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Viable seeds buried in the tropical forest soils of Xishuangbanna, SW China

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Abstract

This paper examines the composition and density of soil seed banks under a mature seasonal rain forest (>150 years old), three secondary forests (4 yr *Trema orientalis* forest, 9 yr *Macaranga denticulata* forest and 25 yr *Mallotus paniculatus* forest) and in a slash-and-burn field of Xishuangbanna, southwest China. Seeds in the secondary forests germinated most rapidly in the first week, while the seeds of the seasonal rain forest and the slash-and-burn field soils germinated slowly over the first 6 weeks and peaked in the seventh and eighth weeks. Seed densities were 4585–65,665 seeds m^{-2} for forest sites and 1130 seeds m^{-2} for the slash-and-burn field in the top 10 cm of the soils. The seed density decreased with soil depth in the forest sites and tended to decline during succession. Herbs accounted for the largest proportion of seeds at all five sites. The importance of woody species, however, increased as forests became older. Slash and burn eliminated a large number of seeds in the upper soil and, consequently, reversed the vertical distribution of seeds in the soil and had a negative impact on family, genus and species richness of the soil seed bank as well.

Keywords: forest regeneration, life form, secondary succession, slash-and-burn agriculture, soil seed bank, tropical forest

Introduction

Viable seeds in soil play an important part in vegetation dynamics (Harper, 1977; Roberts, 1981; Parker *et al*., 1989; Young *et al*., 1989; Skoglund, 1992; Thompson, 1992). In forests they germinate when environmental heterogeneity is created under the canopy by man's activities or natural disturbance. This drives regeneration processes. In tropical forests different disturbance regimes (e.g. tree senescence, earthquake, landslide, cyclone, storm, drought and fire) usually result in the occurrence of canopy gaps (Whitmore, 1975; Brokaw, 1985; Whitmore, 1989a, b, c). Micro-environmental changes following gap creation allow seed germination, seedling establishment and sapling recruitment. This, offers new opportunities for forest trees to compete for environmental resources. Thus, the species composition, abundance and germination performance of viable seeds in the soil seed bank under the forest canopy, along with the advance regeneration and seed rain, lay a foundation for the next forest growth cycle and even control the nature of the regrowth community in some extreme cases.

Many contributions to the ecology of tropical soil seed banks have been made since the Symington (1933) study of the Malayan rain forest soil, where seeds of pioneer tree species existed even under the mature forest canopy. A number of review articles have summarized these efforts (Whitmore, 1983; Vazquez-Yanes and Segovia, 1984; Garwood, 1989; Thompson, 1992; Baskin and Baskin, 1998). It is generally accepted that the seeds of pioneer species are commonly present in tropical forest soils, particularly in secondary forests. In England, Thompson and Grime (1979) defined four types of soil seed banks for herbaceous species, which fell into transient and persistent categories. However, tropical soil seed banks show even more diversified strategies. Garwood (1989) described five soil seed bank strategies from the tropics: transient seed banks, persistent seed banks, pseudo-persistent seed banks, seasonal transient seed banks and delayed-transient seed banks. These arise from the more complex reproductive phenology of tropical plants and germination patterns of tropical seeds. Additional work is still needed to understand the roles of the soil seed bank in regeneration of different forest types.

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Xishuangbanna (21°09′–22°33′ N, 99°58′–101°50′ E) is located in south-western Yunnan, on the borders between China, Laos and Myanmar. This area serves as an ecotone between the Asian tropics and subtropics. Tropical monsoons dominate the local climate. The annual mean air temperature is 21.7°C. The annual rainfall is approximately 1500 mm, more than 80% of which occurs in the rainy season (from May through to October), followed by a distinct dry season (from November through April). Consequently, the rain forest in this area, which maintains some deciduous affinities in species composition and displays seasonality to some extent in forest aspects, is described as a seasonal rain forest (Zhang and Cao, 1995; Cao *et al*., 1996; Zhu, 1997). On the other hand, subtropical forest vegetation, i.e. evergreen broad-leaved forests extending from the central Yunnan, mingles with seasonal rain forests and monsoon forests of Southeast Asia in this region (Zhang and Cao, 1995). Forest fragmentation, however, is becoming increasingly serious owing to the conversion of natural forest in lowlands and on riverbanks into farmland, plantations or fallow fields of slash-and-burn agriculture (Zhang and Cao, 1995; Cao and Zhang, 1996).

The floristic and vegetational mixtures, which resulted from the transitional location in physical geography of Xishuangbanna, have a pronounced impact not only on the structure but also on the function of local forest ecosystems. This, in turn, inevitably gives the local soil seed bank unique regional features as well. In this study we test three a priori hypotheses: (a) that local soil seed banks contain some dominant species of the regional flora; (b) that seed density in soil decreases through the successional stages; (c) that slash and burn decreases seed density. The present paper describes the density, vertical distribution, life forms and dominants of the viable seeds buried in local soils under a seasonal rain forest, secondary forest at different successional stages and in a slash-and-burn field. Finally, we discuss the effect of slash and burn on the seed distribution in the soils.

