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Soil Seedbank in a Dipterocarp Rain Forest in Xishuangbanna, Southwest China[1]

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ABSTRACT

Dipterocarp rain forest reaches its northern latitudinal limit in Xishuangbanna, Southwest China. We studied the soil seedbank of dipterocarp rain forest in Xishuangbanna during the dry and wet seasons. Results showed that there were large seed accumulations in both the dry (mean ± SD; 3925 ± 2533 seeds/m^2) and wet seasons (5415 ± 3232 seeds/m^2). One hundred and sixteen species of seed plants were identified from germination, 66 percent of which were woody species. Weed or pioneer species dominated the seedbank. The soil seedbank in Xishuangbanna had similar species composition as compared to those in tropical Asia, but higher seed storage reflects the intense disturbance and forest fragmentation in this area.

Key words: forest regeneration; soil seed germination; tropical rain forest; Xishuangbanna.

TROPICAL SOIL SEEDBANKS are considered important regeneration resources during secondary succession or gap dynamics within rain forests (Hopkins & Graham 1984, Young *et al.* 1987, Garwood 1989, Thompson 1992, Dupuy & Chazdon 1998). Many soil seedbanks consist primarily of pioneer species or weed species from adjacent disturbed areas (Whitmore 1983, Putz & Appanah 1987, Young *et al.* 1987, Thompson 1992, Dalling & Denslow 1998, Metcalfe & Turner 1998, Saulei & Swaine 1998). The persistence and distribution of seeds in the soil are known to be largely determined by seed size and shape (Thompson 1992, Bekker *et al.* 1998, Guo *et al.* 2000). The size and species composition of the soil seedbank vary seasonally as changes in transient and seasonal-transient seedbanks (Garwood 1989), and this change largely coincides with the fruiting phenology of forests (Grombone-Guaratini & Rodrigues 2002). Seeds of primary species rarely occur in the soil seedbank of tropical rain forests due to large seed size, high water content, and rapid germination strategies (Vazquez-Yanes & Orozco-Segovia 1993). As a result, the species composition of soil seedbanks differs considerably from the species composition of the forest canopy (Garwood 1989). The species composition, density, and distribution of soil seedbanks have been the subject of investigations that also consider forest fragmentation and regional disturbance (Hopkins & Graham 1984, Quintana-Ascencio *et al.* 1996, Cao *et al.* 2000).

Previous work in the dipterocarp rain forest at Mengla Nature Reserve in Southwest China has documented floristic composition and structure. The ecological and floristic characteristics of this dipterocarp rain forest are similar to other tropical rain forests of Southeast Asia. It is considered as a type of tropical seasonal rain forest on the northern margin of tropical Asia (Zhu 2000, Zhu *et al.* 2006). *Shorea wantianshuea* and *Vatica guanxiensis* (Dipterocarpaceae) dominate the forest. Compared to other rain forest types in the area, the dipterocarp forest contains more species, resulting in higher tree species diversity (Cao & Zhang 1997). Soil seedbank studies in other forest types have shown high seed accumulation in this area, ranging from 4585 seeds/m^2 in a mixed seasonal rain forest to 65,665 seeds/m^2 in young slash-and-burn fallow, reflecting forest fragmentation and high disturbance regimes (Cao *et al.* 2000). Although this dipterocarp rain forest is protected, it is still subject to disturbance from intensive slash-and-burn agriculture in the areas surrounding the nature reserve. In this study, we used a germination experiment to explore soil seedbank composition and its seasonal changes in the dipterocarp rain forest of Xishuangbanna, China. We also compared the soil seedbank with other studies from tropical Asia.

METHODS

STUDY AREA AND SAMPLING METHOD.—The study was carried out in a tropical dipterocarp rain forest in the Mengla Nature Reserve (21°42′N, 101°35′E; 850 m elev.), Xishuangbanna, Yunnan Province, Southwest China. The dipterocarp rain forest of the nature reserve occupies a total area of about 800 ha and is separated into 16 patches. Our study was conducted in one of the patches known as Bubeng, located 16 km from the city of Mengla. Xishuangbanna has a typical monsoon climate with pronounced drying–wetting cycles (Cao *et al.* this issue).

