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FLORISTIC CHANGES IN A SUB—TROPICAL RAIN FOREST SUCCESSION

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ABSTRACT

Floristic changes in a subtropical rain forest succession were assessed. Three regrowth forests aged 20 years, 50 years and 60 years and an undisturbed forest were sampled. The series of sites show floristic changes that would be expected in a successional sequence. The regrowth forests were dominated by the secondary species but the primary species occur from the early stage. The oldest regrowth (60 year-old site) was still well short of regaining its original condition.

ABSTRAK

Perubahan flora pada suatu suksesi hutan subtropika basah ditelaah. Tiga lokasi hutan sekunder berumur 20, 50 dan 60 tahun serta satu hutan yang tidak terganggu dicuplik. Pada sederetan lokasi ini memperlihatkan adanya perubahan flora sebagaimana dalam suatu rangkaian suksesi. Hutan-hutan sekunder muda didominasi oleh jenis-jenis sekunder, tetapi jenis-jenis hutan primer sudah hadir sejak awal suksesi. Hutan sekunder tertua (60 tahun) rupanya masih memerlukan waktu yang panjang untuk mencapai keadaan flora seperti sebelum terganggu.

INTRODUCTION

Many studies have been concerned with describing the composition and structure of rain forests. These have usually emphasized trees with the diameter at breast height (DBH) of 10 cm or more. Such studies have shown a considerable variation in species composition among individual stands of rain forest, associated with environmental gradients (Richards 1952, Baur 1964 and Whitmore 1975). However, comparatively few of such studies have examined along the successional sequences.

The floristic composition of several sub-tropical rain forests assumed to form a successional sequence is examined. This examines of how secondary species are replaced by primary forest species and how long the establishment of the primary forest species will take place.

STUDY AREA AND METHODS

The study area was in the vicinity of O'Reilly's Guest House in the Lamington National Park (28°14'S, 153°7'E) Queensland. Rainfall in the area is about 1 880 mm per year mostly falling in the summer months between November—April. There are no temperature measurements available for the area but the environment is probably similar to the nearby Tamborine Mountain where the temperature range varies from a mean daily minimum of 8.3 °C in July to a mean daily maximum of 26.8° C in January. The vegetation in the area has been mapped and described by McDonald & Whiteman (1979) as a tall closed forest alliance dominated, above 800 m, by a *Caldcluvia paniculosa* — *Cryptocarya erythroxylon* — *Dysoxylum fraserianum* association. According to Webb's classification (Webb 1968) this can be described as a cool sub-tropical rain forest or complex notophyll vine forest. A number of study sites were chosen in regrowth forests of different ages (Figure 1) :

Site 1. Twenty year-old regrowth which has developed on abandoned farmland. The original forest was probably burnt or partially burnt at the time of clearing. The site is about 40 ha in area and 500 m wide at the narrowest point. It is surrounded on three sides by intact forest and on fourth by pasture. The elevation is about 860 m.

Site 2. Fifty-year-old regrowth which has developed after an attempt; to clear the original forest failed. The forest was cleared and partially-burnt but weeds colonized and regrowth prevented pasture establishment. The area covers about 16 ha and is 400 m wide at its narrowest point. The site is bounded on two sites by intact forest and by pasture and disturbed forest on the other two sides. The elevation is 800 m.

Site 3. Sixty-year-old regrowth forest which has developed after the original forest was cleared, burnt and converted to pasture for several years before being abandoned. The area is about 16 ha and about 300 m wide at its narrowest point. It is surrounded on three sides by intact forest and bounded on fourth by road and repeatedly disturbed forest dominated by *Acacia melanoxylon*. The elevation is 900 m.

Site 4. Undisturbed forest close to Site 1). The elevation is 860 m.