Materials and methods

Study sites

Four forest types and one slash-and-burn field were chosen as study sites (Table 1). Their soils are ferralsols according to the world soil classification (FAO-UNESCO, 1990). The forest sites included one seasonal rain forest (Srf) and three secondary forests. *Mallotus paniculatus* forest (*Mp*f), *Macaranga denticulata* forest (*Md*f) and *Trema orientalis* forest (*To*f) are secondary forests of different successional ages. *Mp*f is derived from slashing and burning a seasonal rain forest that has been maintained uncultivated for monitoring forest succession. *Md*f and *To*f have developed following disturbance of seasonal rain forests and had been previously cropped with maize and upland rice before they were fallow.

Seasonal rain forest is the climatic climax of this area (Wu *et al*., 1987) and maintains the highest tree species diversity in Xishuangbanna (Cao and Zhang, 1997; Cao *et al*., 1998). The forest patch in which the sample plot was located covers approx. 10 ha in a narrow valley and is surrounded by a 30-yr-old regrowth of evergreen broad-leaved forest – a type of montane forest dominated by tree species of Fagaceae and Lauraceae. The plot is about 200 m from the nearest forest edge. *Pometia tomentosa* (Bl.) Teysm. et Binn., *Terminalia myriocarpa* Heurck et Muell.-Arg., *Barringtonia macrostachya* (Jack) Kurz, *Gironniera subaequalis* Planch. and *Chisocheton siamensis* Craib dominate this forest. Cao *et al*. (1996) described the tree floristic composition and the community structure of this site.

The *Mp*f site is about 4 ha in area. *Mallotus paniculatus* (Lam.) Muell.-Arg. together with *Millettia leptobotrya* Dunn, *Melia toosendan* Sieb. et Zucc. and *Phoebe lanceolata* (Wall. ex Nees) Nees dominate the forest canopy, covering about 90% in the rainy season. The *Md*f site covers about 12 ha. More than four-fifths of the canopy trees are *Macaranga denticulata* (Bl.) Muell.-Arg. which is accompanied by *Aporusa yunnanensis* (Pax et Hoffm.) Metc., *Ficus semicordata* Buck.-Ham. ex Smith, *Cratoxylum cochinchinensis*

Table 1. Basic information on the study sites

Site	Altitude (m)	Slope (degrees)	Canopy height (m)	Stratification (layer)[a]	Forest age (yr)
Seasonal rain forest (Srf)	750	>15	40	5 ($T_1 + T_2 + T_3$ + S + H)	>150
Mallotus paniculatus forest (*Mp*f)	600	5	12	3 (T + S + H)	25
Macaranga denticulata forest (*Md*f)	960	10	10	3 (T + S + H)	9
Trema orientalis forest (*To*f)	620	20	8	3 (T + S + H)	4
Slash-and-burn field (Sbf)	620	20	–	–	–

[a]T = tree layer, S = shrub layer, H = herb layer.

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(Lour.) Bl. and *Eurya groffii* Merr. *Trema orientalis* forest develops from the cleared rain forest or abandoned farmlands in Xishu-angbanna. The *To*f site sampled in the present study covers approx. 6 ha and has a dense canopy (90% of coverage). In addition to *Trema orientalis* (L.) Bl., *Debregeasia longifolia* (Burm. f.) Wedd., *Ficus semicordata* and *Ficus hispida* L.f. occur in the canopy.

The Sbf was produced by slashing and burning a *Trema orientalis* forest for the purpose of cultivating maize. This Sbf site had been a part of the *To*f site and was contiguous with it. We sampled the soil 2 d after the burning took place.

The selected secondary forest sites were scattered in different forest patches. Owing to intensive use of local agriculture, secondary forests, especially those forest patches in sites with easy access, have been mostly converted into either artificial plantations or slash-and-burn agricultural fields. In these kinds of sites, only some individual pioneer trees can be found on the edges of the plantations or slash-and-burn agricultural fields. It is rare to find large areas of mono-dominant secondary forests that are currently undisturbed. Therefore, owing to the disturbance to the forest mentioned above, no appropriate replication of these forest types was available near our institution where the germination trials were performed. All the study sites were selected as representative examples of the corresponding forest types. The *Mp*f site is an experimental plot established for the permanent monitoring of succession by the Xishuangbanna Station of Tropical Ecology (XSTE), and was created by slashing and burning a tropical seasonal rain forest 25 years ago. Since then the *Mp*f site has been kept undisturbed for ecological observations. Both the *Md*f and *To*f sites are farmers' lands and have been maintained by the villagers.

Sampling methods

Twenty soil cores of 10 × 10 × 10 cm were taken, at 2 m intervals along a 40 m long transect, from each of the five sites. Fresh litter on the soil surface was removed before sampling. Each soil core was sampled in three different layers (depths): 0–2 cm, 2–5 cm and 5–10 cm. This was done by using two special flat shovels which were exactly 10 cm wide, together with a steel tape. The soil samples were then placed separately in cloth bags and transported to the XSTE, about 15 km away from the farthest site, for germination testing.

In addition, a geobotanical plot measuring 10 × 10 m was made in each of the *Mp*f, *Md*f and *To*f sites to describe their forest structures.

