# SOIL SEED BANKS IN PLANTATIONS AND TROPICAL SEASONAL RAINFORESTS OF XISHUANGBANNA, SOUTH-WEST CHINA

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**CHEN H, CAO M & TANG Y. 2013. Soil seed banks in plantations and tropical seasonal rainforests of Xishuangbanna, South-West China.** The impacts of land conversion from forests to plantations on seed availability are poorly appraised in terms of future restoration potentials. Seed storage and species composition of soil seed banks were characterised in five natural forests and three plantations. Mean soil seed storage differed significantly between study sites, ranging from 2444 seeds/m$^2$ in a selectively logged forest to 17,946 seeds/m$^2$ in a pomelo orchard. For all sites except for secondary forest 2, herb seeds dominated the soil seed bank. More seeds of pioneer tree species were found in the soil seed banks of secondary forests than in primary rainforests. This suggests that secondary forests have higher seed availability and stronger potential for forest restoration than primary forests. Anthropogenic management activities resulted in abundant but less diverse soil seed bank due to the dominance of a few herbaceous species in the pomelo orchards and rubber plantations. Low tree seed storage was found in soil seed banks of pomelo orchards and rubber plantations and might decelerate forest succession. Thus, the seeds of pioneer trees in soil seed banks of secondary forests could promote natural forest regeneration in abandoned plantations.

Keywords: Invasive herbs, management, pioneer tree species, seed availability, tropical forest

**CHEN H, CAO M & TANG Y. 2013. Kebolehdapatan biji benih di ladang dan hutan hujan tropika bermusim di Xishuangbanna, Barat Daya China.** Kesan penerokaan hutan untuk dijadikan ladang kurang dikaji dari segi kebolehdapatan biji benih bagi pemulihan hutan. Simpanan biji benih dan komposisi spesies di tanah asal lima hutan semula jadi dan tiga ladang dikaji. Purata simpanan biji benih berbeza dengan ketara antara tapak kajian dan berjulat antara 2444 biji benih/m$^2$ di hutan yang mengalami tebangan memilih hingga 17,946 biji benih/m$^2$ di kebun limau bali. Semua tapak kajian kecuali hutan sekunder 2 didominasi oleh biji benih tumbuhan herba. Lebih banyak biji benih spesies pokok perintis ditemui di tapak hutan sekunder berbanding dengan hutan primer. Ini mencadangkan yang hutan sekunder mempunyai sumber biji benih yang lebih banyak. Oleh itu, potensi hutan sekunder untuk memulihkan hutan adalah lebih baik berbanding dengan hutan primer. Aktiviti urusan antropogeni membanyakkan biji benih tetapi mengurangkan kepelbagaian biji benih disebabkan dominasi beberapa spesies tumbuhan herba di kebun limau bali dan ladang getah. Simpanan biji benih yang rendah di kebun limau bali dan ladang getah mungkin melambatkan sesaran hutan. Oleh itu, biji benih pokok perintis di tapak hutan sekunder boleh digunakan sebagai sumber untuk memulihkan hutan semula jadi di tapak ladang yang terbiar.

## INTRODUCTION

Tropical ecosystems are exceptionally rich and exclusive reservoirs of much of the biodiversity on earth (Whitmore 1990). However, human population and industrial timber logging have led to rapid and extensive destruction of tropical forests (Laurance 2007). The conversion of rainforests into secondary forests or agricultural plantations is occurring at an alarming rate. Over the next 50 years, rapid and widespread agricultural expansion poses a serious threat to natural ecosystems worldwide (Tilman et al. 2001). The highest rate of deforestation in any major tropical region occurs in South-East Asia, which can lose three quarters of its original

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forests and up to 42% of its biodiversity by 2100 (Sodhi et al. 2004). Furthermore, the planting of perennial exotic crops, which include rubber (*Hevea brasiliensis*), oil palm (*Elaeis guineensis*) and coconut (*Cocos nucifera*), accounts for 20–30% of the total cultivated area of South-East Asia and has led to extensive deforestation (Flint 1994).