Five strip plots each 10 x 100 m were established in an undisturbed forest as well as in the 20, 50 and 60 year-old regrowth forests (i.e. Sites 4, 1, 2 and 3). Each strip plot was then divided into 10 plots 10 x 10 m. Thus 50 plots, with a total area of 0.5 ha, were established at each site. Trees with a DBH greater than 10 cm in each plot were recorded. The diameter was measured using a diameter tape, about 1.3 m above the ground or 20 cm above buttress. Specimens were collected for identification purpose and voucher specimens were prepared.

RESULTS

Compositional Changes

The number of species, genera and families of trees all tended to increase with an increase in forest age (Table 1). The total number of species in each 0.5 ha sample area ranged from 37 in the 20 year-old regrowth (Site 1) to 66 in the intact forest (Site 4). Similarly the number of families increased from 19 to 25 respectively. In general the changes of species composition led to increase in species diversity and equitability, thus the Shannon diversity index increased from 2.45 in Site 1 to 3.46 in Site 4, and the equitability from 0.68 to 0.83.

Sorensen's similarity index, based on the species presence or absence, and Motyka's similarity index, based on the individual number of plants of each species in each site, both indicate similar trends (Table 2). The degree of similarity between the various sites was low. However, both indices also showed that with time the regrowth forest tended to become more similar to the undisturbed forest. Thus Site 1 (20 year-old site) and Site 4 (undisturbed forest) had a Sorensen index of 33.01 while Site 3 (60 year-old regrowth) and Site 4 had a Sorensen index of 49.60. Not surprisingly the highest similarity index was between 50 and 60 year old regrowth forests (Sites 2 & 3).

In regard of the species functional group, most individual trees in the youngest regrowth forest (Site 1) were early secondary species (91,9) %, i.e., species that are short-lived, fast growing, intolerant of shade and regularly produce large numbers of effectively dispersed seeds (Hopkins *et al.*, 1977 & Shugart *et al.*, 1980). The proportion of these declined dramatically throughout succession. As Figure 2 shows, this decreased to 66 % and 11 % in older regrowth forest (Site 3) and undisturbed forest (Site 4) respectively. In contrast, the proportion of trees belonging to primary species (i.e. slow growing and long-lived trees which are capable of germinating and establishing in shade, and irregularly produced seeds that are usually less effectively dispersed) increased from 6 % at the Site 1 to 84 % at Site 4. The late secondary trees which are intermediate in most characteristics between early and primary species, shows a different trend. The proportion increased from 4 % at Site 1 to 22 % at Site 3, but then declined to 9 % in undisturbed forest.

Although the proportion of individuals belonging to primary forest species in the young regrowth forest was very low, the proportion of primary forest species was similar to that of early secondary species i.e., 35 % and 45 % (Figure 2. B). The proportion of primary species increased slightly to 48 % in the 60 year-old regrowth, and then increased sharply to 71 % in the undisturbed forest (Site 4). The proportion of early secondary species, how

Table 1. Number of species, genera and families of trees in a series of regrowth and undisturbed forests (based on 5 strip plots per site each of 10 x 100 m each).

Site Age (years)	1 20	2 50	3 60	4 UF
Number of species	37	58	55	66
Number of genera	32	46	46	49
Number of families	19	23	23	25
Shannon diversity indices	2.45	3.09	2.98	3.46
Shannon equitability indices	0.68	0.76	0.74	0.83

Table 2. Matrix of Sorensen and Motyka's similarity indices

Site Age (years)	Sorensen's similarity			
	1 20	2 50	3 60	4 UF
1 (20 years)	—	44.21	50.00	33.01
2 (50 years)	20.71	—	60.18	48.16
3 (60 years)	34.54	47.41	—	49.59
4 (UF)	10.83	14.27	16.65	—

Motyka's similarity

ever, declined to 29 % in the 60 year-old, then 11 % in the undisturbed forest. The proportion of late secondary species at each site was intermediate between these two groups, increasing to a maximum of 30 % in the 60 year-old regrowth forest and then declining to 20 % in the undisturbed forest.