Seed germination

Each field soil sample was spread in a clay-baked germination pot (approx. 20 cm deep × 30 cm diameter for upper and middle samples, 20 cm deep × 40 cm diameter for bottom samples) approx. 1 cm deep onto a 3 cm layer of perlite on the day of collection. No soil samples were left overnight in the cloth bags. Each germination pot was covered with a piece of white cloth nearly 40 × 40 cm and wrapped with an elastic cord to prevent seed contamination. This cloth provided approx. 15–20% shade. Thus, a total of 300 germination pots were put on four bamboo trestle tables approx. 80 cm above the ground in a clearing with full sun in order to prevent rain and mud from contaminating the cloth on the pots.

The germination pots were regularly watered to keep the soil samples moist after carefully opening the cloth covers. Seedling censuses were conducted every 2 d and those identified were counted and then removed at once. Seedling emergence began 2 d after sowing the soil samples. Seedlings that were difficult to distinguish were transplanted for continued growth until we could identify them. Soil samples were stirred in the fourth month of the experiment, and the census was continued to the end of emergence, which occurred early in the sixth month.

The soil seed bank sampling and the start of germination trials occurred 4–12 May 1995 and the germination trials ended on 26 October 1995.

Statistical analysis

For the purpose of reducing the heterogeneity of variances, a square-root transformation of seedling count data was made before ANOVA, both one-way and two-way, to analyse the differences in number of seedlings germinated from the soil samples of the five sites and to examine the interaction effect of soil depth and site factors (Underwood, 1997).

Results

Time course of seed germination

Most of the seeds in the soil samples germinated within 70 d (Fig. 1). However, the seeds from various forests differed in germination rate. In general, the germination rate of seeds from secondary forest soils peaked in the first week (*Md*f, *Mp*f and *To*f), while the germination of seeds in Srf and Sbf soils was staggered over the first 6 weeks and peaked in the seventh and eighth weeks.

Seed storage

Seed density ranked as: *To*f > *Md*f > *Mp*f > Srf > Sbf (Table 2). Srf, the climax forest of this area, had the

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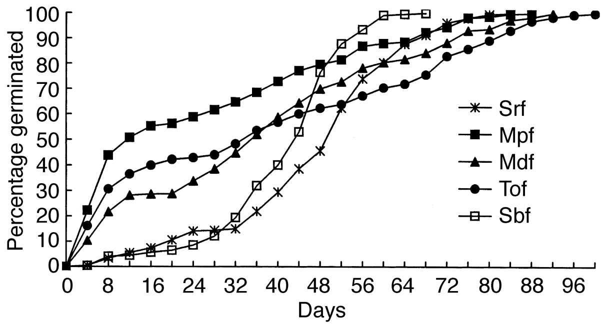

Figure 1. Germination percentages vs. time from soil samples taken from the five study sites. Germination after day 100 was ignored because over 95% of the total seeds germinated within the first 3 months.

lowest soil seed bank density of the forest sites. In contrast, *Tof*, a 4-yr-old forest, showed the most abundant seed bank in these five sites. ANOVA indicated that the difference in seed density among these sites was significant ($p < 0.001$). The Newman–Keuls multiple comparison test confirmed that these sites were significantly different from each other in seed density, at the 0.05 significance level, except for Srf – *Mpf* ($Q = 0.016$, critical $q = 2.812$). *Mpf*, the oldest of the secondary communities surveyed, was in the building phase and had more tree species than the other secondary forests. Its forest structure and microclimate were also somewhat similar to Srf. The interaction effect of site and soil depth on seed density was significant ($p < 0.001$).

The distribution of seeds in different soil layers varied between sites (Fig. 2). The upper soil layer (0–2 cm) had the highest seed density of the forest sites. Multiple comparisons (Tukey's honestly significant difference test) demonstrated that the difference in seed density between the upper and middle layers (2–5 cm) was significant for all the sites. The difference between the middle and lower layers (5–10 cm), however, was significant for *Mpf* and *Tof*, but not significant for Srf and *Mdf* (significance level: 0.995 and 0.515, respectively). The reason for this was the presence of numerous seeds of *Pilea microphylla* (L.) Liebm., *Thysanolaena maxima* (Roxb.) O. Ktze. and *Ageratum conyzoides* L. in deep soil levels of Srf and *Mdf*.

Life forms and dominants

Herbs dominated the life form spectra of the five sites (Table 3). Trees took second place and shrubs third. Liana species were rare in the soil seed banks. In the four forest sites the proportion of herbaceous species decreased and woody species (tree + shrub) increased as the forests became older.

Of the 14 most abundant germinating species, nine were forbs, grasses or sedges (Table 4). Generally speaking, *Ageratum conyzoides* and *Pilea microphylla* dominated the germinated seedlings, particularly in *Tof* and *Mdf*. These two species, however, were rarely found in undergrowth of the forests. *Ageratum conyzoides* is a heliophilous weed which commonly appears in wet habitats on small streams, edges of secondary forests and newly abandoned lands. The filtering of light by tree leaves reduces the germination of the light-requiring seeds of this species (Pons, 1992). In *Mpf*, a bird-dispersed tree species, *Broussonetia papyrifera* (L.) Vent. ranked in second place, although *Cyperus diffusus* Vahl dominated the soil seed bank. The situation in Srf was different from the other three forests. *Pilea microphylla* and *Mussaenda elongata* Hutch., a shrub, were the most abundant seeds in the Srf soil. *Thysanolaena maxima* is a tall grass which usually becomes established and dominates the abandoned lands of slash-and-burn agriculture of this area (cf. Fig. 5e in Zhang and Cao, 1995). The present study revealed that viable seeds stored in soil under the seasonal rain forest might contribute to the sources for *T. maxima* establishment and dominance.