One 200-m transect was established in the core area of the forest. Along the transect, 20 soil cores (10 × 10 × 10 cm) were collected at 10 m intervals in both the rainy (6 November 2000) and dry (10 April 2000) seasons using two small shovels. Each soil core was then divided into upper (0–2 cm), middle (2–5 cm), and lower (5–10 cm) layers and immediately transported to a germination house. A total of 60 soil samples were collected in each of the two seasons.

GERMINATION.—Soil samples were spread over sterilized sand in germination trays to form a 2-cm-thick soil layer. Trays were located in a glasshouse receiving 70 percent sunlight at the Xishuangbanna Tropical Botanical Garden. The samples were watered daily. Observations of germination were made every 2 d during the first 2 mo.

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TABLE 1. *Number of seeds germinated from 20 (10 × 10 × 10 cm) soil samples taken from* Shorea wangtianshuea *forest, Southwest China.*

Sample season	Seed germinated 0–2 cm	2–5 cm	5–10 cm	Total	Average seed germinated/tray[a]	Seed storage (seeds/m^2)[a]
Rainy (October)	333	449	301	1083	18.6 ± 13.3	5415 ± 3232
Dry (April)	279	286	220	785	13.1 ± 11.0	3925 ± 2533

[a]Mean ± standard error, $N = 20$.

Seedlings were removed for identification. Those that could not be identified were transplanted to individual pots for further identification. The experiment ran for approximately 5 mo until no further germination occurred. Plant nomination followed the list of plants in Xishuangbanna (Li *et al.* 1996). Analyses were carried out on the $\log(n + 1)$ transformed germinants from each soil sample, where n is the number of seedlings for each species. Repeated measures ANOVA was used to examine the seasonal change in seed density in the three soil layers. The seed density distribution within soil layers was compared using a paired t-test. To test the distribution of seeds in soil, relative frequency (F) for each species present in the soil samples was calculated ($F =$ number of soil samples in which a species was present/total number of soil samples).

RESULTS

A total of 1868 individuals representing 116 species and 39 families germinated over the course of the study, among which 113 species were identified to species level and 3 to genus only. Woody species dominated the soil seedbanks with 52 species from 24 families, making up nearly 63 percent of total individuals. Herb species included 49 species from 20 families, accounting for 33 percent of total seedlings germinated. Only three lianas species were recorded during the study.

Moraceae and Asteraceae were the most dominant families with 17 species recorded in each, followed by Rubiaceae with 12 species and Urticaceae with 9 species. These four families accounted for 55 percent of the total germinated seedlings. Seedlings from Moraceae accounted for 34 percent of total tree seedlings recorded.

SEED STORAGE.—Large numbers of seeds accumulated in the soil in both the dry and rainy seasons (Table 1). More seedlings germinated from soil samples taken in the rainy season than from the dry season ($F = 4.726$, $P < 0.05$), but seasonal differences were insignificant for individual soil layers ($F = 1.362$, $P = 0.259$). The high standard errors for both seed density and number of seedlings germinated per tray reflect an uneven distribution of seeds in the soil seedbank.

VERTICAL DISTRIBUTION.—We observed significant differences in the distribution of seeds among soil layers (Fig. 1). Seed density decreased drastically from the upper to lower soil depths in the dry season (Paired t-test, $P < 0.01$). Although there was a slight decrease in seed density from the upper to middle depth in the rainy season, differences between the two layers were not significant (Paired t-test, $P = 0.28$). However, seed density in the lower soil depth was significantly different from that in the upper and middle depths (Paired t-test, $P < 0.01$) for both rainy and dry seasons.