These same trends are evident if one considers the identity of species having the highest importance value at each site. As Table 3 shows, all the species with importance value greater than 10 in the 20 and 50 year-old regrowth forests were early secondary species. In a 60 year-old forest, of the eight species with importance values greater than 10, five were early secondary species two were late secondary species (*Decaspermum humile* and *Dysoxylum fraserianum*) and one was primary species (*Elatostachys nervosa*). Conversely, all of those important species in the undisturbed forest were primary species except for *Dendrocnide excelsa*.

Table 3, Rank of the most important species which have importance value greater than 10.0

Rank	Forest age (years)			
	20	40	50	UF
1	<i>Acacia melanoxylon</i>	<i>Alphitonia excelsa</i>	<i>Acronychia oblongifolia</i>	<i>Argyrodendron trifoliolatum</i> *
2	<i>Euodia micrococca</i>	<i>Polyscias elegans</i>	<i>Alphitonia excelsa</i>	<i>Pseudoweinmania lachnocarpa</i> *
2	<i>Polyscias elegans</i>	<i>Acronychia oblongifolia</i>	<i>Polyscias elegans</i>	<i>Streblus pendulinus</i> *
4	<i>Dendrocnide excelsa</i>	<i>Pentaceras australe</i>	<i>Euodia micrococca</i>	<i>Dendrocnide excelsa</i>
5	<i>Duboisia myoporoides</i>	<i>Rhodomyrtus psidioides</i>	<i>Rhodomyrtus psidioides</i>	<i>Pseudocarpa nitidula</i> *
6	<i>Alphitonia excelsa</i>	<i>Acacia melanoxylon</i>	<i>Decaspermum humile</i> **	<i>Diospyros pentamera</i> *
7	<i>Acronychia oblongifolia</i>	<i>Euodia micrococca</i>	<i>Dysoxylum fraserianum</i> **	—
8	<i>Elatostachys</i>		<i>ner-vosa</i> *	
Site	2	3	4	5

* : Primary species

** : Late secondary species

— : I.V less than 10.0

UF : Undisturbed forest

Population Changes of Particular Species

The number of important early secondary species such as *Acacia melanoxylon*, *Alphitonia excelsa*, *Dendrocnide excelsa*, *Duboisia myoporoides*, *Euodia micrococca* and *Polyscias elegans* increased sharply in the first 20 years following the disturbance (Figure 3). Thereafter, some of these such as *Acacia melanoxylon*, *Duboisia myoporoides* and *Euodia micrococca* decreased. However, populations of *Acronychia oblongifolia*, *Alphitonia excelsa*, *Pentaceras australe*, *Polyscias elegans* and *Rhodomyrtus psidioides* reached the highest density in 50 and 60 year-old forest. In general, the early secondary species appeared to dominate the regrowth for up to about 60 years.

Late secondary species follow a similar pattern to these early secondary species. But these species tend to establish and become more prevalent later. Their populations were small in the 20 year-old forest.

The number of individuals of primary species in regrowth forests was very small but increased sharply in the mature forest. Only one primary forest species, *Elattostachys nervosa*, was numerous in 60 year-old regrowth forest.

DISCUSSION

As might be expected in a series of forests differing mainly in age, the number of species, genera and families present increased with time since disturbance. Likewise, diversity also increased with forest age. By 60 years, the regrowth forest had not acquired the species richness or diversity of the undisturbed forest. On the other the two similarity indices showed that the regrowth forests were becoming increasingly like the undisturbed forest as time passed by.

Early secondary species dominated the 20 year-old regrowth site (Figure 2). The abundance of these species may be associated with the fact that their seeds are widely dispersed or that they can be stored, remaining dormant in the soil seed bank. Secondary trees often require at least 75% of full sunlight for establishment (Unesco, 1978). Forest clearing, therefore, allows those species to become established.

