with elucidation of dispersal mechanisms. The assistance and support of the Queensland Department of Environment is acknowledged.

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Appendix A Species germinated from soil seed bank samples taken from four locations in far North Queensland

Dispersal: B, bird; CE, capsule ejection; M, mammal; T, bat; Wd, wind; Wr, water. Habit: f, forb; g, grass; sb, shrub; sd, sedge; t, tree; v, vine. Location: Bk, Backshalls; Br, Barrine; Eu, Eubenangee; Mu, Mulgrave. 7/5, 7/5-year-old plots; con, control.

Family	Species	Habit	Dispersal	Origin	Site										
					Bk7	Bk5	Br7	Br5	Br con	Eu7	Eu5	Eu con	Mu7	Mu5	Mu con
Acanthaceae	Unidentified sp.	f	CE	unknown						2				6	
Acanthaceae	Unidentified sp.	f	CE	unknown								1	2		
Apiaceae	<i>Centella asiatica</i>	f	Wd	native						2					
Asteraceae	<i>Ageratum sp.</i>	f	Wd	exotic	17	20	10	6		55	11	85	14	6	30
Asteraceae	<i>Conzys canadensis</i>	f	Wd	exotic		1									
Asteraceae	<i>Crassacephalum crepidioides</i>	f	Wd	exotic	1	22				1		1	3	3	2
Asteraceae	<i>Eclipta prostrata</i>	f	Wd	native										1	
Asteraceae	<i>Galinsoga parviflora</i>	f	Wd,M	exotic									2	1	
Capparaceae	<i>Cleome sp.</i>	f	CE	unknown									1		
Caryophyllaceae	<i>Drymaria cordata</i>	f	Wd	native	1										
Euphorbiaceae	<i>Phyllanthus sp.</i>	f	Wd	native						1		2			
Onagraceae	<i>Ludwigia octovalvis</i>	f	Ce,Wr	native										4	1
Polygonaceae	<i>Polygonum lapathifolium</i>	f	Wd	native						2	2				
Rubiaceae	<i>Oldenlandia corymbosa</i>	f	Wd	native							2			7	
Solanaceae	<i>Solanum nigrum</i>	f	B	exotic									2		5
Unidentified sp. 1		f		unknown						1					
Unidentified sp. 3		f		unknown	17										1
Unidentified sp. 2		f		unknown	7					1	1	1	1		
Verbenaceae	<i>Stachytarpheta cayennensis</i>	f	Wd	exotic										2	
Verbenaceae	<i>Stachytarpheta jamaicensis</i>	f	Wd	exotic									1	4	
Total no. families					4	1	1	1		7	4	4	6	5	4
Total no. species					5	3	1	1		8	4	5	8	9	5
Total no. individuals					43	43	10	6	0	65	16	90	26	34	39
Poaceae	<i>Eleusine indica</i>	g	Wd	exotic		1							3	5	
Poaceae	<i>Melinis minutiflora</i>	g	Wd	exotic				12	1						
Poaceae	<i>Oplismenus aemulus</i>	g	B,Wd,Wr	native			1								
Poaceae	<i>Panicum maximum</i>	g	Wd	exotic											4
Poaceae	<i>Paspalum paspalodes</i>	g	Wd	native						15	40	53			
Poaceae	Unidentified sp.	g		unknown						1		7			
Unidentified sp. 4		g		unknown	1										
Total no. families					1	1	1	1	1	1	1	1	1	1	1
Total no. species					1	1	1	1	1	2	1	2	1	1	1
Total no. individuals					1	1	1	12	1	16	40	60	3	5	4

Appendix A (*continued*)

Family	Species	Habit	Dispersal	Origin	Site										
					Bk7	Bk5	Br7	Br5	Br con	Eu7	Eu5	Eu con	Mu7	Mu5	Mu con
Mimosaceae	<i>Mimosa pudica</i>	sb	Wd	exotic						2	3				
Solanaceae	<i>Solanum mauritianum</i>	sb/t	B,T	exotic	2	1		1		1					
		Total no. families			1	1		1		2	1				
		Total no. species			1	1		1		2	1				
		Total no. individuals			2	1		1		3	3				
Cyperaceae	<i>Bulbostylis densa</i>	sd	Wd	native	2										
Cyperaceae	<i>Carex sp.</i>	sd	Wd	exotic											1
		Total no. families			1										1
		Total no. species			1										1
		Total no. individuals			2										1
Rubiaceae	<i>Nauclea orientalis</i>	t	B	native										1	
Urticaceae	<i>Pipturus argenteus</i>	t	B	native										1	
		Total no. families												2	
		Total no. species												2	
		Total no. individuals												2	
Fabaceae	<i>Desmodium sp.</i>	v	CE	exotic	1			10	5						
		Total no. families			1			1	1						
		Total no. species			1			1	1						
		Total no. individuals			1			10	5						

