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Regeneration of native plant species in restored forests on degraded lands in Singapore

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Abstract

The pattern of natural regeneration was studied in three 1-year old and three 4-year old native species reforestation sites on degraded lands in Singapore. On each site, twenty 25 m^2 plots were set up and plant regeneration was surveyed. For each woody species regeneration, life form, mature height, dispersal mode and successional status were accessed. We also investigated how the successional status and condition of the surrounding forest influence the course of early succession on these sites. A predictable suite of typical early pioneer species of degraded lands dominated all 1-year old reforestation sites. Natural regeneration on a site surrounded by primary forest was not any more diverse nor was the rate of succession accelerated compared to other sites surrounded by mature and degraded secondary forest. Principle components analysis (PCA) showed that the type of landscape matrix and seed dispersal become increasingly important in determining succession as the planted saplings grow and canopy cover is restored. The regenerating woody community on the 4-year old reforestation sites was fairly species rich with 73 species observed. However, the community was dominated by a subset of small-seeded secondary forest species of medium stature, while some of the prominent primary forest families such as Dipterocarpaceae were completely missing from the regeneration. The results showed that reforestation has been successful in promoting native forest development, but it also illustrated the need for management intervention in restoring the floristic diversity and structural complexity of a primary forest especially where the natural successional processes are hampered by soil degradation, habitat fragmentation and the loss of native fauna.

Keywords: Forest restoration; Pioneer species; Succession; Forest regeneration; Seed dispersal

1. Introduction

Restoring biodiversity on degraded lands across the increasingly fragmented tropical landscape poses a challenge to forest managers and conservationists (Lamb et al., 2005; Carnus et al., 2006). The regeneration of native tree species following land clearance is constrained by a combination of factors that include low seed availability, predation of seeds and seedlings, competition with grasses and other non-woody vegetation, soil degradation and unfavorable microclimate (Uhl and Jordan, 1984; Uhl, 1987, 1988; Uhl et al., 1988; Lugo, 1988; Holl and Kappelle, 1999; Hardwick et al., 2004). In some conditions, weed species can arrest succession on degraded sites (Aide et al., 1995; Cohen et al., 1995; Kuusipalo et al., 1995; Otsamo et al., 1995), necessitating human intervention to initiate forest restoration. Numerous studies have shown that the establishment of plantations or restoration plantings on degraded lands can ameliorate unfavorable microclimatic and soil conditions, and provide habitat for seed-dispersing wildlife, thereby greatly accelerating natural forest regeneration (Parrotta et al., 1997a; Carnus et al., 2006). Regeneration of native tree, shrub, palm, herbaceous and epiphyte communities can also promote the restoration of animal communities (Yu et al., 1994; Jansen, 1997; Parrotta et al., 1997a; Tucker, 2000; Sanchez-DeLeon et al., 2003). Despite evidence for the importance of physical and chemical barriers on the natural forest successional processes, studies suggest that the lack of propagules is perhaps the most important constraint on secondary forest succession (Holl and Kappelle, 1999).

In the early 1800s, a significant fraction of Singapore's native forest, which was mostly lowland dipterocarp forest similar to that in Peninsular Malaysia, was cleared for

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agriculture (Corlett, 1991; LaFrankie et al., 2005). Farming activities in Singapore declined sharply after World War II (Corlett, 1992) due to unsustainable agricultural practices and rise in land prices. After abandonment, fire-prone lalang (*Imperata cylindrica*) grasslands developed on former farmlands, which regenerated to secondary forest known as *Adinandra* belukar (named for its dominant species, *Adinandra dumosa*) after suppression of fire (Corlett, 1991, 1992). Persistence at this stage is variable (Corlett, 1991), but eventually, the *Adinandra* forest is replaced by a more diverse secondary forest (Turner et al., 1997). The soils under these secondary forests are known to have extremely low levels of total N and P with pH values of 3.5–4.2 at 0–10 cm (Grubb et al., 1994). Within the secondary forest mosaic are patches of open scrubland covered by dense growth of *Dicranopteris linearis* ferns and *Smilax setosa* vines that have apparently remained in this condition for 40 years or more. Soil factors, fire and removal of timber from the regenerating forest may have led to the formation of such areas of degraded vegetation (Burkill, 1961; Corlett, 1991). *Dicranopteris* is an aggressive weed that can prevent establishment of tree regeneration by forming dense thickets, thereby arresting succession. Dominance by these ferns may persist for decades or even centuries (Russell et al., 1998). Understanding the factors constraining the regeneration of native forest in these degraded, *Dicranopteris*-dominated lands is important for both land management and conservation.

Since 1991, the National Parks Board has been reforesting these degraded areas within the nature reserves in Singapore using native tree species. The principal reforestation objective is to accelerate succession thereby restoring lands of degraded vegetation to mature secondary forest that contains significant primary forest components. In addition to species return, forest restoration is thought to have other benefits, such as watershed protection, buffer zone development to ameliorate the effects of fragmentation, creation of better habitat for wildlife and provision of more forest areas for recreation. In this study, we investigated the effects of restoration plantings on native forest regeneration on degraded lands. Life form, mature height, dispersal mode and successional status of each naturally regenerating species were assessed to predict whether these restoration plantings are likely to develop into a floristically diverse and structurally complex rain forest. We also examined how the variation in surrounding forest type, thus the difference in composition of seed rain, and the presence of *Dicranopteris* rootmat influence the course of early succession in the restored forests. The results of this study will contribute to the development of a more effective restoration strategy that takes into account the self-recuperating potential of the ecosystem and to provide feedback in evaluating the success of forest restoration.