LIFE-FORM COMPOSITION.—Seeds of tree and shrub species dominated the life-form spectrum in soil seedbanks of both seasons, contributing 57 percent of the total seedlings germinated from the dry season, and 65 percent from the rainy season (Fig. 2). Shrub seeds were the most abundant group, comprising 38 percent of the total seedlings germinated from soils collected during the rainy season, whereas herb seeds were more dominant in the dry season, and the proportion of shrub seeds dropped to 22 percent. Liana seeds accounted for only 1 percent of the total seeds germinated in both seasons. A greater number of species germinated from samples taken during the rainy season than in the dry season (Table 2). The largest seasonal change was found in herb species, with ten more species

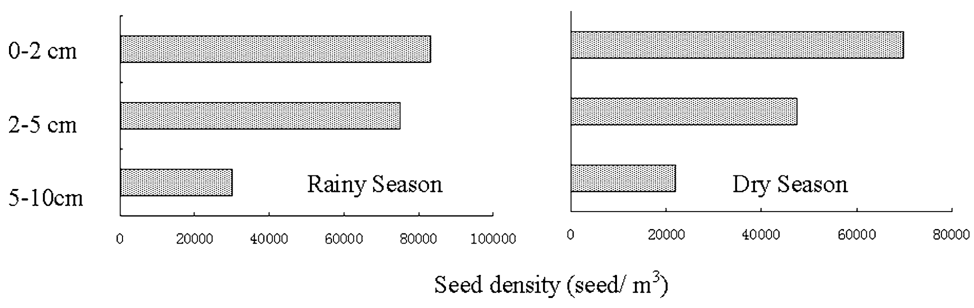

FIGURE 1. Vertical distribution of seeds in the soil seedbank of *Shorea wangtianshuea* forest in Mengla, Southwest China.

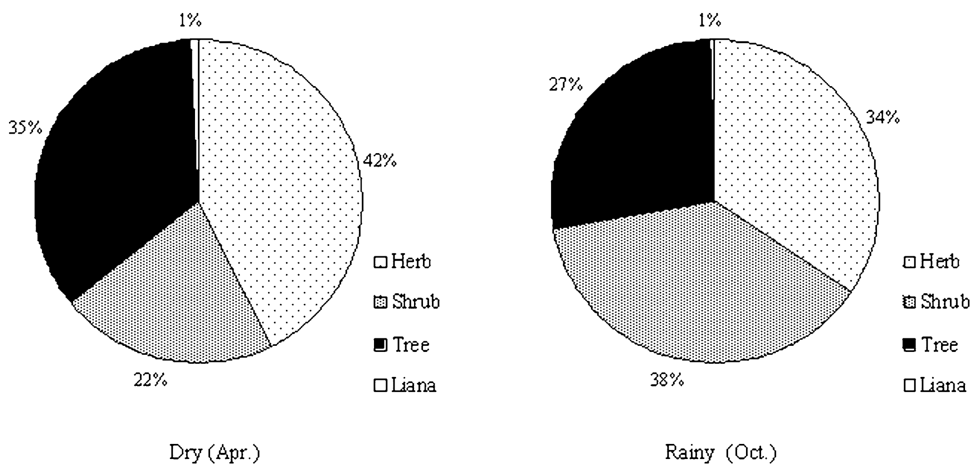

FIGURE 2. Proportion of seeds germinated from 20 soil samples according to life-form composition from *Shorea wangtianshuea* forest in Mengla, Southwest China.

in the soil seedbank of the rainy season than that of the dry season. Twenty-six tree species occurred in soil samples from both the rainy and dry seasons, and the same species dominated both seasons. Few species occurred only in the rainy or dry season. Three liana species were recorded in soil from the dry season, and only two species were present in samples from the rainy season.

DOMINANTS AND THEIR SEASONAL DISTRIBUTION.—*Anthocephalus chinensis* was the most dominant tree species in the seedbank, followed by *Ficus langkokensis* (Table 3). Some widely distributed tropical pioneer tree species, such as *Trema orientalis*, *Macaranga* spp., and *Mallotus* spp., were also recorded in our study. The dominant shrub was *Pouzolzia elegans*, a typical bird dispersed species with abundant mature individuals, distributed along the stream in the center of the study area. In a previous study, seeds of *Mussaenda elongata*, had the highest abundance in the soil seedbank of a mixed seasonal rain forest (Cao *et al.* 2000), and this species also had a high seed accumulation in our study. The most dominant herb species was *Thysanolaena maxima*, a common weed species in the Asia-Pacific region, which occurs in recently disturbed and abandoned slash-and-burn areas. *T. maxima* seeds accounted for 54.6 percent of the total herb seeds in soil samples taken during the dry season and 42.5 percent taken in the rainy season. It was also the dominant species in the mixed seasonal rain forest and secondary forests following slash-and-burn in this area (Cao *et al.* 2000). No mature individuals of *T. maxima* were found in the dipterocarp rain forest during the study. The seeds may have come from adjacent secondary forests or roadside vegetation.