Appendix B Native plant species colonising study sites

Dispersal: B, bird; C, insect; G, gravity; M, mammal; T, bat; S, cassowary; Wd, wind; Wr, water; ?, probable dispersal. Succession: E, early; I, intermediate; L, late. *, indicates possible contribution by planted stock. Habit: ct, canopy tree; gt, gap tree; ut, understorey tree; sh, shrub; g, grass; v, vine; h, herb; f, fern; e, epiphyte. Seed size: S, small (<10 mm); I, intermediate (10–20 mm); L, large (>20 mm). Site: Bk, Backshalls; Br, Barrine; Eu, Eubenagee; Mu, Mulgrave. 7, 7-year-old; 5, 5-year-old; con, control.

Family	Species	Habit	Dispersal	Successional stage	Seed size	Site										
						Bk7	Bk5	Br7	Br5	Brcon	Eu7	Eu5	Eucon	Mu7	Mu5	Mucon
Anacardiaceae	<i>Euroschinus falcata</i> var. <i>falcata</i>	ct	B C?	E-I	S	2		9	5						2	
Anacardiaceae	* <i>Semecarpus australiensis</i>	ct	G Wr T M S	I-L	I									105		
Anacardiaceae	<i>Blepharocarya involucrigera</i>	ct	Wd	I-L				1								
Apocynaceae	<i>Alstonia muelleriana</i>	ct	Wd	E				9	163							
Apocynaceae	<i>Alstonia scholaris</i>	ct	Wd	E-I-L											12	
Araliaceae	* <i>Polyscias elegans</i>	ct	B C?	E-I	S			12	16							
Araliaceae	<i>Polyscias murrayi</i>	ct	B C?	E	S				5							
Araucariaceae	<i>Araucaria cunninghamii</i>	ct	Wd B? M	E-I				1	1							
Arecaeae	<i>Archontophoenix alexandrae</i>	ct	B Wr T M? S	E-I-L	I							9				
Burseraceae	<i>Canarium acutifolia</i>	ct	B T M S	I-L	I							1				
Clusiaceae	<i>Calophyllum sil</i>	ct	B Wr T? S	I-L	S									1		
Combretaceae	<i>Terminalia sericocarpa</i>	ct	B T M S	I-L	S						49	29		19	3	1
Dilleniaceae	<i>Dillenia alata</i>	ct	B C?	I-L	S						29	5				
Elaeocarpaceae	* <i>Elaeocarpus angustifolius</i>	ct	B Wr G T M S	E-I-L	I		1					1				
Elaeocarpaceae	<i>Elaeocarpus eumundi</i>	ct	B T? M S	I-L	I			2	2							
Elaeocarpaceae	<i>Elaeocarpus angustifolius</i>	ct	B Wr G T M S	E-I-L	I									245	83	
Euphorbiaceae	<i>Aleurites moluccana</i> var. <i>rockinghamensis</i>	ct	M	E	L			1	2							
Euphorbiaceae	<i>Bischofia javanica</i>	ct	B	I-L	S										2	
Euphorbiaceae	<i>Drypetes lasiogyna</i> var. <i>australasica</i>	ct	B	E-I	I						3			1		
Euphorbiaceae	<i>Mallotus mollissimus</i>	ct	B C	E-I	S			1								
Fabaceae	<i>Castanospermum australe</i>	ct	Wr M G	I-L	L									115		17
Lauraceae	<i>Beilschmiedia obtusifolia</i>	ct	B M S	I-L	I						147	953		1		
Lauraceae	<i>Cryptocarya mackinnoniana</i>	ct	B S	I-L	I			5								
Lauraceae	<i>Cryptocarya murrayi</i>	ct	B S	I-L	I						4					
Lauraceae	<i>Cryptocarya grandis</i>	ct	B M? S	I-L	I									4		1
Lauraceae	<i>Cryptocarya hypospodia</i>	ct	B M? S	I-L	I									16	2	18
Lauraceae	<i>Litsea lefeana</i>	ct	B	I-L	I	2	3	20			4	5	1	4		1
Lecythidaceae	<i>Barringtonia calyptrata</i>	ct	Wr M T S	L	L									30	19	
Meliaceae	<i>Dysoxylum papuanum</i>	ct	B T? M? S	I-L	S							1				
Meliaceae	<i>Dysoxylum gaudichaudianum</i>	ct	B T? M? S	E-I	S									409	137	
Meliaceae	<i>Dysoxylum muelleri</i>	ct	B T? M? S	E-I	S									28	12	
Meliaceae	<i>Toona ciliata</i>	ct	Wd	E				1	3							