2. Methods

2.1. Study area

The Republic of Singapore lies at the southern tip of the Malay Peninsula, approximately 137 km north of the equator (1°14N, 103°55E). This study was conducted in the Central Catchment Nature Reserve, which encompasses about 1600 ha of mostly secondary vegetation with patches of primary forest, and the Bukit Timah Nature Reserve which is adjacent to the Catchment and contains ca. 70 ha of primary forest surrounded by regenerating secondary forest.

In this study, six reforestation sites ranging in size from 2200 to 2500 m^2 were surveyed in the two nature reserves. Three of the sites were planted in 1999 and 2000 (approximately four years prior to the field work) and three were planted in 2003 (one year before the field work). The plantings at each site consisted of a mixture of about 30 native tree species planted at an average spacing of 3 m. The three 4-year old sites were all surrounded by mature secondary forests, while each of the three 1-year old sites were surrounded by primary forest, mature secondary forest, and degraded secondary forest next to an urban landscape (Table 1). Land use history of the sites is not clear, except for Site 3 which was a rubber (*Hevea brasiliensis*) plantation that was abandoned around 60 years ago (Corlett, 1992). Sites 5 and 6 are located nearly adjacent to each other. Prior to reforestation, the six sites were cleared of all *Dicranopteris* ferns and other vegetation except for the mature remnant trees using grass cutters. The debris was left to decompose, and the *Dicranopteris* rootmat was left untouched. The only maintenance operation implemented after planting was the periodic removal of *Smilax* vines that sprouted from rhizomes.

2.2. Natural recruitment survey

Natural recruitment in the restored forest was studied by randomly placing twenty 5 m × 5 m plots at each of the six

Table 1
Features of the six reforestation sites

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Time[a] (year)	1	1	1	4.5	4	4
Canopy	Open, 1–5 m	Open, 1–5 m	Open, 1–5 m	Closed, 5–11 m	Closed, 4–10 m	Closed, 4–10 m
Slope	5°	Very slight	8°	Level	Level	Level
Topography	Ridge top	Lowland	Lowland	Next to reservoir	Next to reservoir	Next to reservoir
Aspect	NE	East	North	N/A	N/A	N/A
Prior condition	Fern thicket	Fern thicket	Fern thicket	Fern thicket	Fern thicket	Fern thicket
Past land use	Unknown	Plantation?	Rubber plantation	Agriculture?	Plantation?	Plantation?
Surrounding forest type	Primary and secondary	Mature secondary	Degraded secondary	Mature secondary	Mature secondary	Mature secondary

[a] Time indicates time since reforestation.

reforestation sites. Natural regeneration of woody plants ≥10 cm in length that had established after reforestation were identified to species and counted. Common species were identified in the field, and unknown species were identified using the Singapore National Herbarium specimens. For each species, size at maturity, tree longevity, and dispersal agents were described based on literature survey (Hsuan, 1990; Corner, 1940) and field observation. Percentage area covered by grasses and *Dicranopteris* ferns was visually assessed using a modified Braun–Blanquet cover class scale where >75% cover = 6, 50–75% = 5, 25–50% = 4, 5–25% = 3, 1–5% = 2, and individual cover = 1. Numbers of herbs (≥5 cm), vines (≥10 cm), *S. setosa* and sedges (*Gahnia tristis*) were counted. For statistical analyses, species richness and density data was log transformed. Species diversity (estimated by the Shannon–Wiener index), species richness, density of woody regeneration, sedges, herbs, *Smilax* and other vines, and percentage cover of grasses and *Dicranopteris* were compared among the six sites using nested analysis of variance with age as the main effect and sites nested within ages. Test of significant difference among the six sites were made with Tukey's HSD tests, and between 1-year old and 4-year old sites using Student's *t*-test. Regression analyses were performed to evaluate the effects of grass cover on species richness, diversity, and density of woody regeneration. Finally, principle components analysis (PCA) was used to compare the community composition of natural regeneration among the six reforestation sites using abundance data. SAS® software version 8.02 (1999–2001) and JMP 5.1 (2003) were used for statistical analyses of the data.

2.3. Effects of Dicranopteris rootmat on natural regeneration

To evaluate the effects of *Dicranopteris* rootmat on preventing the establishment of natural regeneration, six $5\ m \times 5\ m$ plots were randomly placed on $800\ m^2$ of *Dicranopteris*-dominated land near Site 1 after the ferns were cleared using grass cutters. An experimental plot with the rootmat removed and a control plot were paired and placed at the same distance from the forest margin. In the rootmat removal plots, all roots and rhizomes of *Dicranopteris* near the soil surface were manually dug up and removed together with leaflitter. The soil was scarified in the process and mineral soil was exposed. Control plots were left untouched. The regenerating vegetation was surveyed after 6 and 10 months using the same method as the natural recruitment survey. Student's *t*-tests were used to compare density and species richness of natural regeneration between treatment and control plots.

3. Results

3.1. Effects of Dicranopteris rootmat on natural regeneration

The density and species richness of woody regeneration were significantly elevated on the treatment plots six and ten months after the removal of *Dicranopteris* rootmat. The treatment also resulted in the establishment of more vines, sedges, and herbs (Table 2). On the treated plots, plant regeneration started to appear four weeks after the removal of the rootmat, and their density and diversity continued to increase. Succession proceeded more slowly on the control plots as the network of *Dicranopteris* roots and rhizomes continued to suppress vegetative regeneration even though their above-ground biomass had been removed. After ten months, the desiccated *Dicranopteris* rootmat showed no clear signs of decomposing.

3.2. Overall structure of natural regeneration

The 4-year old sites supported a significantly more diverse and species rich community of woody recruitment than the 1-year old sites ($P < 0.05$). The 1-year old sites had significantly greater abundance of sedges, grasses, *Dicranopteris*, *Smilax* and other vines than the 4-year old sites ($P < 0.05$) clearly due to the favorable light conditions under the open canopy (Table 3). Ground cover by herbaceous plants was sparse as non-woody vegetation is naturally uncommon in secondary forests in Singapore (Grubb et al., 1994; Turner et al., 1997). The particular abundance of herbs on Site 5 was due to the profusion of understory ferns.