Figure 3 shows the number of taxa germinated from soil samples of different sites. *Mdf* (9 yr old) clearly had the most species-rich seed bank, higher even than *Tof* (4 yr old) which had the highest seed density in the soil (Fig. 3 and Table 2) and Srf (mature

Table 2. Number of seeds germinated from the five sites (20 soil samples of 10 × 10 × 10 cm)

Site	Seedlings germinated				Seed density
	0–2 cm	2–5 cm	5–10 cm	Total	(seeds m^{-2})[a]
Seasonal rain forest (Srf)	244	249	424	917	4585 ± 344
Mallotus paniculatus forest (*Mpf*)	367	313	275	955	4775 ± 553
Macaranga denticulata forest (*Mdf*)	1994	1783	2612	6389	31,945 ± 2973
Trema orientalis forest (*Tof*)	8349	3557	1227	13133	65,665 ± 6906
Slash-and-burn field (Sbf)	21	70	135	226	1130 ± 142

[a] Mean ± standard error, $n = 20$.

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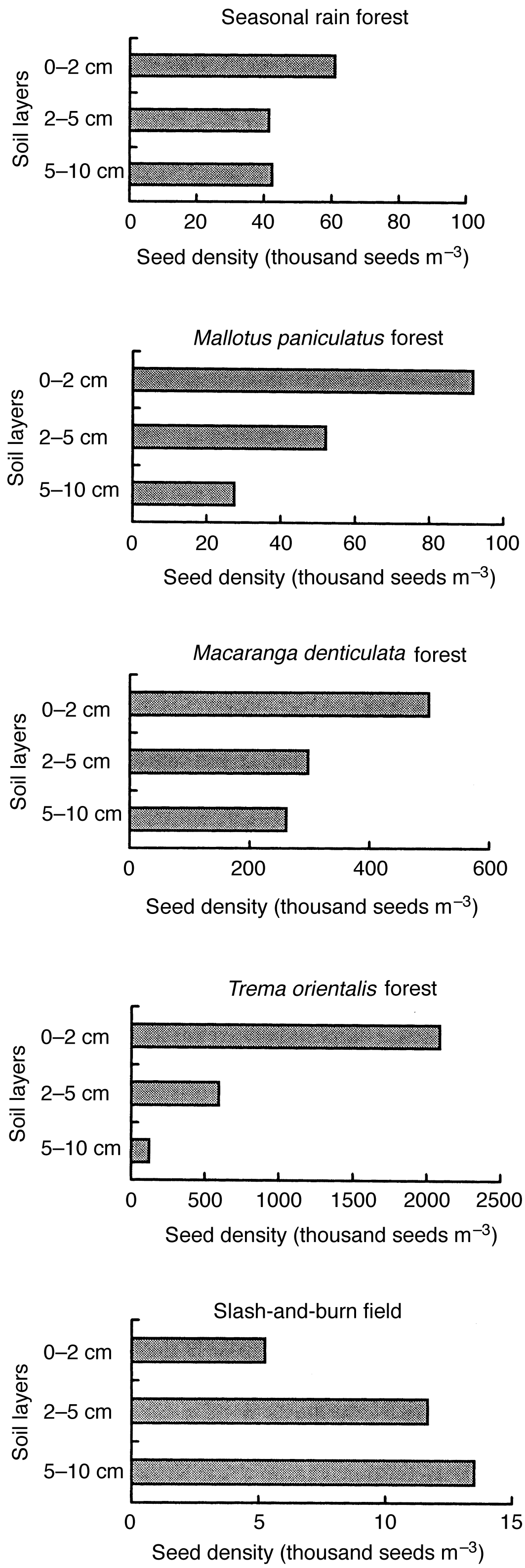

Figure 2. Vertical distribution of the seeds in soils.

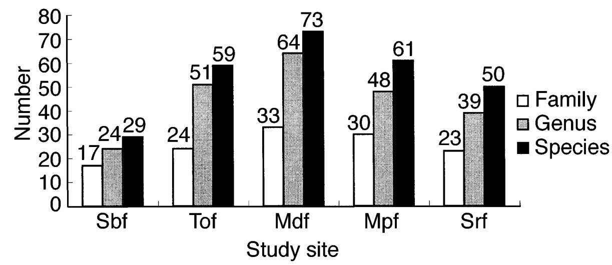

Figure 3. Seed composition of soil samples at different taxonomic levels in five habitats.

forest) which had the highest tree species diversity in the vegetation (Cao and Zhang, 1997).