Appendix B (continued)

Family	Species	Habit	Dispersal	Successional stage	Seed size	Site										
						Bk7	Bk5	Br7	Br5	Brcon	Eu7	Eu5	Eucon	Mu7	Mu5	Mucon
Mimosaceae	* <i>Acacia aulacocarpa</i>	ct	B C	E	S			9	47							
Moraceae	<i>Ficus racemosa</i>	ct	B M T C S	E-I-L	S									1	24	
Moraceae	<i>Ficus virgata</i>	ct	B M T C S	I-L	S									2		
Moraceae	<i>Ficus albipila</i>	ct	B M T C S	I-L	S										1	
Moraceae	<i>Ficus fraseri</i>	ct	B M T C Wr S	I-L	S										3	
Myrtaceae	<i>Syzygium tierneyanum</i>	ct	B Wr T? M S	E-I-L	I							8		160	88	194
Myrtaceae	* <i>Tristaniaopsis exiliflora</i>	ct	Wr G	E	S	60										
Oleaceae	<i>Chionanthus ramiflorus</i>	ct	B M? S	E-I-L	I									36		
Proteaceae	<i>Cardwellia sublimis</i>	ct	Wd	E-I				42			1					
Proteaceae	* <i>Darlingia darlingiana</i>	ct	Wd	E-I		12	1	12	11							
Proteaceae	* <i>Grevillea baileyana</i>	ct	Wd	E-I		34										
Proteaceae	<i>Grevillea robusta</i>	ct	Wd	E					1							
Rhamnaceae	* <i>Alphitonia whitei</i>	ct	B M	E-I	S			4	7							
Rhamnaceae	* <i>Emmenosperma alphonoides</i>	ct	B	I	S	25	2									
Rubiaceae	<i>Nauclea orientalis</i>	ct	B Wr T M C S	E-I-L	S									1		
Rutaceae	<i>Acronychia acidula</i>	ct	B T M S	I	S			3								
Rutaceae	<i>Euodia bonwickii</i>	ct	B C?	E-I	S			2								
Rutaceae	<i>Flindersia brayleyana</i>	ct	Wd	E-I-L				3	1							
Rutaceae	<i>Flindersia pimenteliana</i>	ct	Wd	E-I-L				1	3							
Rutaceae	* <i>Melicope elleryana</i>	ct	B C?	E-I	S		1		10		120	228	4	6	1	
Sapindaceae	<i>Ganophyllum falcatum</i>	ct	B T? M S	I-L	S							1		3	2	
Sapindaceae	<i>Harpullia pendula</i>	ct	B M	I-L	I									1		
Sapotaceae	<i>Palaquium galactoxylum</i>	ct	B T M S	L	I									8	1	
Sapotaceae	<i>Planchonella chartacea</i>	ct	B T? M S	I-L	S						37					
Sapotaceae	<i>Planchonella obovoidea</i>	ct	B T? M S	I-L	I							1		18		
Sterculiaceae	* <i>Brachychiton acerifolius</i>	ct	M	I	S		1									
Tiliaceae	<i>Trichospermum pleiostigma</i>	ct	Wd	E											1	
Ulmaceae	<i>Aphananthe philippinensis</i>	ct	B	I	S				2					9	1	
Verbenaceae	<i>Gmelina fasciculiflora</i>	ct	B T? M S	I-L	I						6	1		1		
Xanthophyllaceae	<i>Xanthophyllum octandrum</i>	ct	B G T? M?	I-L	S						29					
For canopy trees						5	6	12	11	1	9	12	2	19	15	4
Total no. families						6	6	19	15	1	11	13	2	25	18	6
Total no. species						135	9	138	277	2	429	1243	5	1224	394	232