Successional change in the composition of naturally regenerating woody species is shown in Appendices A and B. The colonizing woody community on the 1-year old sites was dominated by the classic light-demanding pioneers of degraded lands, among which *Macaranga heynei*, *Mallotus*

Table 2
Vegetative recruitment after removal of *Dicranopteris* rootmat

Time (month)	Treatment	Number of species	Density of woody regeneration	Density of vines	Density of sedges	Density of herbs
0	Rootmat removed	0	0	0	0	0
	Control	0	0	0	0	0
6	Rootmat removed	5.67 ± 1.33a	19.33 ± 1.20a	3.00 ± 1.15a	5.67 ± 2.60a	0.33 ± 0.33a
	Control	0.67 ± 0.33b	2.00 ± 1.53b	1.00 ± 0.58a	0.33 ± 0.33a	0 ± 0a
10	Rootmat removed	8.00 ± 0.58a	25.33 ± 1.33a	3.67 ± 1.20a	6.00 ± 2.08a	7.00 ± 1.53a
	Control	4.33 ± 1.20b	8.00 ± 0.58b	0.67 ± 0.67a	0.67 ± 0.33a	1.33 ± 0.88b

Number of species and density are per $25\ m^2$ plot. Standard errors are followed by different letters (a and b) when the differences are significant ($P < 0.05$) as determined by paired Student's *t*-test. Wood regeneration and vines, ≥10 cm; herbs, ≥5 cm; sedges counted by clumps.

Table 3
Comparison of diversity and structure of natural regeneration in the six sites

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Time (year)	1	1	1	4.5	4	4
Species diversity						
Shannon–Wiener index	1.59 ± 0.10cd	1.86 ± 0.09bc	1.24 ± 0.14d	2.17 ± 0.07ab	2.03 ± 0.11ab	2.28 ± 0.07a
Species richness						
No. of species per site	29	43	21	56	44	54
No. of species per 25 m^2 plot	7.50 ± 0.43b	10.90 ± 0.25ab	5.00 ± 0.15c	11.85 ± 0.79a	11.35 ± 0.83a	13.20 ± 0.90a
Regeneration density (individuals/ha)						
Woody species	8,480 ± 257b	18,460 ± 702a	4,580 ± 160c	11,400 ± 280b	11,740 ± 237ab	11,300 ± 268ab
Vines	4,500 ± 309a	3,580 ± 118ab	1,880 ± 112bc	900 ± 40c	1,980 ± 68abc	2,460 ± 50ab
Sedges	700 ± 44a	440 ± 40abc	600 ± 40ab	80 ± 11c	140 ± 10bc	20 ± 5c
Herbs	1,500 ± 53b	2,520 ± 141b	620 ± 93c	1,700 ± 72b	4,880 ± 160a	2,060 ± 106b
Smilax	880 ± 80a	500 ± 44b	880 ± 72b	0 ± 0c	0 ± 0c	20 ± 0.01c
Dicranopteris (cover scale)	1.10 ± 0.01a	1.25 ± 0.02a	1.20 ± 0.02a	1.00 ± 0.00a	1.00 ± 0.00a	1.05 ± 0.01a
Grass (cover scale)	2.20 ± 0.17a	1.35 ± 0.06ab	1.95 ± 0.07ab	1.2 ± 0.02b	1.10 ± 0.02b	1.00 ± 0.00b

Wood regeneration and vines (including *Smilax*), ≥10 cm; herbs, ≥5 cm; sedges counted by clumps. Standard errors are followed by different letters (a–d) when the differences are significant ($P < 0.05$) as determined by Tukey's HSD test.

paniculatus, *Trema tomentosa* and *Acacia auriculiformis* were the fastest growing, reaching heights of up to 2 m within a year of reforestation. Other species that achieved significant growth in the first year were *Ficus grossularioides*, *Macaranga gigantea*, *Melastoma malabathricum* and *Dillenia suffruticosa*. At the sites reforested 4 years ago, some of the naturally recruited species, e.g., *M. heynei, Macaranga conifera* and *M. paniculatus*, comprised the canopy with the planted trees. However, these shade-intolerant pioneers were senescing with no regeneration in the understory to indicate that they would be a major component of the stand in the future. Other highly light-demanding species such as *M. malabathricum*, *F. grossularioides* and *T. tomentosa* were reduced to small scattered individuals under the closed canopies. With the elimination of the initial pioneers, typical components of secondary forests in Singapore (e.g., *Rhodamnia cinerea*, *A. dumosa*, *Timonius wallichianus*, and species of *Syzygium*, *Garcinia*, *Calophyllum* and *Litsea*) became increasingly abundant as seedlings (mostly ≤50 cm in height). The three 1-year old sites and the three 4-year old sites had accumulated a total of 52 species belonging to 22 families and 73 species belonging to 27 families, respectively.

Canopy emergents that will exceed a height of 30 m at maturity were poorly represented in the natural regeneration at all sites, with only four species (*Ixonanthes reticulata*, *Alstonia angustiloba*, *Fagraea fragrans* and *Campnosperma auriculatum)* recorded in the 1-year old sites and five species (*I. reticulata*, *A. angustiloba*, *F. fragrans*, *Paraserianthes falcataria*, and *Calophyllum wallichianum)* in the 4-year old sites. Common secondary forest species with small seeds dispersed by open country birds, bats and small mammals comprised most of the recruits. *Alstonia angustifolia, A. angustiloba* and *I. reticulata* were the only wind-dispersed species recruited into the sites (Appendices A and B). *Horsfieldia brachiata* (Myristicaceae), whose seeds are generally dispersed by the locally extinct hornbills, was found regenerating on one of the 4-year old sites. Long-tailed macaques (*Macaca fascicularis*) are common in the area and they may be assisting the dispersal of large, fleshy fruited species.