Slash-and-burn agriculture

Slash-and-burn agriculture had a strong impact on the soil seed bank. It greatly reduced seed storage in the soil in comparison with that of *Tof* (Table 2) and changed the depth profile of the soil seed bank, leading to an inverted pattern in vertical distribution (Fig. 2). Most of the seeds in the upper soil layer were burned out during the fire and only a small proportion remained. Consequently, the middle and lower soil layers held more seeds than the upper soil layer (Fig. 2). ANOVA showed that there was a significant difference in seed density between the upper and middle soil layers ($p <$ 0.05), but the difference between the middle and lower layers was not significant (significance level: 0.448). In the slash-and-burn field there was a change in dominant species. *Thysanolaena maxima* and *Trema orientalis* were the most abundant seeds in the Sbf site, in contrast to *Ageratum conyzoides* and *Pilea microphylla* which dominated the *Tof* site before slashing and burning (Table 4). On the other hand, woody species (tree + shrub) accounted for more than half of the soil seed bank (Table 3). The taxonomic diversity of the seeds in the soil seed bank also decreased at the levels of family, genus and species (Fig. 3).

Discussion

The soil seed density of seasonal rain forests is within the range of seed densities of mature forest soils (maximum 3350 seeds m^{-2} from the 0–5 cm soil layer), summarized by Garwood (1989), although the highest value in her review was from a forest edge. Compared with forests in Thailand, Malaysia, Singapore, Papua New Guinea and Australia, however, the Xishuangbanna seasonal rain forest displays an extraordinarily abundant soil seed bank (Table 5), although nearly half of the seeds in the soil seed bank were weeds (Table 3). Regardless of herbs and

Table 3. Numbers of species germinated from the soils (20 samples for each)[a]

Site	Life form				
	Tree	Shrub	Herb	Liana	Total
Srf	15 (30.0%)	7 (14.0%)	27 (54.0%)	1 (2.0%)	50 (100.0%)
Mpf	17 (27.9%)	5 (8.2%)	34 (55.7%)	5 (8.2%)	61 (100.0%)
Mdf	10 (13.7%)	11 (15.1%)	47 (64.4%)	5 (6.8%)	73 (100.0%)
Tof	11 (18.6%)	7 (11.9%)	40 (67.8%)	1 (1.7%)	59 (100.0%)
Sbf	10 (34.5%)	6 (20.7%)	12 (41.4%)	1 (3.4%)	29 (100.0%)

[a] Figures in parentheses are percentages for the numbers of species in the total number of species germinated from the 20 soil samples of each site, i.e. life form spectra.

Table 4. The 14 species with the most abundant seedlings that germinated from the soil samples of the five sites (20 samples for each)[a]

Species	Life form	Site				
		Srf	*Mpf*	*Mdf*	*Tof*	Sbf
Ageratum conyzoides L.[b]	Herb		5 (0.5%)	**2199 (34.4%)**	**8265 (62.9%)**	
Broussonetia papyrifera (L.) L'Herit. ex Vent.	Tree		**93 (9.7%)**			
Cyperus diffusus Vahl	Herb	25 (2.7%)	**171 (17.9%)**		**906 (6.9%)**	**18 (8.0%)**
Hedyotis diffusa Willd.[b]	Herb	21 (2.3%)	20 (2.1%)	**274 (4.3%)**	17 (0.1%)	2 (0.9%)
Lindernia viscosa (Hornem.) Boldingh[b]	Herb	**113 (12.3%)**	7 (0.7%)	26 (0.4%)	90 (0.7%)	5 (2.2%)
Macaranga denticulata (Bl.) Muell.-Arg.	Tree			**256 (4.0%)**		2 (0.9%)
Mariscus sumatranus (Retz.) T. Koyama	Herb	1 (0.1%)	26 (2.7%)		**242 (1.8%)**	4 (1.8%)
Microstegium ciliatum (Trin.) A. Camus	Herb		**66 (6.9%)**	1	6	
Mollugo pentaphylla L.[b]	Herb		**67 (7.0%)**			
Mussaenda elongata Hutch.	Shrub	**145 (15.8%)**		8 (0.1%)	1	1 (0.4%)
Mussaenda hossei Craib	Shrub	2 (0.2%)		1		**27 (11.9%)**
Pilea microphylla (L.) Liebm.[b]	Herb	**147 (16.0%)**		**2088 (32.7%)**	**1814 (13.8%)**	
Thysanolaena maxima (Roxb.) O. Ktze.[b]	Herb	**133 (14.5%)**	47 (4.9%)	41 (0.6%)	102 (0.8%)	**57 (25.2%)**
Trema orientalis (L.) Bl.	Tree	5 (0.5%)	30 (3.1%)	4	163 (1.2%)	**31 (13.7%)**

[a]Total number of seedlings of each species, and percentages (in parentheses) of total number of seedlings, germinated from the 20 soil samples. Figures in bold are those ranked in the first four places in each site.
[b]Weeds commonly occurring in farmland and on road-sides.

Table 5. Mean seed densities in soil seed banks of mature tropical forests in some Asian-Oceanic sites.