Xishuangbanna ($1.96 \times 10^6$ ha) is famous in China for being a biodiversity hotspot with diverse tropical flora and fauna (Zhang & Cao 1995, Zhu et al. 2006). However, the forest cover of Xishuangbanna declined from 69% in 1976 to less than 50% in 2003 because of rapid development of the local economy leading to increased demand for natural resources (Li et al. 2007, 2009). Since reforms and clearing of lands in the late 1970s, traditional agriculture such as slash-and-burn cultivation has been replaced by permanent cash crop cultivation. The development of rubber plantations is a major threat to local tropical rainforests, which are usually distributed below 900 m above sea level in Xishuangbanna. From 1976 till 2003, a total of 139,576 ha of tropical rainforests were converted into rubber plantations at lower altitudes. Furthermore, during the last decade, the rising market price of rubber further increased its demand and caused more severe clearance of natural forests distributed at higher altitudes or steep slopes for new arable land (Li et al. 2007, 2009). Meanwhile, pomelo (*Citrus maxima*) orchards expanded rapidly to meet market demand. The change in landuse from natural forests to plantations causes not only biodiversity loss but also deterioration of soil seed banks (Lemenih & Teketay 2006).

Soil seed bank is the aggregation of viable seeds in the superficial soil (Simpson et al. 1989). Seed inputs into the soil seed bank are determined by seed rain from the standing vegetation (Guevara 2005). Both the species diversity and size of soil seed bank are reduced in primary forests compared with secondary forests because of the depletion and limited seed inputs of pioneer trees (Plue et al. 2010). Natural or anthropogenic disturbances of standing vegetation might also affect the seed density and species composition of soil seed bank (Mamede & de Araujo 2008). Extensive and frequent disturbances lead to larger soil seed bank, which is due to large inputs of seeds from light-demanding and small-seeded plant species (Alvarez-Aquino et al. 2005). Viable pioneer tree seeds in soil seed bank can promote forest regeneration after natural or anthropogenic disturbances (Zimmerman et al. 2000). In contrast, a lack of pioneer tree seeds in soil seed bank impedes the secondary succession of indigenous forest in abandoned pastures (Wijdeven & Kuzee 2000, Zimmerman et al. 2000). Therefore, seed availability, which hereafter refers to the viable seed storage of pioneer tree species in soil seed bank, serves as a key indicator for the assessment of the restoration potential of vegetation. Ex-situ transplant of soil seed bank that contains seeds of many pioneer trees is often a recommended low-cost technique for restoration of vegetation that is degraded by mine tailings (Parrotta & Knowles 2001, Zhang et al. 2001, Mackenzie & Naeth 2010).

In Xishuangbanna, studies have revealed higher seed storage in a seasonal rainforest and a dipterocarp rainforest than in some other rainforests of tropical Asia, reflecting the effects of local forest fragmentation (Cao et al. 2000, Tang et al. 2006). In addition, a majority of non-native species, especially wind-dispersed weeds, comprises the soil seed bank of forest-edge areas and is induced by human disturbance (Lin et al. 2006). Although slash-and-burn agriculture eliminates most of the superficial seeds in the soil seed bank, abundant seed storage (65,665 seeds/$m^2$) was found in young slash-and-burn fallow (Cao et al. 2000).

Based on previous findings, the present study was conducted to examine the restoration potential of different types of lands by comparing the seed availability of soil seed bank. We hypothesise that secondary forests have more abundant storage of pioneer tree seeds than primary rainforests or plantations or pomelo orchards, thereby resulting in relatively high seed availability in its soil seed bank. Reduced seed availability in soil seed bank is a main barrier to forest recovery in rubber plantations and pomelo orchards. The reduced availability is due to depletion of tree seeds stored in the soil and predominance of exotic/non-native herbs after long-term plantation practices. The objectives of this study were to (1) investigate the changes in species composition and seed density of soil seed bank following deforestation and conversion into plantations and (2) examine the natural restoration potentials of sites by comparing the seed availability in the soil seed bank. We also presented some perspectives on the promotion of forest restoration.

## MATERIALS AND METHODS

### Study area

This study was conducted in Xishuangbanna, South-West China, where tropical seasonal forests are distributed (Cao et al. 2006). The climate is tropical monsoon with annual mean temperature of 21.7 °C. Average annual rainfall is approximately 1500 mm and more than 80% of it occurs during the rainy season from May till October. During the dry season, especially from November till February, there is high frequency of heavy fog in the lower hills and valleys in the night and morning (Liu et al. 2004, 2005, Cao et al. 2006). The primary vegetation is tropical seasonal rainforest that consists of *Pometia tomentosa*, *Terminalia myriocarpa*, *Barringtonia macrostachya*, *Shorea wantianshuea*, *Gironniera subaequalis* and *Chisocheton siamensis* (Zhu et al. 2006).