3.3. Natural recruitment as influenced by the landscape matrix

Species composition on the initial pioneer community was similar in all 1-year old sites despite the variation in surrounding forest type and the presumed difference in the species composition of seed rain. Only two species, *Dysoxylum cauliflorum* and *Campnosperma auriculata*, were unique to Site 1 in spite of the great floristic diversity of the surrounding primary forest. The density and species richness of woody regeneration was significantly greater on Site 2 than the other 1-year old sites ($P < 0.05$). Abundance of vines, sedges and herbs were similar in all three sites ($P > 0.05$).

Among the 4-year old sites, natural regeneration community was relatively consistent in species richness and density, but showed greater variation in species composition, although the three sites were surrounded by mature secondary forest in

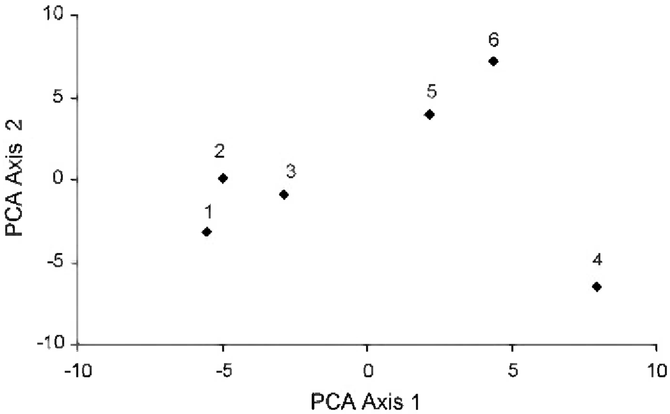

Fig. 1. First two axes of PCA ordination of natural regeneration community on six reforestation sites showing similar floristic compositions of the 1-year old plots (Sites 1–3) and more variation among the 4-year old plots (Sites 4-6).

similar floristic state. Many of the recruits were present in small numbers and unique to a particular site.

3.4. Principle components analysis

PCA using abundance data of all 83 species of woody regeneration recorded revealed two groups of floristically similar communities: the three 1-year old sites and the two adjacent 4-year old sites. Site 4 was distinct from all other sites in species composition (Fig. 1). The first and second components explained 34.4 and 29.3% of the variation in species composition, respectively. The first axis was associated with successional development and separated the younger plots (Sites 1–3) from the older plots (Sites 4–6). On one end of the eigenvector values were the highly shade-intolerant early pioneers while more shade-tolerant later-successional species had higher eigenvector values on the other end. The second axis was related to the gradient in floristic composition among the three 4-year old sites. Species with strongly positive eigenvector values on axis 2 included *Syzygium grande*, *Cinnamomum iners* and *H. brasiliensis*, which probably regenerated from the remnant cultivated trees in the area. Past land use around Site 4 may have been less intensive as the cultivated species were absent and late-secondary species were more frequent. No axis showed any relationship to the variation in surrounding forest type.

4. Discussion

4.1. Succession in restored forests

D. linearis is unrivaled in its ability to colonize open low-nutrient sites due to its indeterminate growth form, shallow rhizomes, mat-forming capacity and exceptionally high phosphorus-use efficiency (Russell et al., 1998). The fern maintains its dominance and suppresses rain forest regeneration by blanketing the site with slow-decomposing leaves and an extensive root system. In this study, removing the rootmat after cutting the above-ground biomass facilitated the natural establishment of herbs, vines, shrubs and trees as was demonstrated in Sri Lanka by Cohen et al. (1995). While successional processes were definitely slowed by the presence of the *Dicranopteris* rootmat, it was observed to decompose soon after canopy closure. The network of roots also appears to prevent soil erosion in the absence of canopy and leaflitter cover.

The results of this study suggest that the extreme microclimatic and soil factors of severely degraded lands pose significant barriers to natural forest regeneration, especially to the establishment of primary forest species. Seed rain from the surrounding secondary forest gave rise to the dense regeneration of common successional species on Site 2, while being surrounded by a primary forest resulted in lower density and species richness of woody regeneration on Site 1. The relative lack of regeneration on Site 3 can be explained by the poor floristic state of the adjacent forest and the scarcity of seed dispersers. As the restoration plantings grow, understory microclimatic conditions are ameliorated, and this allows for the establishment of a wider range of species. Dispersal factor begins to play a more crucial role in determining the species composition of the regenerating forest, and life history variation among the species brings about further successional changes (Finegan, 1996). Many characteristic species of mature secondary forest were fairly abundant in regeneration on the 4-year old sites. These species are evidently capable of surviving in the understory for some years until the shorter-lived pioneers begin to decline, presenting them with a window of opportunity to usurp the canopy.

The natural recruitment community and the shift in species composition during the course of early secondary succession was similar to the pattern observed in Singapore and elsewhere in the region (Wyatt-Smith, 1963; Kochummen, 1966; Kochummen and Ng, 1977; Corlett, 1991), but the process was greatly accelerated by the restoration plantings. In a study of natural plant succession after farming in peninsular Malaysia, it was reported that *M. malabathricum* and *Dicranopteris* ferns effectively blocked woody succession for 13 years, requiring 21 years for the site to accumulate 51 species and sufficient tree growth to shade out the ferns (Kochummen and Ng, 1977). In Singapore, a secondary forest with 35–64 tree species naturally regenerated on land degraded by intensive agriculture 20–50 years after the establishment of weedy vegetation (Corlett, 1991). In this study, similar species richness was achieved in the naturally regenerating community in just 4 years after reforestation.

