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香港乡土树种幼苗在次生林下生长的研究

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摘要: 通过苗木移植试验，测定了21种香港乡土树种在次生林下的成活率及生长状况。结果表明，大多数种类的幼苗具有一定的耐荫性，可在林下生长；只有极少数种类表现出极耐荫或极不耐荫，导致林下先锋树种幼苗死亡率高的主要原因是荫蔽或因荫蔽而生长不良受病虫害致死。在香港次生林演替中占优势的种类通常具有生长快、稍耐荫，或生长稍慢但耐胁迫等特点。这是对香港退化土地长期适应的结果。鸟播植物在香港次生林中占有重要地位，建议加强鸟播树种生态学特性的研究及其在植树造林中应用。结合本实验结果，对一些现代植物群落演替假说进行了简要的讨论。

关键词: 香港；次生林；树苗成活率；生长；次生演替
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SURVIVAL AND GROWTH OF NATIVE TREE SEEDLINGS IN SECONDARY FOREST OF HONG KONG

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Abstract: The seedling survival and growth of 21 native tree species were studied by transplanting into two natural forest sites and an open site for approximately 22 months during June-August 1989 and April-October 1991. The results showed that the seedlings of most species had some tolerance to shading and could survive in forests. Only a few species showed extreme tolerance or intolerance to shade. The seedlings of most pioneer species died directly from shading or insect damage and pathogens in forests. The extremely shade-intolerant species in the study were *Pinus massoniana*, *Sapium discolor*, and *Trema tomentosa*. These species with a typical syndrome of pioneer characters do not play an important role in secondary succession in Hong Kong. The major components in current secondary forest, such as *Machilus chekiangensis* and *Gordonia axillaris*, have mixed and intermediate characters, which may be an adaptation to the soil degradation caused by centuries of fire and erosion. Bird-dispersed species play an important role in secondary forest of Hong Kong. Research and application of the bird-dispersed woody flora must be enhanced. Some hypotheses on the current floristic succession are briefly discussed.

Key words: Hong Kong; Secondary forest; Seedling survival; Growth; Secondary succession

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As a result of past human impacts, all the original forests of Hong Kong have been cleared and the flora and fauna are degraded. Secondary succession is a major process of forest restoration on degraded hillsides of Hong Kong. In the absence of any disturbance, most of the degraded grassland and shrubland can potentially recover to secondary forest with a good canopy within 30－40 years[1]. There have been several studies of forest succession in Hong Kong[2,3], but all of them were descriptive.

Recent hypotheses have suggested that the floristic dynamics of forest succession mainly result from differentiation of life histories of the plants[4－6]. The knowledge of ecophysiological characteristics of the plant seedlings in forest is necessary to understand the mechanisms of secondary succession[7－9]. However, the relevant information of most native trees is not available in Hong Kong and South China. As a part of the research on forest succession of Hong Kong, the major aim of this study is to investigate the seedling survival and growth of native tree species in secondary forests of Hong Kong, because the species at seedling stage are the most sensitive in the plant's life. The second aim is to verify some current hypotheses regarding forest succession and shade tolerance of the seedlings.

1 Materials and methods

1.1 Study sites

Hong Kong (22°N, 114°E) has a transitional subtropical to tropical monsoon climate with a long, hot and humid summer and a short, cool and dry winter. The mean annual temperature is 23 ℃ and mean annual rainfall is 2678.8 mm[10].

The study was conducted during June-August 1989 and April-October 1991 at two natural secondary forest sites (Shing Mun and Pokfulam) and a non-forest control site at the Kadoorie Agricultural Research Centre (KARC). The Shing Mun site is located on the northern side of Shing Mun Reservoir in the New Territories. It is a remnant of an old Feng shui wood, which is well protected for reasons connected with the Chinese system of geomancy ("Feng shui"). It has been estimated to be about 300 years old and is dominated by *Pygeum topengii*, *Endospermum chinense*, *Sarcosperma laurinum* and *Cryptocarya chinensis*. The Pokfulam forest site is located on the northern slope of Victoria Peak on Hong Kong Island. The forest has developed since 1945 and is currently dominated by *Machilus chekiangensis* and *M. breviflora*. The composition and structure of these forests are much simpler than those of Shing Mun Feng shui wood. The control site was set on a terrace (9 × 20 m^2) at KARC of the University of Hong Kong in the New Territories. A brief physical description of these sites is given in Table 1.