Location and sites	Forest type	Soil depth (cm)	Seed density (m^{-2})	Reference
Xishuangbanna, China	Seasonal rain forest (750 m alt.)	**10**	**4585**	Present study
Xishuangbanna, China	Seasonal rain forest (750 m alt.)	**5**	**2464**	Present study
Chiang Mai, Thailand	*Castanopsis* forest (1350 m alt.)	5	161–243	Cheke *et al*. (1979)
Chiang Mai, Thailand	Dry dipterocarp forest (550 m alt.)	5	137	Cheke *et al*. (1979)
Pasoh, Malaysia	Lowland dipterocarp forest	10	131	Putz and Appanah (1987)
Sabah, Malaysia	Lowland dipterocarp forest	15	60	Liew (1973)
Bukit Timah Natl. Park, Singapore	Lowland rain forest (<162 m alt.)	5	approx. 1000	Metcalfe and Turner (1998)
Mt. Susu, Papua New Guinea	*Araucaria* rain forest (900 m alt.)	7.5	1325	Enright (1985)
Gogol, Papua New Guinea	Tropical rain forest (<100 m alt.)	5	398	Saulei and Swaine (1988)
North Queensland, Australia	Lowland rain forest (≤250 m alt.)	5	588–1068	Hopkins and Graham (1983)
North Queensland, Australia	Lowland rain forest (<70 m alt.)	5	592	Hopkins and Graham (1984)
North Queensland, Australia	Lowland rain forest (360–600 m alt.)	4	240	Graham and Hopkins (1990)

herbaceous lianas, there still were 1580 seeds m^{-2} of woody species in the seasonal rain forest soil at 10 cm depth, of which over 75% were trees and shrubs occurring only in secondary forests or on forest edges (e.g. *Anthocephalus chinensis* (Lam.) Rich. ex Walp., *Ficus hispida*, *Duabanga grandiflora* (Roxb. et DC.) Walp., *Rhus chinensis* Mill., *Mussaenda elongata*, and *Kydia calycina* Roxb.). The fractions of the seeds in soils contributed by pioneer tree species in tropical forests in Sabah and Peninsular Malaysia were: 61% (Liew, 1973) and 29% (Putz and Appanah, 1987), respectively, lower than that from Xishuangbanna seasonal rain forest.

Graham and Hopkins (1990) predicted that any forest development tending to increase areas of persistent high light intensity would allow invasion and reproduction of weeds. It is believed that high seed density may occur if the forest surveyed is close to an extensive secondary forest or if the forest is suffering disturbance (Hopkins and Graham, 1984; Putz and Appanah, 1987; Graham and Hopkins, 1990). Seasonal rain forests in this area are only distributed in some narrow wet valleys and lowlands below 1000 m altitude, usually along rivers or streams between ridges. Because Xishuangbanna lies on the northern border of tropical Asia and experiences a relatively dry and cool season, the development of seasonal rain forests requires habitats with sufficient water supply. This is particularly important for the rain forest that has to survive a dry season from November to April every year. Its mountainous topography, in addition, contributes to the patchy distribution of seasonal rain forests (Zhang and Cao, 1995). Tropical forests in Xishuangbanna have also become seriously fragmented through intensive agricultural use in recent decades. Of the 40,000 ha of remaining primary tropical rain forest and monsoon forest, only 25,000 ha lie within nature reserves and the forest has been broken up into over 400 patches. It is very difficult to find a continuous seasonal rain forest fragment larger than 10 ha in area that has not been disturbed. Our sample plot was chosen in one of the patches. The occurrence of abundant weed seeds in the soil seed bank under the seasonal rain forest could be a result of local forest fragmentation and disturbance. Because both seed density and the proportion of weed species decrease with distance to the forest edge, weed regrowth or farmlands (Garwood, 1989), some tropical mature forest stands contain hardly any herbaceous species in the soil seed bank (Dalling and Denslow, 1998).

Similarly, the secondary forests examined in this study support an even more numerous seed bank

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(Table 2). The top value (59,530 seeds m^{-2} for the 0–5 cm soil layer of *Tof*) far exceeds the upper limit for secondary regrowth, disturbed vegetation and farms (18,900 seeds m^{-2} for the 0–5 cm soil layer) given by Garwood (1989). Most of the seeds are agricultural weeds and road-side herbs (e.g. *Ageratum conyzoides*, *Hedyotis diffusa* Villd., *Mollugo pentaphylla* L. and *Pilea microphylla*), which do not seem to germinate and flourish in the shade of the forest canopy. In contrast, *Chromolaena odorata* (L.) R. (= *Eupartorium odoratum* L.), an invasive weed of South American origin which dominates abandoned lands of slash-and-burn agriculture in this area, occupies a very small proportion in the soil seed banks (less than 1% in general), although it was abundant (8424 seeds m^{-2} in the 0.5 cm soil) in an African tropical secondary forest (Epp, 1987). It is even absent from the soil of freshly slashed and burned fields, which implies the allochthonous origin of *Chromolaena odorata* in fallow fields of slash-and-burn agriculture.

Trema orientalis is a pioneer tree species in the eastern tropics (Whitmore, 1990). In Xishuangbanna it can become established and may even form mono-dominant stands in fields abandoned after slash-and-burn agriculture (Cao and Zhang, 1996). However, it does not germinate under the forest canopy because the filtering of light by leaf litter prevents germination (Chang, 1996). Once disturbance occurs in the forest and its seeds are exposed to full sunlight, they germinate immediately, although temperature fluctuations may also promote germination (Chang, 1996). The regeneration of *Trema orientalis* forest, therefore, depends upon forest clearance. On the other hand, some birds disperse the tree species by ingesting and dropping its seeds. Thousands of *Pycnonotus jocosus monticola* McClelland in flocks visit *Tof* during the peak seeding season of *Trema orientalis* (August–October) (Cao and Tang, pers. obs.). Therefore, both soil seed bank and bird dispersal (or seed rain) may contribute to the establishment of this species.