Appendix B (continued)

Family	Species	Habit	Dispersal	Successional stage	Seed size	Site										
						Bk7	Bk5	Br7	Br5	Brcon	Eu7	Eu5	Eucon	Mu7	Mu5	Mucon
Apocynaceae	<i>Parsonsia straminea</i>	v	Wd	E-I		1	2				9	5				
Apocynaceae	<i>Parsonsia latifolia</i>	v	Wd	E-I					2							
Arecaceae	<i>Calamus moti</i>	v	B T? M S	I-L	S			7	1	1						
Aristolochiaceae	<i>Aristolochia tagala</i>	v	Wd	I										4	3	
Convolvulaceae	<i>Erycibe coccinea</i>	v	B T? M?	I-L	I						12	1				
Dilleniaceae	<i>Hibbertia scandens</i>	v	B C?	E-I	S						2	4				
Dilleniaceae	<i>Tetracera nordtiana</i>	v	B C?	E-I	S			23	20		642	145	8	4	1	
Dioscoreaceae	<i>Dioscorea transversa</i>	v	Wd	E-I-L											4	
Elaeagnaceae	<i>Elaeagnus triflora</i>	v	B M T S?	E-I	S		5	54	5	1				1		
Fabaceae	<i>Derris trifoliata</i>	v	G Wd Wr M?	I-L					2		20	1		3	2	
Fabaceae	<i>Mucuna gigantea</i>	v	G Wr M?	E-I-L	I										3	
Flagellariaceae	<i>Flagellaria indica</i>	v	B T?	E-I	S									12		
Menispermaceae	<i>Hypserpa decumbens</i>	v	B	E-I-L	S		1									
Menispermaceae	<i>Pychnarrhena novoguineensis</i>	v	B	I-L	S						64	23				
Menispermaceae	<i>Stephania japonica</i>	v	B	E-I-L	S			11		1				3	7	1
Monimiaceae	<i>Palmeria scandens</i>	v	B T?	E-I	S			5	1		2					
Moraceae	<i>Maclura cochinchinensis</i>	v	B,T	E	S	2	5	9	7	1				1		
Moraceae	<i>Malaisia scandens</i>	v	B T M C?	E-I-L	S			3			13	4	5			
Myrsinaceae	<i>Embelia grayi</i>	v	B C?	I-L	S			4			20	2				
Myrsinaceae	<i>Embelia australiana</i>	v	B C?	I-L	S							2				
Piperaceae	<i>Piper novae-hollandiae</i>	v	B T? M? C? S	I-L	S			69	26							
Piperaceae	<i>Piper caninum</i>	v	B T? M? C? S	I-L	S						2	12		156	80	3
Rubiaceae	<i>Morinda coeleosperma</i>	v	B T? M? C?	I-L	S							12				
Rubiaceae	<i>Psychotria coeleospermum</i>	v	B C?	I-L	S						7					
Smilacaceae	<i>Eustrephus latifolius</i>	v	B C?	I-L	S								1			
Smilacaceae	<i>Smilax australis</i>	v	B C?	I	S									1		
Unidentified	Unidentified	v						1		1						
Unidentified	Unidentified	v						1		11					1	
Unidentified	Unidentified	v						1								
Vitaceae	<i>Cayratia acris</i>	v	B T? M? C? S	I-L	S			2						47	2	1
Vitaceae	<i>Cayratia japonica</i>	v	B T? M? C? S	E-I	S								4			
Vitaceae	<i>Cissus hypoglauca</i>	v	B T? M? C? S	I-L	S			9	1							
Vitaceae	<i>Cissus hastata</i>	v	B T? M? C? S	E-I-L	S						4	1			1	
Vitaceae	<i>Tetrastigma nitens</i>	v	B T? M C? S	E-I-L	S									2	2	
Vitaceae	<i>Tetrastigma thorsbornianum</i>	v	T? M? C?	I-L	S										1	
Lauraceae	Unidentified												1			
		For vines		Total no. families		2	4	14	10	7	13	11	6	12	11	4
				Total no. species		2	4	17	12	7	16	14	7	15	15	4
				Total no. individuals		3	13	529	304	31	990	264	30	324	129	7