1.2 Species studied

A total of 21 native tree species, belonging to 11 families and 18 genera, from various

Table 1 Natural condition of the study sites

Site no.	Location	Habitat	PAR* (%)
1	Shing Mun Country Park	Feng shui wood	0.7
2	Pokfulam Country Park	Lowland secondary forest	2.0
3	KARC	Open site	100.0

* Photosynthetically active radiation

stages of secondary forest of Hong Kong were included in this study (Table 2). The seedlings were either grown from seeds in the greenhouse or bought from a local nursery (Table 2). The seedlings used varied from 6 to 25 months old, but the seedling sizes and ages were relatively uniform within the same species. Twenty seedlings of each species were planted in each site.

1.3 Transplanting of the seedlings

The seedlings for the experiment were transplanted into the three experimental sites between June and August 1989. All the seedlings were planted randomly at spacing of 1.5 m × 1.5 m. They were harvested between April and August 1991 except *Sterculia lanceolata,* whose seedlings were harvested in October 1991 because they shed their leaves in summer.

All the planted seedlings were fertilized with 0.2 g solid N-P-K (15-15-15) fertilizer one month after planting, since the seedlings in the open exhibited symptoms of nutrient deficiency at the control site. The seedlings at KARC were watered with sprinklers when the weather was dry. In order to decrease the influence of weeds on the growth of the experimental seedlings, weeds in the control site were eradicated before and after summer.

1.4 Data collection and analysis

The survival of the seedlings was surveyed monthly. The causes of death were recorded. At harvest, major stem height was measured. Dry weights of roots, stems and leaves of every tree were measured after drying at 105 ℃ for 48 hours. Tukey's studentized range test was used for pair-wise comparisons of significant differences between the seedling growth in different sites.

2 Results

2.1 Seedling survival in the three sites

Seedling survival rates at the end of the experiment varied significantly among species and sites (Table 2). Survival rates were generally higher in the control site than in the forest sites. The light-demanding species had much higher survival rates and growth rates in the open, but weak growth and high mortality in the forest. The most light-demanding species were

Table 2 Main causes of seedling death

Species	Site no.[1]	Total mortality (%)	Killed by insects (%)	Desiccation (%)	Others[2] (%)
Bischofia javanica	1	55	30	25	0
	2	17	7	10	0
	3	0	0	0	0
Castanopsis fissa	1	35	0	35	0
	2	40	0	40	0
	3	90	0	90	0
Celtis sinensis[3]	1	70	20	50	0
	2	95	30	65	0
	3	5	0	5	0
Cinnamomum camphora	1	95	0	95	0
	2	100	0	100	0
	3	0	0	0	0
Diospyros morrisiana	1	30	0	30	0
	2	70	0	70	0
	3	5	0	5	0
Gordonia axillaris	1	90	0	90	0
	2	90	5	85	0
	3	55	0	55	0
Liquidambar formosana[3]	1	95	20	75	0
	2	90	0	90	0
	3	5	0	5	0
Lithocarpus glaber	1	68	15	53	0
	2	65	30	30	5
	3	82	0	82	0
Machilus breviflora	1	47	0	47	0
	2	30	10	15	5
	3	15	0	15	0
Machilus chekiangensis	1	100	0	100	0
	2	100	0	100	0
	3	35	0	35	0
Machilus velutina	1	70	0	70	0
	2	80	0	80	0
	3	35	0	35	0
Mallotus paniculatus	1	80	5	75	0
	2	75	20	55	0
	3	0	0	0	0
Ormosia emarginata	1	50	0	50	0
	2	70	20	50	0
	3	72	0	72	0
Pinus massoniana[3]	1	100	0	100	0
	2	100	0	100	0
	3	42	0	42	0
Cyclobalanopsis neglecta	1	75	0	70	5
	2	35	0	35	0
	3	57	0	57	0
Cyclobalanopsis myrsinifolia	1	53	14	39	0
	2	66	0	66	0
	3	73	0	73	0
Reevesia thyrsoidea[3]	1	5	0	5	0
	2	5	5	0	0
	3	0	0	0	0

(Continued)

Species	Site no.[1]	Total mortality (%)	Killed by insects (%)	Desiccation (%)	Others[2] (%)
Sapium discolor	1	100	20	80	0
	2	100	15	85	0
	3	45	5	40	0
Schefflera octophylla	1	50	0	50	0
	2	10	0	10	0
	3	35	0	35	0
Sterculia lanceolata[3]	1	30	20	5	5
	2	10	0	10	0
	3	0	0	0	0
Trema tomentosa	1	100	30	70	0
	2	100	65	30	5
	3	0	0	0	0

[1]For site number see Table 1; [2]Death caused by trampling or landslides; [3]Seedlings were bought from the Tai Tong Nursery Station.