Numerous studies on natural forest regeneration under plantations or restoration plantings report colonization dominated by small-seeded, bird or bat dispersed species of early to intermediate successional stage and the absence of large-seeded taxa of late successional vegetation (Nepstad et al., 1990; Cohen et al., 1995; Tucker and Murphy, 1997; Parrotta et al., 1997b; Otsamo, 2000). Similar results were obtained in this study, with no regeneration of dipterocarps recorded in the restored forests. Other prominent primary forest families such as Burseraceae, Anacardiaceae, Meliaceae, Ebenaceae, Sapotaceae, Annonaceae, and Myristicaceae were either completely missing from regeneration or poorly represented by only the small-seeded species. Secondary forest in Singapore is much simpler in structure than the primary forest it replaced because of the lack of emergent canopy (Turner et al., 1996, pers. obs.). Likewise, recovery of mature forest species composition after disturbance was found to be the slowest in the canopy layer in the Bolivian Amazon (Pena-Claros, 2003).

Trees of the emergent canopy and large-seeded species should therefore be given priority in planting to ensure that the regenerating forest will have the structural complexity and provide resource heterogeneity to support the native fauna.

4.2. Management implications

The results of this study suggest that reforestation has been successful in controlling invasive weeds and accelerating the natural forest successional processes on degraded lands previously occupied for decades by dense cover of *Dicranopteris* ferns and *Smilax* vines.

The only exotic species that showed significant presence in natural regeneration were *A. auriculiformis*, *Paraserianthes falcataria* and *Clidemia hirta*. *A. auriculiformis* and *P. falcataria* were both introduced from the New Guinea region (Corner, 1940) and now grow wild on wastelands in Singapore. The regeneration of these species should be removed in order to contain their spread on the island. *Clidemia hirta* is an exotic shrub that has become widespread in the rain forests of peninsular Malaysia and oceanic islands. In Singapore, however, *C. hirta* dominates only in disturbed forest edges and is not considered a conservation threat (Teo et al., 2003).

Smilax continued to sprout from rhizomes on the open canopy sites. *Smilax* and other vines were abundant in some areas and stifled the growth of some of the planted trees and natural regeneration. Under the current reforestation strategy in Singapore of planting 1.5 m saplings at 3 m spacing, it would be prudent to remove vines in order to protect the investment in the planted trees and to ensure quick canopy closure. *Dicranopteris* were not able to recover after the initial site clearance and did not pose a threat after reforestation. Although grass had significant negative impact on the density and species richness of woody species recruitment, grass cover was patchy and its growth was suppressed soon after canopy closure. So it appears that only periodic cutting in the first years to facilitate maintenance operations is required.

Some of the tree species abundant in natural regeneration were also used as restoration plantings. These species offer little in improving biodiversity and should not be given priority in planting unless the particular species grows exceptional well or is an important attracter of seed dispersers. Restoration planting should instead focus on adding species and functional groups of trees that are unlikely to establish naturally and those species threatened due to habitat loss. The approach of inter-planting late successional species that are tolerant of open conditions at the initial planting stage, then adding exposure-intolerant species under the canopy of the developing stand has been shown to be a viable forest restoration method in Singapore and elsewhere (Parrotta and Knowles, 2001; FORRU, 2005; Shono et al., in press). This approach, however, requires significant ecological knowledge, and continuous field testing is needed to determine appropriate strategies for establishing each species.

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Appendix A

Woody regeneration (≥10 cm) in the three 1-year old sites

Species	Family	Frequency	No. (ha^{-1})	IV[a]	Size at maturity[b]	Longetivity[c]	Dispersal agent[d]
Macaranga heynei	Euphorbiaceae	0.75	40,267	27.3	2	1	B
Ficus grossularioides	Moraceae	0.65	22,533	24.3	1	1	B
Melastoma malabathricum	Melastomataceae	0.73	31,067	22.8	1	1	B
Trema tomentosa	Ulmaceae	0.60	10,133	13.5	2	1	B
Macaranga conifera	Euphorbiaceae	0.47	15,467	10.7	2	1	B
Ixonanthes reticulata	Linaceae	0.40	11,467	10.3	3	3	W
Macaranga bancana	Euphorbiaceae	0.37	4,267	8.6	2	1	B
Acacia auriculiformis	Fabaceae	0.25	4,000	8.3	2	2	B
Cratoxylum cochinchinense	Hypericaceae	0.27	7,600	8.1	1	1	B
Fagraea fragrans	Loganiaceae	0.33	4,800	7.8	3	3	B
Syzygium lineatum	Myrtaceae	0.23	19,333	7.6	2	2	B, M
Mallotus paniculatus	Euphorbiaceae	0.33	6,400	6.9	1	1	B
Alstonia angustiloba	Apocynaceae	0.30	3,600	5.7	3	3	W
Dillenia suffruticosa	Dilleniaceae	0.23	2,800	4.5	1	1	B
Ficus aurata	Moraceae	0.13	2,133	3.8	1	1	B

Appendix A (*Continued*)