Macaranga denticulata and *Mallotus paniculatus* occur in secondary forests as pioneer tree species in Xishuangbanna. In the forest dominated by *Macaranga denticulata*, we found abundant seeds of this species in the soil, but they were unable to germinate under the *Mdf* canopy. The germination performance of this tree species is similar to that of *Trema orientalis*. In contrast, the seeds of *Mallotus paniculatus* were very rare in the soil seed bank of *Mpf*. Only 17 seeds of this species (1.8% of total) germinated from the soil samples. A seed burial experiment conducted in the Pasoh primary forest showed that the mean life of buried *Mallotus paniculatus* seeds was much shorter than that of *Trema orientalis* seeds (Kheong *et al*., 1996).

Slash-and-burn agriculture is widely practised in this region. It drastically decreases the size of the soil seed bank and changes the depth profile. Brinkmann and Vieira (1971) found that the heat effect during burning was deadly to the soil seed bank at the 2 cm depth and extremely serious at the 5 cm depth in a Brazilian forest. A comparison of seed reserves in burned and unburned Amazonian tierra firme forest soils confirmed that burning significantly reduced the size of the seed bank (752 seeds m^{-2} vs. 157 seeds m^{-2}) (Uhl *et al*., 1981). Repeated fires changed the composition of a soil seed bank which had abundant grass and forb seeds rather than successional woody species (Uhl and Clark, 1983). Of course, fire with moderate temperatures can promote seed germination of some species. Higher heat intensity and prolonged exposure, however, can burn the seed coats and destroy the seed embryos, resulting in reduction of seed germination (Mucunguzi and Oryem-Origa, 1996). Frequent fires cause a shift in species composition, favouring species capable of vegetative reproduction (Hoffmann, 1998). Results from Mexican tropical deciduous forests also revealed that fire modifies species dominance and depletes the original seed bank (Rico-Gray and Garcia-Franco, 1992; Miller, 1999). The ecological implications of this in forest regeneration need to be examined by monitoring the dynamics of the soil seed bank following cultivation activities.

In conclusion, the tropical forests surveyed in this study maintained a conspicuously abundant soil seed bank, ranging from 4585 to 65,665 seeds m^{-2} in the 0–10 cm soil layer. The fact that herbs made up approx. half of the seeds in the soil seed bank suggests that these forests, both mature and secondary, are suffering fragmentation and disturbances. Slash-and-burn agriculture changed the depth profile of the soil seed bank. This deserves further investigations in terms of site dynamics.

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References

Baskin, C.C. and Baskin, J.M. (1998) *Seeds: ecology, biogeography, and evolution of dormancy and germination*. San Diego, Academic Press.

Brinkmann, W.L.F. and Vieira, A.N. (1971) The effect of burning on germination of seeds at different soil depths of various tropical tree species. *Turrialba* **21**, 77–82.

Brokaw, N.V.L. (1985) Treefalls, regrowth, and community structure in tropical forests. pp. 53–69 *in* Pickett, S.T.A.; White, P.S. (Eds) *The ecology of natural disturbance and patch dynamics*. Orlando, Academic Press.

Cao, M. and Zhang, J. (1996) An ecological perspective on shifting cultivation in Xishuangbanna, SW China. *Wallaceana* **78**, 21–27.

Cao, M. and Zhang, J. (1997) Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodiversity and Conservation* **6**, 995–1006.

Cao, M., Zhang, J., Feng, Z., Deng, J. and Deng, X. (1996) Tree species composition of a seasonal rain forest in Xishuangbanna, southwest China. *Tropical Ecology* **37**, 183–192.

Cao, M., Zheng, Z. and Zhang, J. (1998) Long-term ecological research in a tropical seasonal rain forest of Xishuangbanna, southwest China. pp. 71–78 *in* Iwakuma, T. (Ed.) *Long-term ecological research in the east Asia-Pacific region: biodiversity and conservation of terrestrial and freshwater ecosystems*. Tsukuba, Japan, National Institute of Environmental Studies.

Chang, N.-H. (1996) Effects of light on seed germination of three pioneer tree species (*Alnus formosana*, *Trema orientalis*, *Broussonettia papyrifera*). *Taiwan Journal of Forestry Science* **11**, 195–199. (In Chinese.)

Cheke, A.S., Nanakorn, W. and Yankoses, C. (1979) Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. *Biotropica* **11**, 88–95.

Dalling, J.W. and Denslow, J.S. (1998) Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. *Journal of Vegetation Science* **9**, 669–678.

Enright, N. (1985) Existence of a soil seed bank under rainforest in New Guinea. *Australian Journal of Ecology* **10**, 67–71.

Epp, G.A. (1987) The seed bank of *Eupatorium odoratum* along a successional gradient in a tropical rain forest in Ghana. *Journal of Tropical Ecology* **3**, 139–149.

FAO–UNESCO (1990) Soil map of the world, revised legend. Rome, FAO.

Garwood, N.C. (1989) Tropical soil seed banks: a review. pp. 149–209 *in* Leck, M.A.; Parker, V.T.; Simpson, R.L. (Eds) *Ecology of soil seed banks*. San Diego, Academic Press.