Most of the species with high seed storage, such as *T. maxima, P. elegans*, *A. chinensis*, and *M. elongata*, scored a high frequency in both the dry and rainy seasons (Table 3), indicating a stable seed input and even distribution. Some wind dispersed seeds such as *Blumea balsamifera*, *Eupatorium odoratum, Crassocephalum crepidioides,* and *Conyza canadensis* also had a high frequency value ($F > 0.5$), although their seed storage was relatively low. In contrast, some species such as *Saurauia macrotricha* had a lower frequency, despite considerably high seed storage, indicating a patchy distribution.

TABLE 2. *Life-form composition of soil seedbank in* Shorea wangtianshuea *forest, Southwest China.*

Sample season		Herb	Shrub	Tree	Liana	Total
Rainy (October)	Species (#)	38	21	26	2	87
	Percentage of total species	44	24	30	2	100
Dry (April)	Species (#)	28	16	26	3	73
	Percentage of total species	38	22	36	4	100

DISCUSSION

In contrast to other studies of dipterocarp rain forests, this study recorded extremely high seed storage values in both the dry and rainy seasons (Table 4). High seed storage might reflect the intensive disturbance from slash-and-burn agriculture in this area. Disturbance promotes agricultural weed species and creates large areas of secondary forest, which could act as sources for the soil seedbank (Quintana-Ascencio *et al.* 1996). The mountainous topography and fragmented distribution of local vegetation were also cited as the reasons for high seed storage in soil seedbanks of seasonal rain forest in this area (Cao *et al.* 2000).

The dipterocarp forest in Mengla has the same family composition and almost the same generic composition as typical rain forests in tropical Asia (Zhu 2000). Evidence from our study also demonstrates this similarity. Some typical pioneer tree species (*e.g.*, *T. orientalis*, *Macaranga denticulata*, *Mallotus paniculatus*, and *Aralia armata*), have been reported to be dominant in soil seedbanks in Thailand (Cheke *et al.* 1979), and were also present in our study.

TABLE 3. *Dominant species (> 10 seedlings germinated) and their seasonal distribution in the soil seedbank of* Shorea wangtianshuea *forest, Southwest China.*

	Dry season					Rainy season				
Species	Upper	Middle	Bottom	Total	Frequency	Upper	Middle	Bottom	Total	Frequency
Asteraceae										
Blumea balsamifera	6	6	5	17	0.7	15	10	10	35	0.75
Conyza canadensis	15	6	2	23	0.65	1	3	–	4	0.2
Crassocephalum crepidioides	11	6	–	17	0.6	11	4	–	15	0.5
Eupatorium odoratum	2	1	1	4	0.15	12	3	–	15	0.45
Begoniaceae										
Begonia angustinei	8	6	9	23	0.5	3	1	4	8	0.3
Campanulaceae										
Campanula mekongensis	7	8	3	18	0.4	1	3	3	7	0.2
Loganiaceae										
Buddleia sp.	7	8	7	22	0.6	4	7	2	13	0.45
Moraceae										
Ficus auriculata	3	2	4	9	0.45	4	4	5	13	0.45
Ficus chrysocarpa	2	2	–	4	0.15	5	–	5	10	0.25
Ficus hispida	7	4	1	12	0.5	1	1	–	2	0.1
Ficus langkokensis	17	20	5	42	0.5	18	20	–	38	0.45
Myrsinaceae										
Measa indica	10	23	11	44	0.65	6	4	9	19	0.3
Oxalidaceae										
Oxalis corniculata	5	7	6	18	0.4		–	1	1	0.01
Poaceae										
Thysanolaena maxima	36	62	60	158	1	42	58	59	159	0.95
Rubiaceae										
Anthocephalus chinensis	10	25	14	49	0.75	34	23	24	81	0.8
Mussaenda elongata	18	11	8	37	0.8	24	25	11	60	0.75
Mycetia bracteata	13	15	8	36	0.6	18	11	8	37	0.6
Randia yunnanensis	3	6	6	15	0.25	10	6	4	20	0.4
Saurauiaceae										
Saurauia macrotricha	2	49	4	55	0.45	2	20	12	34	0.2
Saurauia tristyla	5	8	14	27	0.6	4	5	1	10	0.3
Sonneratiaceae										
Duabanga grandiflora	8	3	1	12	0.35		2	–	2	0.15
Theaceae										
Eurya austro-yunnanensis	13	14	13	40	0.55	–	5	3	8	0.3
Ulmaceae										
Trema orientalis	–	1	4	5	0.3	2	7	6	15	0.55
Urticaceae										
Pouzolzia elegans	36	71	49	156	0.8	15	26	16	57	0.85