Species	Family	Frequency	No. (ha^{-1})	IV[a]	Size at maturity[b]	Longetivity[c]	Dispersal agent[d]
Gynotroches axillaris	Rhizophoraceae	0.15	2,533	3.3	2	2	B
Syzygium grande	Myrtaceae	0.08	1,733	3.0	2	2	B, M
Macaranga trichocarpa	Euphorbiaceae	0.12	1,867	2.5	1	1	B
Clerodendrum laevifolium	Verbenaceae	0.08	3,867	2.0	1	1	B
Caryota mitis	Arecaceae	0.10	933	1.9	2	2	B, M
Rhodamnia cinerea	Myrtaceae	0.13	2,133	1.8	2	2	B, M
Macaranga gigantea	Euphorbiaceae	0.08	800	1.8	2	2	B
Adinandra dumosa	Theaceae	0.12	1,067	1.5	2	2	B
Timonius wallichianus	Rubiaceae	0.08	1,600	1.2	2	2	B
Sapium discolor	Euphorbiaceae	0.05	400	0.8	2	2	B, M
Cinnamomum iners	Lauraceae	0.03	267	0.8	2	2	B, M
Guioa pubescens	Sapindaceae	0.03	267	0.8	2	2	B
Litsea firma	Lauraceae	0.07	533	0.8	2	3	B, M
Campnosperma auriculata	Anacardiaceae	0.03	267	0.6	3	2	B
Dysoxylum cauliflorum	Meliaceae	0.03	267	0.6	2	2	B, M
Ficus sps.	Moraceae	0.05	400	0.6	–	–	–
Unidentified	–	0.05	400	0.6	1	1	–
Hevea brasiliensis	Euphorbiaceae	0.02	133	0.5	2	2	G
Clerodendrum villosum	Verbenaceae	0.03	533	0.5	1	1	B
Porterandia anisophylla	Rubiaceae	0.03	400	0.4	1	2	B, M
Calamus sp.	Arecaceae	0.02	267	0.4	2	2	B, M
Trigonachras acuta	Sapindaceae	0.02	267	0.4	2	2	B, M
Gnetum gnemon	Gnetaceae	0.03	267	0.4	2	2	B, M
Endospermum diadenum	Euphorbiaceae	0.02	133	0.3	2	3	B
Syzygium attenuatum	Myrtaceae	0.02	133	0.3	2	2	B, M
Ficus variegata	Moraceae	0.02	267	0.2	2	3	B, M
Macaranga hypoleuca	Euphorbiaceae	0.02	267	0.2	2	2	B
Vitex pinnata	Verbenaceae	0.02	267	0.2	2	2	B
Lindera lucida	Lauraceae	0.02	133	0.2	2	2	B
Archidendron clypearia	Fabaceae	0.02	133	0.2	2	2	B
Ficus fistulosa	Moraceae	0.02	133	0.2	2	1	B, M
Leea indica	Sapindaceae	0.02	133	0.2	2	1	B
Litsea elliptica	Lauraceae	0.02	133	0.2	2	3	B, M
Macaranga griffithiana	Euphorbiaceae	0.02	133	0.2	1	1	B
Prunus polystachya	Rosaceae	0.02	133	0.2	2	2	B, M
Morella esculenta	Myricaceae	0.02	133	0.2	1	2	B

[a] Importance value was calculated as the sum of relative frequency and relative density.
[b] Size at maturity indicates normal adult height: 1, <10 m; 2, 10–30 m; 3, >30 m.
[c] Longevity indicates typical life span in natural forest: 1, <20 years; 2, 20–80 years; 3, >80 years.
[d] Seeds typically dispersed by birds and/or bats (B), mammals (M), wind (W), and gravity (G).

Appendix B

Woody regeneration (≥10 cm) in the three 4-year old sites

Species	Family	Frequency	No. (ha^{-1})	IV[a]	Size at maturity[b]	Longetivity[c]	Dispersal agent[d]
Syzygium grande	Myrtaceae	0.68	27,467	18.5	2	3	B, M
Dillenia suffruticosa	Dilleniaceae	0.57	11,200	9.8	1	1	B
Rhodamnia cinerea	Myrtaceae	0.47	11,733	9.2	2	2	B, M
Caryota mitis	Arecaceae	0.48	10,267	8.8	2	2	B, M
Syzygium lineatum	Myrtaceae	0.38	11,467	8.6	2	2	B, M
Cinnamomum iners	Lauraceae	0.47	10,000	8.5	2	2	B, M
Ficus grossularioides	Moraceae	0.47	9,333	8.2	1	1	B, M
Litsea elliptica	Lauraceae	0.42	7,733	7.0	2	3	B, M
Ixonanthes reticulata	Linaceae	0.43	6,800	6.8	3	3	W
Timonius wallichianus	Rubiaceae	0.38	7,733	6.7	2	2	B
Macaranga heynei	Euphorbiaceae	0.33	7,200	6.2	2	1	B
Adinandra dumosa	Theaceae	0.38	5,467	5.7	2	2	B
Clerodendrum laevifolium	Verbenaceae	0.38	4,800	5.4	1	1	B
Alstonia angustiloba	Apocynaceae	0.32	5,067	5.1	3	3	W
Guioa pubescens	Sapindaceae	0.22	6,267	4.6	2	2	B
Archidendron clypearia	Fabaceae	0.22	5,467	4.3	2	2	B
Ficus aurata	Moraceae	0.25	4,667	4.2	1	1	B

Appendix B (*Continued*)