The length of time for which the secondary species persist at a site seems to depend on their life spans. As Figure 2 shows, the population of the more important secondary species increased then decreased with increasing forest age. Species such as *Acacia melanoxylon*, *Duboisia myoporioides* and *Euodia micrococca* probably had a life span no longer than about 60 years since their number had decreased sharply by this age. Others such as *Alphitonia excelsa*, *Pentaceras australe* and *Polyscias elegans* lived longer but their population densities began to decline after 50 or 60 years. *Acrotychia* and *Rhodomyrtus psidioides* all had their highest population number in the 60 year-old forest but were virtually absent from the undisturbed forest. According to Shugart *et al.* (1980) these have a life span in the order of 100 years, but *Rhodomyrtus* only about 55 years.

These data support the earlier conclusion by Hopkins *et al.* (1977) that the life span of many secondary tree species in these subtropical rain forest is less than 60 years. Likewise Riswan *et al.* (1987) noted a similar longevity for many secondary tropical species. Interestingly King & Chapman (1983) found secondary species disappeared from logged forest in New South Wales within 30 years. Presumably this is because only the shorter lived secondary species had been able to invade the gaps left by logging.

The well known secondary species *Dendrocnide excelsa*, differed from the other species since the population increased in undisturbed forest after decreasing in older regrowth. As this species is an early secondary species, it is thought to be intolerant of shade conditions under canopy. It is believed

that this abundance is due to *Dendrocnide* invading gaps in the mature forest, since it is very common in soil seed banks (Abdulhadi, 1989).

Despite sites is being colonized by the early secondary species, many of the species characteristic of late and primary species also became established soon after abandonment. It is well known that seeds of these species are often of limited viability (Budowski, 1970; Shugart *et al.*, 1980 and Whitmore, 1984). Hence the occurrence of these species in the youngest regrowth forest may have been due to seed rain from nearby parent trees in the undisturbed forest or to resprouting of suckers from persistent roots (Webb *et al.*, 1972 and Stacker, 1981).

Although the primary species were present in the young regrowth forest, their individual numbers were small. In time however, populations of primary species increased. The early occurrence of primary species has also been reported from regrowth forest elsewhere. Riswan *et al.* (1987) found high numbers of these species (60% of all species) in 0.8 ha plot of 35 year-old tropical rain forest regenerating on an area used for some years- as a pepper plantation. This plot was close to an area of undisturbed primary forest.

Assuming a uniform rate of change, an estimate of how long it takes the number of primary species in this successional process to be established or reach an equilibrium can be made by calculating the rate of influx of these species (Riswan *et al.*, 1987). Since the number of primary species in the 20 and 50 year-old forests were 13 and 22 respectively, the rate of influx of these species over the 30 years would be nine (i.e., $22 - 13$) species. To achieved 47 species (as found in undisturbed forest), would require an additional 25 (i.e., $47 - 22$) species. Thus the period to reach 47 species would be $25 \times 30/9 + 50 = 133$ years.

Another way of estimating the time needed to reach maturity is to assess the rate of change in the proportion of primary species. The proportion of primary species in the 20, 50 year-old and undisturbed forests was 35, 38 and 71% respectively (Figure 2). Thus, the period to reach the 71% in the mature phase would be $(71-38) \times [(50-20)/(38-35)] + 50 = 380$ years."

These estimates are necessarily approximation. They make no allowance for the different histories and areas of each site. They also assumed that the rate at which primary species arrived and become established at a site remain constant over time. However they are of the same order as other estimates of the time required for recovery of primary forest. Thus Knight (1975) concluded that after 120 — 150 years, one of his sites in Barro Colorado Island was still not a climax. The similar estimation has also been noted by Riswan *et al.* (1987). They suggested that for successful reestablishment of a mixed dipterocarp forest be time required would be between 150 and 500 years.