A total of eight forest types were chosen that represented different levels of disturbances. They were two seasonal rainforests (rainforest 1, RF1; rainforest 2, RF2), one selectively-logged rainforest (SLF), two secondary forests (secondary forest 1, SF1; secondary forest 2, SF2), one *Senna siamea* plantation (SSP), one monoculture rubber plantation (RUP) and one monoculture pomelo orchard (POO) (Table 1). The rainforest 1 and rainforest 2 sites are located in the core zones of Menglun and Mengla Nature Reserves respectively, where collection and hunting are forbidden. The other six sites are located in the Xishuangbanna Tropical Botanical Garden (XTBG). The selectively logged rainforest is a fragmented, tropical seasonal rainforest. It was selectively logged in 1959. Since then, it has been protected as an in-situ reserve for indigenous plant species. Secondary forest 1 and secondary forest 2 are secondary forests that naturally regenerated after slash-and-burn cultivation approximately 30 years ago. The *S. siamea* plantation is a fuelwood plantation that was established by clearing the secondary forest 30 years ago. Since XTBG assumed its management approximately 15 years ago, fuelwood harvest has been forbidden. The rubber plantation and pomelo orchard sites were planted after slashing and burning of secondary forests. Intensive management activities, which include manual weeding or three herbicide (glyphosate) applications during the rainy season to eliminate weeds, are conducted in the rubber plantation and pomelo orchard every year. In August, a compound fertiliser containing N, P and K was applied under each rubber tree in the rubber plantation. At the end of the rainy season, the farmers fertilise the pomelo orchard. In addition, the rubber plantation site has rubber latex tapped once every 2 days in April till November of each year. In the pomelo orchard site, fruits are harvested from July till August of each year.

### Soil sampling

In May 2009, 20 soil samples (diameter 10 cm, depth 5 cm) were collected using a steel tube at 10 m intervals along a 200 m transect in the core area of each site. The surface area of the soil sampled at each stand was 78.5 $cm^2$ and the soil volume was 392.7 $cm^3$. A total of 160 soil samples were collected from the eight sites.

**Table 1** Characteristics of study sites

| Parameter | RF1 | RF2 | SLF | SF1 | SF2 | SSP | RUP | POO |
|---|---|---|---|---|---|---|---|---|
| Altitude (m) | 700 | 850 | 566 | 630 | 640 | 620 | 600 | 590 |
| Latitude N | 21° 57' | 21° 42' | 21° 55' | 21° 54' | 21° 54' | 21° 54' | 21° 54' | 21° 54' |
| Longitude E | 101° 12' | 101° 35' | 101° 35' | 101° 16' | 101° 16' | 101° 16' | 101° 16' | 101° 16' |
| Area (ha) | CF | CF | 100 | 14 | 8.7 | 15.7 | 10.8 | 22.3 |
| Canopy height (m) | 35 | 40 | 30 | 16 | 16 | 18 | 15 | 3 |
| Age (years) | > 200 | > 200 | > 200 | 30 | 30 | 30 | 19 | 15 |
| Disturbance | Low | Low | Low | Medium | Medium | Medium | High | High |

RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard, CF = continuous forest

## Seed germination

The number of viable seeds in each soil sample was estimated through germination trials. We refer to viable seeds as those germinated under our germination condition settings. Each soil sample was placed in a separate tray at a depth of approximately 1 cm in a non-temperature controlled greenhouse (30% of full light). The trays were watered daily to keep the soil samples moist. Seedlings were counted and identified seedlings were removed. Seedlings that were difficult to distinguish were transplanted into pots for continued growth until identification was possible. After emerged seedlings were removed from the trays, soil samples were carefully stirred. Trays were kept and observed until no seedlings had emerged for a period of 1 month. There might be some seeds dormant in the soil, even at the end of the germination trial. However, we might also germinate seeds that persisted in the soil for a long time and those which dormancy was broken during our germination trials. These serve as mutual complementation in theory.

## Data analysis

Frequency at a site was defined as the percentage of soil samples with an identified species in the soil seed bank of that site. Seed abundances between sites were compared by one-way analysis of variance using log (n + 1) transformations where n = number of seedlings germinated (Tang et al. 2006). The proportions of tree seeds to herb seeds were tested for differences between sites using Pearson chi-squared tests.