Trema tomentosa, *Pinus massoniana*, and *Sapium discolor*. All the seedlings of *Trema tomentosa* died within 6 months at the two forest sites, compared with 100% survival in the open. The seedlings of *Pinus massoniana*, *Sapium discolor*, and *Machilus chekiangensis* were all dead within 10, 16, and 21 months, respectively, compared with more than 50% survival in the open. *Celtis sinensis*, *Cinnamomum camphora*, *Gordonia axillaris*, *Liquidambar formosana*, and *Mallotus paniculatus* also had much lower survival rates in forests than in the open. In contrast, *Bischofia javanica*, *Cyclobalanopsis neglecta*, *C. myrsinifolia*, *Lithocarpus glaber*, *Reevesia thyrsoidea*, *Schefflera octophylla*, and *Sterculia lanceolata* were more shade-tolerant and had similar survival rates at all sites (Table 2).

The causes of seedling mortality in the three sites were different (Table 2). The seedlings in the open site died mainly from desiccation of the soil or failure of competition with fast-growing weeds. The mortality was usually higher in slow-growing species, such as *Machilus chekiangensis*, *M. velutina*, *Gordonia axillaris*, *Ormosia emarginata*, and the species of Fagaceae. These slow-growing species were inferior in the open. Mortality in the forest sites was more complicated. Most deaths in potentially fast-growing species were directly attributed to shading, which could be confirmed by the species having similar performance in the two forest sites. However, about 50% of seedlings of *Trema tomentosa* (30% in Pokfulam, 65% in Shing Mun) were killed by insects. Some seedlings of *Celtis sinensis* were also attacked by insects. The slow-growing species were generally susceptible to physical damage by litterfall, mammal trampling and landslides (Table 2). However, the seedlings of *Reevesia thyrsoidea* and *Sterculia lanceolata* were able to resprout and resume growth after being damaged by insects, trampling and treefalls.

2.2 Height growth and total biomass

The height growth and biomass accumulation of seedlings differed greatly from species to species and also from site to site (Table 3). Almost all of the tested species in the open site exhibited higher growth height and greater total biomass than in forest sites, althouth the difference was not significant for *Castanopsis fissa*, *Cyclobalanopsis neglecta*, *C. myrsinifolia*, *Lithocarpus glaber*, *Ormosia emarginata* and *Reevesia thyrsoidea* (Table 3). Differences in growth varied with species. For *Bischofia javanica*, *Machilus breviflora*, *M. velutina*, *Schefflera octophylla* and *Sterculia lanceolata*, the significant differences in biomass allocation resulted mainly from much differences in habitats between the forest and the open sites, while differences in biomass accumulation between the two forest sites were usually minor (Table 4). Seedlings of most species which showed major differences in survival between forest and open sites also showed significant differences in growth. However, some other species with little difference

Table 3 Height and total biomass of the seedlings at harvest

Species	Site no.[1]	Height (cm)	Total biomass (g)	Species	Site no.[1]	Height (cm)	Total biomass (g)
Bischofia javanica	1	38.2	9.2	*Mallotus paniculatus*	1	66.1	4.1
	2	40.5	9.5		2	72.3	5.1
	3	126.1	505.3		3	101.4	167.0
Castanopsis fissa	1	14.2	1.0	*Ormosia emarginata*	1	10.5	0.3
	2	22.6	1.0		2	15.1	1.5
	3	*	*		3	11.3	0.8
Celtis sinensis	1	33.8	0.1	*Pinus massoniana*	1	*	*
	2	34.5	*		2	*	*
	3	96.9	24.6		3	128.9	593.1
Cinnamomum camphora	1	*	*	*Cyclobalanopsis neglecta*	1	10.6	1.0
	2	*	*		2	11.3	0.8
	3	84.3	359.1		3	20.5	2.8
Diospyros morrisiana	1	17.4	1.9	*Cyclobalanopsis myrsinifolia*	1	16.2	1.4
	2	24.1	2.4		2	19.0	1.4
	3	81.9	48.2		3	33.4	9.2
Gordonia axillaris	1	*	*	*Reevesia thyrsoidea*	1	35.1	5.9
	2	*	*		2	43.8	9.3
	3	11.2	2.1		3	49.6	21.8
Liquidambar formosana	1	46.8	*	*Sapium discolor*	1	*	*
	2	36.0	*		2	*	*
	3	85.2	185.4		3	76.1	40.8
Lithocarpus glaber	1	10.5	0.4	*Schefflera octophylla*	1	12.5	3.4
	2	17.9	1.4		2	20.0	6.4
	3	17.9	3.8		3	51.4	184.2
Machilus breviflora	1	11.9	0.7	*Sterculia lanceolata*	1	42.4	7.5
	2	16.0	1.4		2	71.6	21.6
	3	46.1	24.7		3	86.1	128.6
Machilus chekiangensis	1	*	*	*Trema tomentosa*	1	*	*
	2	*	*		2	*	*
	3	23.1	5.5		3	146.0	1147.6
Machilus velutina	1	9.8	0.5				
	2	12.5	1.1				
	3	17.6	4.6				