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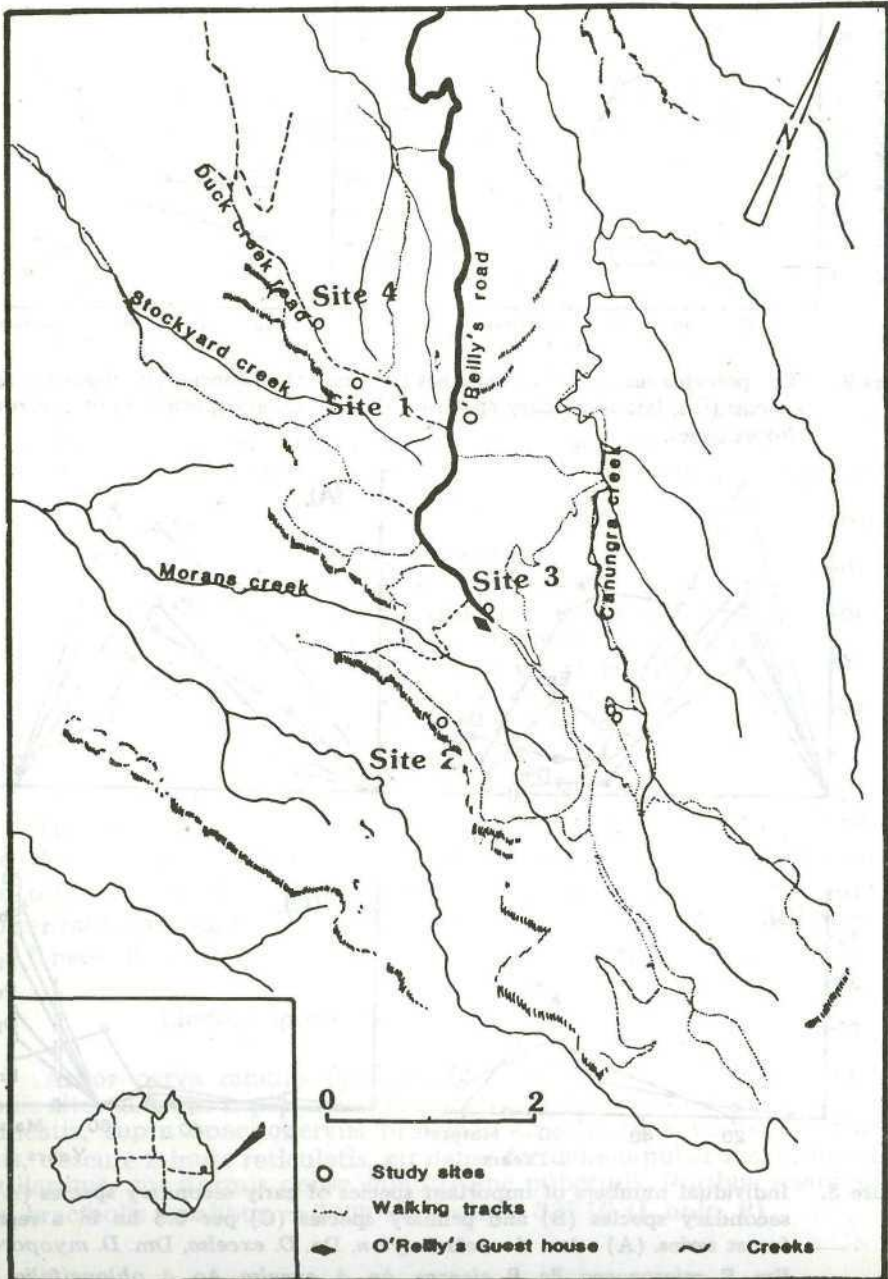


Figure 1. Map showing the situation of the study area and location of the study sites.