Species	Family	Frequency	No. (ha^{-1})	IV[a]	Size at maturity[b]	Longetivity[c]	Dispersal agent[d]
Macaranga bancana	Euphorbiaceae	0.30	3,600	4.2	2	1	B
Alstonia angustifolia	Apocynaceae	0.22	5,067	4.1	2	2	W
Ficus fistulosa	Moraceae	0.25	3,600	3.7	2	1	B, M
Calophyllum ferrugineum	Clusiaceae	0.20	3,867	3.4	2	3	B
Macaranga conifera	Euphorbiaceae	0.25	2,667	3.4	2	1	B
Diospyros lanceifolia	Ebenaceae	0.15	3,733	2.9	2	2	B, M
Melastoma malabathricum	Melastomataceae	0.20	2,533	2.9	1	1	B
Garcinia parvifolia	Clusiaceae	0.13	3,600	2.7	2	3	M
Macaranga gigantea	Euphorbiaceae	0.20	2,000	2.6	2	2	B
Litsea firma	Lauraceae	0.15	2,533	2.5	2	3	B, M
Albizia falcataria	Fabaceae	0.20	1,733	2.5	3	2	B
Anisophylla disticha	Rhizophoraceae	0.17	1,867	2.2	1	1	B, M
Prunus polystachya	Rosaceae	0.12	2,400	2.2	2	2	B, M
Streblus elongatus	Moraceae	0.15	1,733	2.0	2	2	B, M
Macaranga griffithiana	Euphorbiaceae	0.15	1,333	2.0	2	1	B
Mallotus paniculatus	Euphorbiaceae	0.13	1,333	1.8	2	1	B
Elaeocarpus petiolatus	Elaeocarpaceae	0.13	1,333	1.7	2	2	B
Fagraea fragrans	Loganiaceae	0.13	1,333	1.7	3	3	B
Acacia auriculiformis	Fabaceae	0.12	1,333	1.6	2	2	B
Payena lucida	Sapotaceae	0.10	1,467	1.5	2	2	B, M
Elaeocarpus mastersii	Elaeocarpaceae	0.12	1,200	1.5	2	2	B
Archidendron confertum	Fabaceae	0.12	1,333	1.5	2	2	B
Vitex pinnata	Verbenaceae	0.12	933	1.4	2	2	B
Calophyllum pulcherrimum	Clusiaceae	0.08	1,467	1.4	2	3	B, M
Lindera lucida	Lauraceae	0.07	1,467	1.2	2	2	B
Hevea brasiliensis	Euphorbiaceae	0.08	800	1.0	2	2	G
Syzygium polyanthum	Myrtaceae	0.08	533	1.0	2	2	B
Gynotroches axillaris	Rhizophoraceae	0.07	667	0.9	2	2	B
Pternandra echinata	Melastomataceae	0.05	800	0.8	2	1	B
Arthrophyllum diversifolium	Araliaceae	0.07	533	0.8	2	1	B
Unidentified	–	0.05	533	0.7	1	1	–
Vitex sps.	Verbenaceae	0.05	533	0.7	–	–	–
Ficus sps. 1	Moraceae	0.03	533	0.5	–	–	–
Calophyllum wallichianum	Clusiaceae	0.03	400	0.5	3	3	B, M
Syzygium microcalyx	Myrtaceae	0.03	400	0.5	2	2	B
Ficus sps. 2	Moraceae	0.03	400	0.5	–	–	–
Porterandia anisophylla	Rubiaceae	0.03	400	0.4	2	2	B, M
Horsefiledia brachiata	Myristicaceae	0.03	400	0.4	2	3	B, M
Ficus sps. 3	Moraceae	0.03	267	0.4	–	–	–
Artocarpus dadah	Moraceae	0.03	267	0.4	2	2	M
Elaeocarpus ferrugineus	Elaeocarpaceae	0.03	267	0.4	2	2	B
Bhesa paniculatus	Celastraceae	0.03	267	0.4	2	3	B
Breynia reclinata	Euphorbiaceae	0.03	267	0.4	1	1	B
Garcinia scortechinii	Clusiaceae	0.02	267	0.3	1	2	B, M
Clerodendrum vilosum	Verbenaceae	0.02	267	0.2	1	1	B
Gnetum gnemon	Gnetaceae	0.02	267	0.2	2	2	B, M
Macaranga hypoleuca	Euphorbiaceae	0.02	133	0.2	2	2	B
Agrostistachys longifolia	Euphorbiaceae	0.02	133	0.2	1	1	B
Garcinia eugeniaefolia	Clusiaceae	0.02	133	0.2	2	2	B, M
Garcinia griffithii	Clusiaceae	0.02	133	0.2	2	2	B, M
Gironniera nervosa	Ulmaceae	0.02	133	0.2	2	3	B
Glochidion superbum	Euphorbiaceae	0.02	133	0.2	2	2	B
Morella esculenta	Myricaceae	0.02	133	0.2	1	2	B
Unidentified	–	0.02	133	0.2	–	–	–
Ficus glandulifera	Moraceae	0.02	133	0.2	2	2	B, M
Ficus variegata	Moraceae	0.02	133	0.2	2	3	B, M

[a] Importance value was calculated as the sum of relative frequency and relative density.

[b] Size at maturity indicates normal adult height: 1, <10 m; 2, 10–30 m; 3, >30 m.

[c] Longevity indicates typical life span in natural forest: 1, <20 years; 2, 20–80 years; 3, >80 years.

[d] Seeds typically dispersed by birds and/or bats (B), mammals (M), wind (W), and gravity (G).

References

Aide, M.T., Zimmerman, J.K., Herrara, L., Rosario, M., 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. For. Ecol. Manage. 77, 77–86.

Burkill, H.M., 1961. Protection of wild life on Singapore Island. In: Wyatt-Smith, J., Wycherley, R.P. (Eds.), Nature Conservation in Western Malaysia. Malayan Nature Society, Kuala Lumpur, Malaysia, pp. 152–164.

Carnus, J.M., Parrotta, J., Brockerhoff, E.G., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. J. Forestry 104, 65–77.

Cohen, A.L., Singhakumara, B.M.P., Ashton, P.M.S., 1995. Releasing rain forest succession: a case study in the *Dicranopteris linearis* fernlands of Sri Lanka. Rest. Ecol. 3, 261–270.

Corlett, R.T., 1991. Plant succession on degraded land in Singapore. J. Trop. For. Sci. 4, 151–161.

Corlett, R.T., 1992. Ecological transformation of Singapore, 1819–1990. J. Biogeol. 19, 411–420.

Corner, E.J.H., 1940. Wayside Trees of Malaya. Government Printer, Singapore.

Finegan, B., 1996. Patterns and process in neotropical secondary rain forests: the first 100 years of succession. T. Ecol. Evol. 11, 119–124.