[1]For site number see Table 1; *Seedlings were less than 2 survived individuals.

Table 4　Tukey's test for significant difference in stem weight (S), root weight (R), leaf weight (L) and total biomass (TB) of the survived seedlings between the sites

Species	Site no.[1]	S (g)		R (g)		L (g)		TB (g)	
		2	3	2	3	2	3	2	3
Bischofia javanica	1	228.1*	227.8*	134.3*	135.3*	133.4*	133.3*	495.7*	496.2*
	2	–	0.33	–	0.97	–	0.16	–	0.48
Lithocarpus glaber	1	0.25	0.47	1.83	2.23	0.33	0.70	2.40	3.39
	2	–	0.22	–	0.40	–	0.37	–	0.99
Machilus breviflora	1	6.90*	7.04*	9.69*	10.14*	7.20*	7.33*	23.28*	23.99*
	2	–	0.14	–	0.45	–	0.13	–	0.71
Machilus velutina	1	15.62*	15.48*	20.06*	19.45*	9.22*	10.79*	46.29*	45.73*
	2	–	0.14	–	0.56	–	1.57	–	0.57
Mallotus paniculatus	1	89.36	88.85	37.41	37.27	35.98	35.73	162.9	162.0
	2	–	0.52	–	0.19	–	0.24	–	0.95
Ormosia emarginata	1	0.13	0.22	0.36	0.18	0.05	0.34	0.08	0.56
	2	–	0.35*	–	0.53*	–	0.29	–	0.64
Cyclobalanopsis neglecta	1	0.55*	0.53*	0.97*	0.91*	0.50	0.42	2.02*	1.85*
	2	–	0.03	–	0.06	–	0.50	–	0.17
C. myrsinifolia	1	1.82*	1.90*	4.97*	1.88*	0.98	0.82	7.76*	7.77*
	2	–	0.08	–	0.09	–	0.16	–	0.01
Reevesia thyrsoidea	1	2.69*	3.71*	3.75*	6.16*	1.44	1.65*	7.97*	11.18*
	2	–	1.02	–	2.42	–	0.20	–	3.12
Schefflera octophylla	1	63.58*	64.97*	59.12*	60.47*	54.88	55.16*	177.6*	180.6*
	2	–	1.39	–	1.36	–	0.28	–	3.01
Sterculia lanceolata	1	33.42*	36.75*	49.37*	55.22*	12.29*	14.04*	106.4*	117.2*
	2	–	3.33	–	5.85	–	1.75	–	10.79

[1] For site number see Table 1;　* Significant differences at $p<0.05$.

in survival between the two sites had less differences in growth, such as *Reevesia thyrsoidea*. Such species could survive in shade but barely grow or grow almost equally well under sun and shade. Finally, *Lithocarpus glaber, Ormosia emarginata, Machilus breviflora, M. velutina, Cyclobalanopsis neglecta,* and *C. myrsinifolia* grew slowly at all sites. The decrease in height and biomass accumulation in some species was caused by physical damage. Only *Ormosia emarginata* showed significant differences in growth between the two forest sites.

By the end of the experiment, three species, *Mallotus paniculatus, Pinus massoniana* and *Trema tomentosa*, had started to flower and fruit in the open site.