Graham, A.W. and Hopkins, M.S. (1990) Soil seed banks of adjacent unlogged rainforest types in North Queensland. *Australian Journal of Botany* **38**, 261–268.

Harper, J.L. (1977) *Population biology of plants*. New York, Academic Press.

Hoffmann, W.A. (1998) Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* **35**, 422–433.

Hopkins, M.S. and Graham, A.W. (1983) The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica* **15**, 90–99.

Hopkins, M.S. and Graham, A.W. (1984) Viable soil seed banks in disturbed lowland tropical rainforest sites in North Queensland. *Australian Journal of Ecology* **9**, 71–79.

Kheong, Y.S., Tuck, C.H., Kimura, K., Kanzaki, M., Okauchi, Y. and Yamakura, T. (1996) Seed dispersal and buried seed dynamics. pp. 161–172 *in Collected abstracts for the papers of program "Study on tropical forest ecosystems"*. Tsukuba, Japan, CGER, National Institute for Environmental Studies.

Liew, T.H. (1973) Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. *Malaysian Forester* **36**, 185–193.

Metcalfe, D.J. and Turner, I.M. (1998) Soil seed bank from lowland rain forest in Singapore: canopy-gap and litter-gap demanders. *Journal of Tropical Ecology* **14**, 103–108.

Miller, P.M. (1999) Effects of deforestation on seed banks in a tropical deciduous forest of western Mexico. *Journal of Tropical Ecology* **15**, 179–188.

Mucunguzi, P. and Oryem-Origa, H. (1996) Effects of heat and fire on the germination of *Acacia sieberiana* D.C. and *Acacia gerrardii* Benth. in Uganda. *Journal of Tropical Ecology* **12**, 1–10.

Parker, V.T., Simpson, R.L. and Leck, M.A. (1989) Pattern and process in the dynamics of seed banks. pp. 367–384 *in* Leck, M.A.; Parker, V.T.; Simpson, R.L. (Eds) *Ecology of soil seed banks*. San Diego, Academic Press.

Pons, T.L. (1992) Seed responses to light. pp. 259–284 *in* Fenner, M. (Ed.) *Seeds: the ecology of regeneration in plant communities*. Wallingford, UK, CAB International.

Putz, F.E. and Appanah, S. (1987) Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* **19**, 326–333.

Rico-Gray, V. and Garcia-Franco, J.G. (1992) Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *Journal of Vegetation Science* **3**, 617–624.

Roberts, H.A. (1981) Seed banks in soils. pp. 1–55 *in* Coaker, T.H. (Ed.) *Advances in applied biology 6*. London, Academic Press.

Saulei, S.M. and Swaine, M.D. (1988) Rain forest seed dynamics during succession at Gogol, Papua New Guinea. *Journal of Ecology* **76**, 1133–1152.

Skoglund, J. (1992) The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science* **3**, 357–360.

Symington, C.F. (1933) The study of secondary growth on rain forest sites in Malaya. *Malayan Forester* **2**, 107–117.

Thompson, K. (1992) The functional ecology of seed banks. pp. 231–258 *in* Fenner, M. (Ed.) *Seeds: the ecology of regeneration in plant communities*. Wallingford, UK, CAB International.

Thompson, K. and Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* **67**, 893–921.

Uhl, C. and Clark, K. (1983) Seed ecology of selected Amazon Basin successional species. *Botanical Gazette* **144**, 419–425.

Uhl, C., Clark, K., Clark, H. and Murphy, P. (1981) Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. *Journal of Ecology* **69**, 631–649.

Underwood, A.J. (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge, Cambridge University Press.

Vazquez-Yanes, C. and Segovia, A.O. (1984) Ecophysiology of seed germination in the tropical humid forests of the world: a review. pp. 37–50 *in* Medina, E.; Mooney, H.A.; Vazquez-Yanes, C. (Eds) *Physiological ecology of plants of the wet tropics*. The Hague, Dr W. Junk Publishers.

Whitmore, T.C. (1975) *Tropical rain forests of the Far East*. Oxford, Clarendon Press.

Whitmore, T.C. (1983) Secondary succession from seed in tropical rain forests. *Forestry Abstracts* **44**, 767–779.

Whitmore, T.C. (1989a) Canopy gaps and the two major groups of forest trees. *Ecology* **70**, 536–538.

Whitmore, T.C. (1989b) Changes over twenty-one years in the Kolombangara rain forests. *Journal of Ecology* **77**, 469–483.

Whitmore, T.C. (1989c) Forty years of rain forest ecology 1948–1988 in perspective. *GeoJournal* **19**, 347–360.

Whitmore, T.C. (1990) *An introduction to tropical rain forests*. Oxford, Clarendon Press.

Wu, Z., Zhu, Y. and Jiang, H. (1987) *The vegetation of Yunnan*. Beijing, Science Press. (In Chinese.)

Young, K.R., Ewel, J.J. and Brown, B.J. (1987) Seed dynamics during forest succession in Costa Rica. *Vegetatio* **71**, 157–173.

Zhang, J. and Cao, M. (1995) Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation* **73**, 229–238.

Zhu, H. (1997) Ecological and biogeographical studies on the tropical rain forest of south Yunnan, SW China with a special reference to its relation with rain forests of tropical Asia. *Journal of Biogeography* **24**, 647–662.

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