Forest Restoration Research Unit (FORRU), 2005. How to Plant a Forest: The Principles and Practice of Restoring Tropical Forests. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Grubb, P.J., Turner, I.M., Burslem, D.F.R.P., 1994. Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: analysis of soil, leaves and litter. J. Trop. Ecol. 10, 559–577.

Hardwick, K., Healey, J.R., Elliott, S., Blakesley, D., 2004. Research needs for restoring seasonal tropical forests in Thailand: accelerated natural regeneration. New Forests 27, 285–302.

Holl, K.D., Kappelle, M., 1999. Tropical forest recovery and restoration. T. Ecol. 14, 378–379.

Hsuan, K., 1990. The Concise Flora of Singapore: Gymnosperms and Dicotyledons. Singapore University Press, Singapore.

Jansen, A., 1997. Terrestrial invertebrate community structure as an indicator of the success of a tropical rainforest restoration project. Rest. Ecol. 5, 115–124.

Kochummen, K.M., 1966. Natural plant succession after farming. Sg. Kroh. Malayan. Forester 29, 170–181.

Kochummen, K.M., Ng, F.S.P., 1977. Natural plant succession after farming in Kepong. Mal. For. 40, 61–78.

Kuusipalo, J., Adjers, G., Jafarsidik, Y., Antii, O., Tuomela, K., Vuokko, R., 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understory development in forest plantations. J. Veg. Sci. 6, 205–210.

LaFrankie, J.V., Davies, S.J., Wang, L.K., Lee, S.K., Lum, S.K.Y., 2005. Forest Trees of Bukit Timah: Population Ecology in a Tropical Forest Fragment. Simply Green, Singapore.

Lamb, D., Erskine, P., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632.

Lugo, A.E., 1988. The future of the forest—ecosystem rehabilitation in the tropics. Environment 30 (16–20), 41–45.

Nepstad, D., Uhl, C., Serrao, E.A., 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragomina, Para, Brazil. In: Anderson, A. (Ed.), Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest. Columbia University Press, New York, pp. 215–229.

Otsamo, A., Adjers, G., Hadi, T.S., Kuusipalo, J., Tuomela, K., Vuokko, R., 1995. Effect of site preparation and initial fertilization on the establishment and growth of four plantation tree species used in reforestation of *Imperata cylindrica* (L.) Beauv. Dominated grasslands. For. Ecol. Manage. 73, 271–277.

Otsamo, R., 2000. Secondary forest regeneration under fast-growing forest plantations on degraded *Imperata cylindrica* grasslands. New Forests 19, 69–93.

Parrotta, J.A., Turnbull, J.W., Jones, N., 1997a. Catalyzing native forest regeneration on degraded tropical lands. For. Ecol. Manage. 99, 1–7.

Parrotta, J.A., Knowles, O.H., Wunderle, J.M., 1997b. Development of floristic diversity in 10-year-old restoration forests on a bauxite mined site in Amazonia. For. Ecol. Manage. 99, 21–24.

Parrotta, J.A., Knowles, O.H., 2001. Restoring tropical forests on lands mined for bauxite: examples from the Brazilian Amazon. Ecol. Eng. 17, 219–239.

Pena-Claros, M., 2003. Changes in forest structure and species composition during secondary succession in the Bolivian Amazon. Biotropica 35, 450–461.

Russell, A.E., Raich, J.W., Vitousek, P.M., 1998. The ecology of the climbing fern *Dicranopteris linearis* on windward Manua Loa, Hawaii. J. Ecol. 86, 765–779.

Sanchez-DeLeon, Y., Zou, X., Borges, S., Ruan, H., 2003. Recovery of native earthworms in abandoned tropical pastures. Cons. Biol. 17, 999–1006.

Shono, K., Davies, S.J., Chua, Y.K. Performance of 45 native tree species on degraded lands in Singapore. J. Trop. For. Sci. (2007), in press.

Teo, D.H.L., Tan, H.T.W., Corlett, R.T., Wong, C.M., Lum, S.K.Y., 2003. Continental rain forest fragments in Singapore resist invasion by exotic plants. J. Biogeol. 30, 305–310.

Tucker, N.I.J., Murphy, T.M., 1997. The effects of ecological rehabilitation on vegetative recruitment: some observations from the Wet Tropics of North Queensland. For. Ecol. Manage. 99, 133–152.

Tucker, N.I.J., 2000. Wildlife colonization on restored tropical lands: what can it do, how can we hasten it and what can we expect? In: Elliot, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K., Anusarnsunthorn, V. (Eds.), Forest Restoration for Wildlife Conservation. International Tropical Timber Organization, The Forest Restoration Research Unit. Chiang Mai University, Thailand, pp. 279–295.

Turner, I.M., Wong, Y.K., Chew, P.T., Ibrahim, A., 1996. Rapid assessment of tropical rain forest successional status using aerial photographs. Biol. Cons. 77, 177–183.

Turner, I.M., Wong, Y.K., Chew, P.T., Ibrahim, A., 1997. Tree species richness in primary and old secondary tropical forest in Singapore. Biodivers. Conserv. 6, 537–543.

Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75 (2), 377–407.

Uhl, C., 1988. Restoration of degraded lands in the Amazon basin. In: Wilson, E.O. (Ed.), Biodiversity. National Academy Press, Washington, pp. 326–332.

Uhl, C., Jordan, C.F., 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65, 1476–1490.

Uhl, C., Buschbacher, R., Serráo, E.A., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. J. Ecol. 76, 663–681.

Wyatt-Smith, J., 1963. Manual of Malayan Silviculture for Inland Forests. Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia.

Yu, Z.Y., Wang, Z.H., He, S.Y., 1994. Rehabilitation of eroded tropical costal land in Guagdong, China. J. Trop. For. Sci. 7, 28–38.