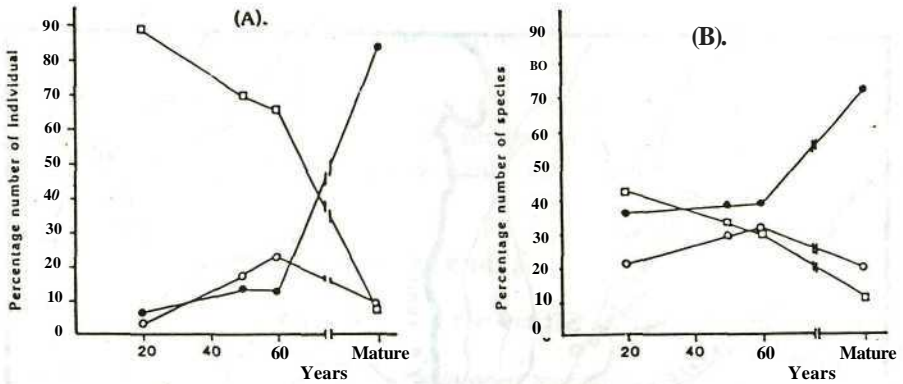


Figure 2. The percentages of individual trees (A) and actual species (B) classed as early species (•), late secondary species (O) and primary species (◻) in a regrowth forest series.

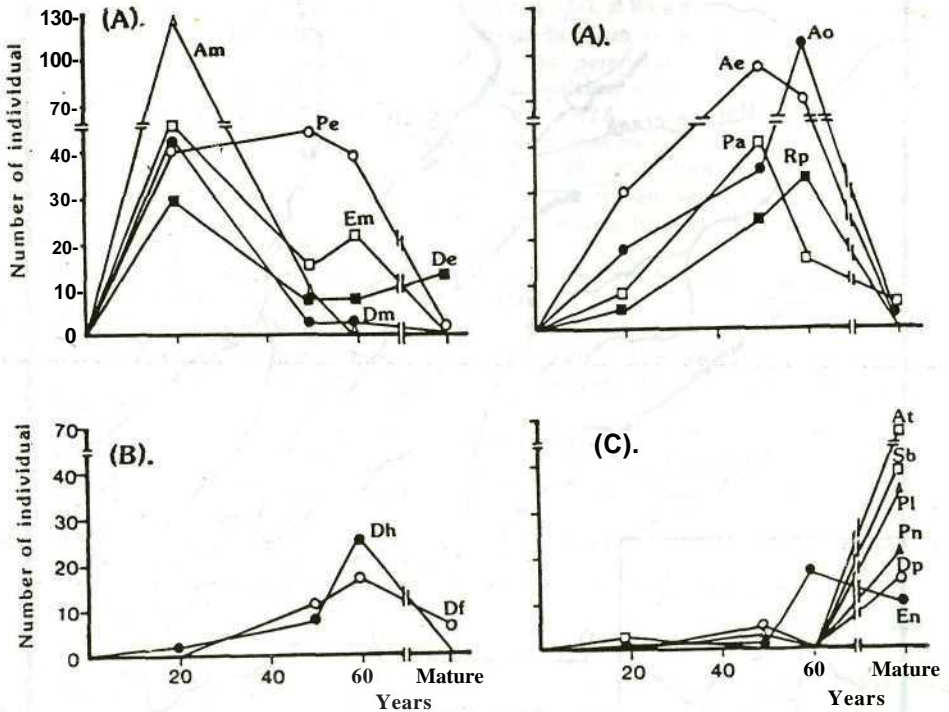


Figure 3. Individual numbers of important species of early secondary species (A), late secondary species (B) and primary species (C) per 0.5 ha in a regrowth forest series. (A) : Am. *A. melanoxylon*, De. *D. excelsa*, Dm. *D. myoporoides*, Em. *E. micrococca*, Pe. *P. elegans*, Ae. *A. excelsa*, Ao. *A. oblongifolia*, Pa. *P. australe.*, Rp. *R. psidioides*; (B) : Dh. *D. humile*, Df. *D. fraserianum*; (C) : At. *A. trifoliolatum*, Dp. *D. pentamera*, En. *E. nervosa*, PL. *P. lachnocarpa* and Sb. *S. pendulinus*.

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