3 Discussion

3.1 Major limitation for tree seedling survival and growth in forest

Seeds which are dispersed into the forest and germinate there are faced with many problems, including low photosynthetically active radiation (PAR), seedling predators, pathogens, and physical damage. The present study confirms that light is the major limiting factor for the survival and growth of the seedlings in forest. Mean PAR in the two forest sites was only 0.7% − 2.0% of full light. Under such light intensities, many pioneer species failed to survive or grew poorly. On the other hand, physical damage caused by litterfall, mammal trampling or landslides also inhibited the establishment of the seedlings in forest. The impact of physical damage varied with habitats and ages of the seedlings. The mortality caused by physical damage was higher in Shing Mun forest than in the Pokfulam forest. The seedlings of slow-growing species were more likely to suffer physical damage than those of fast-growing ones. In addition, there was evidence for an impact of insect damage, but it seemed species specific. The extreme case was *Trema tomentosa*, where about half of the seedlings were killed by insects in the forest. In comparison with the seedling mortality in forest sites, the causes of seedling mortality in the open (at the control site) were simpler, most seedlings failed to compete for light and water. The fast-growing species were usually superior in the open, while the slow-growing species often died from desiccation of the soil and shading by weeds or other fast-growing species.

3.2 Successional status and seedling establishment

One of the oldest and most widely accepted generalizations in plant ecology is the set of characteristics used to distinguish ealy- from late-successional species[11]. Several species included in this study, such as *Pinus massoniana*, *Sapium discolor* and *Trema tomentosa*, exhibited a distinct pioneer syndrome. They posses small seeds with dormancy, which are copiously produced from early in life and well dispersed, have rapid height growth and a short life span[12]. In conflict with the hypothesis of Swaine and Whitmore[11], however, none of these species play a major role in the current forest succession at most sites in Hong Kong. They mainly grow on the forest edge and in disturbed places and seldom exist in the old forest. One of the major reasons for their rarity in secondary forest with a closed canopy is because their seedlings are extremely shade-intolerant. The main canopy in young secondary forest in Hong Kong is formed by the species with intermediate or mixed characters. Two of the major forest canopy species in this study, *Machilus chekiangensis* and *Gordonia axillaris*, grow slowly even in light. Our field observations also showed that the seeds of these species could easily germinate and the seedlings could survive in forest for some time. However, most of the seedlings would die within one year after emergence. This behaviour is typical of gap-dependent species. The seedlings of these species require canopy gaps for growth. *Gordonia axillaris*, a common pioneer species with wind-dispersed seeds, is often dominant in shrubland and at some early stages of secondary forest. Although this species had very slow growth in all experimental sites, its wide distributions on degraded hillsides in Hong Kong shows that it can tolerate degradation of the soil. *Schefflera octophylla*, another common species in secondary forest, can germinate in forest shade and its seedlings show moderate growth and are relatively shade tolerant. This dominance of species with mixed and intermediate characteristics in early succession reflects the predominant environmental conditions in the region. The poor soil resulting from centuries of fire and erosion makes fast growth impossible and favors stress tolerance.

This study suggests that the inhibition and tolerance models of Connell and Slatyer[5] are the major mechanisms determining the floristic composition of the forest. Both direct and indirect effects of inhibition were shown in the study. The seedling growth and biomass accumulation of all the tested species were directly inhibited in the forest and the most shade intolerant species died. The activities of some animals and microbes were found to be a very important limiting factor for the colonization of some pioneer species elsewhere[8], but did not affect all species in this study.

3.3 Implication of this study

Although forest rehabilitation in Hong Kong commenced as early as the 1880s, most of the plantations depended on a few exotic, fast growing species. Only a few native species are currently planted in plantations, such as *Castanopsis fissa* and *Schima superba*. Neither exotic species nor native species grown in current plantations could produce fruits for wildlife. This study revealed that several native pioneer species, such as *Diospyros morrisiana, Liquidambar formosana*, *Mallotus paniculatus*, *Sapium discolor*, and *Trema tomentosa*, could be potentially used in afforestation in Hong Kong and South China. These species not only have potentially high growth and produce a forest canopy in the open but also mature early in the life and produce fruits favored by the local avifauna[13]. Plantation with these species can accelerate native forest regeneration on degraded areas in this region and also favor the wildlife conservation. *Pinus massoniana* is suitable for planting in HK and South China, but the pinewood nematode and pine-needle scale make this impossible in HK and adjacent parts of Guangdong.

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