These species also dominated soil seedbanks of mixed seasonal rain forest, and secondary forests fallowed after slash-and-burn agriculture in Xishuangbanna (Cao *et al.* 2000). *Ficus* was reported to be the most abundant genus in the soil seedbanks in tropical Asia (Whittaker 1995, Metcalfe & Turner 1998). Twelve species from the genus *Ficus* were recorded in our study, reflecting the wide distribution of this small-seeded, bird dispersed tree. Aboriginal people also propagate fig trees for religious purposes, which might also contribute to their wide distribution.

The fate of seeds in the soil seedbank largely depends on the particular conditions under which they are buried (Garwood 1989, Dalling & Hubbell 2002). The distribution of seeds therefore

TABLE 4. *Soil seedbank studies in dipterocarp rain forests in tropical Asia.*

Study area	Forest type	Soil depth (cm)	Seed density (seeds/m^2)	Reference
Xishuangbanna, China	Dipterocarp rain forest	10	3925–5415	Present study
Chiang Mai, Thailand	Dry dipterocarp forest	5	137	Cheke *et al.* (1979)
Bukit Timah, Malaysia	Lowland dipterocarp forest	5	1000	Metcalfe & Turner (1998)
Pasoh, Malaysia	Lowland dipterocarp forest	10	131	Putz & Appanah (1987)
Sabah, Malaysia	Lowland dipterocarp forest	15	60	Liew (1973)
Sri Lanka	Mixed dipterocarp forest	5	2273	Singhakumara *et al.* (2000)

interacts with variations in microenvironmental conditions encountered in the rain forest to determine the success of seedling germination and growth. For example, widely distributed species might have a higher proportion of seeds dispersed into microsites that meet germination requirements than narrowly distributed species. In this study, most wind and bird dispersed seeds showed a wide distribution in the soil seedbank. However, some species, such as *S. macrotricha*, had a narrow distribution despite relatively high seed storage. This pattern could be due to poor dispersal ability or to lack of an effective dispersal agent.

Soil seedbanks of primary tropical forest are often composed of seeds from species absent or rare in the forest canopy (Saulei & Swaine 1988). In this study, few canopy species were present in the soil seedbank, except *Gironniera subaequalis* (one seedling from the dry season and two seedlings from the rainy season), and *Acrocarpus fraxinifolius* (one seedling in the rainy season only). No seeds of *S. wantianshuea* were recorded in this study, as this typical viviparous seed usually germinates within 4 d after it matures. Some seeds of this species even germinate before dropping from the mother tree (Li 2002).

In conclusion, the dipterocarp rain forest in Xishuangbanna was found to have a considerably large number of seeds in the soil seedbank, and indicated seasonal fluctuation. Most germinated seeds were from woody species. The large seed storage and floristic composition of this soil seedbank reflect the regional disturbance regimes and forest fragmentation patterns. The dominant species in the soil seedbank of this rain forest in Xishuangbanna have also been found in other studies around tropical Asia. The majority of species present in the soil seedbank can be found in secondary forests or roadside vegetation nearby.

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