## RESULTS

## Seed stocks and plants

A total of 6517 seeds germinated from the soil seed banks of the eight sites (Table 2). Mean seed density (number of germinated seeds/m$^2$) in the top 5 cm of soil varied significantly from 2445 ± 975 seeds /m$^2$ (mean ± SD) in the selectively logged rainforest to 17,946 ± 8366 seeds /m$^2$ in the pomelo orchard (Figure 1) ($p < 0.05$). Seed density of the soil seed bank was significantly higher in the pomelo orchard and secondary forest 2 than the other sites. Only 39 and 41 species germinated from soil samples of rubber plantation and pomelo orchard respectively, whereas at least 50 species germinated from each of the other six sites (Table 2).

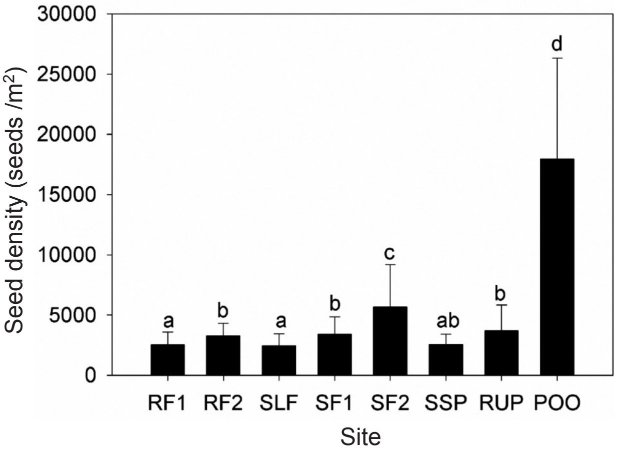


**Figure 1** Seed densities in soil seed banks of the eight study sites (mean ± SD); the different letters indicate significantly different sites at $p < 0.05$; RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard

Herb seeds dominated the soil seed banks of all the sites except for secondary forest 2, which was dominated by tree species (Table 2). Herbs represented more than 82.1% of the species and 95.9% of the plants found in the rubber plantation and pomelo orchard. However, the proportions of woody (tree + shrub) to herbaceous seeds in the soil seed bank were significantly smaller in the rubber plantation and pomelo orchard than in other sites. No vine seeds germinated from the soil samples of the rubber plantation or pomelo orchard. In the *S. siamea* plantation and in five forest sites except for secondary forest 2, woody species accounted for less than half of the seeds. Secondary forest 2 had the most tree seeds followed by secondary forest 1, *S. siamea* plantation and rainforest 2. Although there were fewer tree seeds stored in the soil seed banks of rainforest 1 and selectively logged rainforest, species diversity represented in the soil seed bank was comparable with those found in the soil seed banks of secondary forest 1 and secondary forest 2 (Table 2).

**Table 2** Plant and seed compositions in the soil seed banks of the eight study sites

| Site | Seed composition | | | | | Species composition | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Tree | Shrub | Herb | Vine | Total | Tree | Shrub | Herb | Vine | Total |
| RF1 | 76 (19.3%) | 81 (20.5%) | 230 (58.2%) | 8 (2.0%) | 395 | 15 (28.3%) | 4 (7.6%) | 30 (56.6%) | 4 (7.5%) | 53 |
| RF2 | 90 (17.5%) | 35 (6.8%) | 370 (71.8%) | 20 (3.9%) | 515 | 14 (28.0%) | 9 (18.0%) | 24 (48.0%) | 3 (6.0%) | 50 |
| SLF | 80 (21.0%) | 57 (14.9%) | 232 (60.7%) | 13 (3.4%) | 382 | 14 (28.0%) | 6 (12.0%) | 25 (50.0%) | 5 (10.0%) | 50 |
| SF1 | 127 (23.7%) | 81 (15.2%) | 318 (59.4%) | 9 (1.7%) | 535 | 13 (24.5%) | 10 (18.9%) | 26 (49.1%) | 4 (7.5%) | 53 |
| SF2 | 341 (38.2%) | 209 (23.4%) | 323 (36.2%) | 20 (2.2%) | 893 | 15 (27.3%) | 8 (14.5%) | 26 (47.3%) | 6 (10.9%) | 55 |
| SSP | 101 (25.5%) | 52 (13.1%) | 219 (55.3%) | 24 (6.1%) | 396 | 8 (13.1%) | 9 (14.8%) | 33 (54.1%) | 11 (18.0%) | 61 |
| RUP | 9 (1.5%) | 15 (2.6%) | 558 (95.9%) | 0 (0%) | 582 | 3 (7.7%) | 4 (10.3%) | 32 (82.1%) | 0 (0%) | 39 |
| POO | 10 (0.4%) | 3 (0.1%) | 2806 (99.5%) | 0 (0%) | 2819 | 3 (7.3%) | 2 (4.9%) | 36 (87.8%) | 0 (0%) | 41 |

RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard

### Pioneer tree species

There were more pioneer tree seeds in secondary forest 1 and secondary forest 2 than in rainforest 1, selectively logged rainforest and rainforest 2 (Figure 2a). Only three tree species were observed in the soil seed bank of rubber plantation (Figure 2b). They were *Ficus hirta*, *F. hispida* and *Macaranga denticulata* (Table 3). Similarly, we found only three tree species in the soil seed bank of pomelo orchard and they were *Alchornea davidii*, *Trema orientalis* and *F. hirta*. All tree seeds in the soil seed banks of rubber plantation and pomelo orchard were pioneer tree species. *Trema orientalis* dominated the tree species recorded in the soil seed banks of the eight sites with a total of 281 seeds. A total of 215 *T. orientalis* seeds were found in the soil seed banks of secondary forest 1 and secondary forest 2. *Ficus* was the most abundant genus in the eight sites with a total of 396 seeds belonging to nine species. In all sites, *F. hirta* was the only tree species found in the soil seed banks. Bird-dispersed seeds of *T. orientalis*, *M. denticulata* and *Ficus* spp. accounted for more than 80% of the animal-dispersed seeds of woody species in all sites. The only two wind-dispersed woody species, *Duabanga grandiflora* (15 seeds) and *Tetrameles nudiflora* (11 seeds), were found in the soil seed banks of the rainforest 1 and selectively logged rainforest.

### Exotic herbs

The pomelo orchard had the most exotic herb seeds, followed by rubber plantation, secondary forest 2, secondary forest 1, *S. siamea* plantation, rainforest 1, selectively logged rainforest and rainforest 2 (Figure 3a). The most abundant exotic herbs were *Ageratum conyzoides*, *Crassocephalum crepidioides*, *Spermacoce latifolia*, *Conyza sumatrensis* and *Chromolaena odorata* with 1041, 223, 190, 155 and 143 seeds respectively (Table 4). The less diverse exotic herbs accounted for nearly half of the herb seeds stored in the secondary forest 2, rubber plantation and pomelo orchard, whereas the diverse native herb seeds accounted for more than 70% of the herb seeds stored in the other sites (Figures 3a and b). Although herbs dominated the soil seed banks of rubber plantation and pomelo orchard, only *C. crepidioides*, *C. sumatrensis*, *C. odorata*, *Vernonia cinerea* and *Stevia rebaudiana* were wind-dispersed, and all of these species belong to the Asteraceae. Furthermore, 116 (result not shown) and 159 (Table 4) wind-dispersed seeds were found in the soil seed banks of the rubber plantation and pomelo orchard respectively.

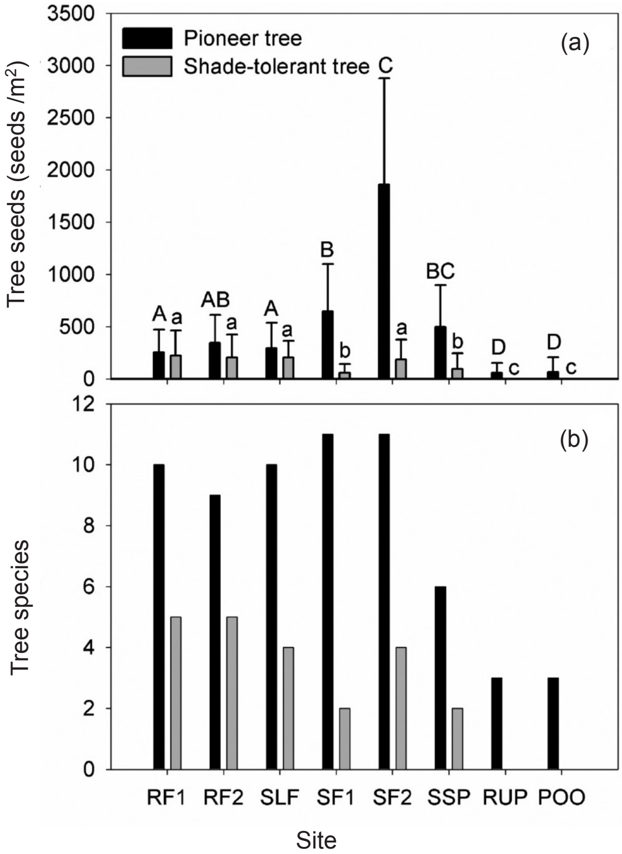


**Figure 2** Tree seed storage as determined by (a) seeds and (b) species in the eight sites (mean ± SD); different letters indicate significantly different sites at $p < 0.05$; RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard

## DISCUSSION

### Conversion of rainforest to secondary forests

The results of our study confirmed that seed density was significantly higher at earlier stages of succession than in later stages. More seeds were stored in the soil seed banks of secondary forest 1 and secondary forest 2 than rainforest 1 and selectively logged rainforest (Table 2 and Figure 1). Although relatively high numbers of seeds (2514 to 3284 seeds/m$^2$; results not shown) were recorded in this study in seasonal rainforests

**Table 3** Tree seed storage in the soil seed banks of the eight sites

| Species | Family | Functional group | Seed dispersal | RF1 | RF2 | SLF | SF1 | SF2 | SSP | RUP | POO | Total | Frequency |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Trema orientalis* | Ulmaceae | Pioneer | Animal | 3 | 21 | 9 | 26 | 189 | 30 | 0 | 3 | 281 | 0.875 |
| *Ficus nervosa* | Moraceae | Pioneer | Animal | 19 | 4 | 8 | 35 | 62 | 19 | 0 | 0 | 147 | 0.75 |
| *Ficus hirta* | Moraceae | Pioneer | Animal | 4 | 14 | 3 | 14 | 20 | 7 | 1 | 2 | 65 | 1.000 |
| *Ficus langkokensis* | Moraceae | Shade-tolerant | Animal | 7 | 19 | 20 | 2 | 6 | 11 | 0 | 0 | 65 | 0.75 |
| *Macaranga denticulata* | Euphorbiaceae | Pioneer | Animal | 0 | 1 | 0 | 23 | 6 | 19 | 1 | 0 | 50 | 0.625 |
| *Ficus hispida* | Moraceae | Pioneer | Animal | 0 | 2 | 4 | 7 | 17 | 13 | 7 | 0 | 46 | 0.75 |
| *Ficus auriculata* | Moraceae | Shade-tolerant | Animal | 24 | 1 | 1 | 7 | 0 | 0 | 0 | 0 | 33 | 0.500 |
| *Euodia trichotoma* | Rutaceae | Shade-tolerant | Animal | 2 | 9 | 0 | 0 | 20 | 0 | 0 | 0 | 31 | 0.375 |
| *Ficus semicordata* | Moraceae | Pioneer | Animal | 2 | 4 | 7 | 3 | 3 | 0 | 0 | 0 | 19 | 0.625 |
| *Ficus cyrtophylla* | Moraceae | Pioneer | Animal | 3 | 6 | 4 | 4 | 0 | 0 | 0 | 0 | 17 | 0.500 |
| *Duabanga grandiflora* | Sonneratiacea | Pioneer | Wind | 6 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 15 | 0.250 |
| *Mallotus paniculatus* | Euphorbiaceae | Pioneer | Animal | 1 | 2 | 1 | 3 | 6 | 1 | 0 | 0 | 14 | 0.750 |
| *Tetrameles nudiflora* | Tetramelaceae | Shade-tolerant | Wind | 1 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 11 | 0.250 |
| *Alchornea davidii* | Euphorbiaceae | Pioneer | Others | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 5 | 9 | 0.500 |
| *Aralia armata* | Araliaceae | Pioneer | Others | 0 | 4 | 2 | 1 | 2 | 0 | 0 | 0 | 9 | 0.500 |
| *Rhus chinensis* | Anacardiaceae | Pioneer | Animal | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0.125 |
| *Ficus* sp. | Moraceae | Pioneer | Animal | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0.125 |
| *Ficus fistulosa* | Moraceae | Shade-tolerant | Animal | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0.125 |
| *Glochidion assamicum* | Euphorbiaceae | Unknown | Others | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0.250 |
| *Garuga floribunda* var. *gamblei* | Burseraceae | Shade-tolerant | Others | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0.250 |
| *Saurauia macrotricha* | Saurauiaceae | Shade-tolerant | Animal | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.125 |
| *Maesa ramentacea* | Myrsinaceae | Pioneer | Animal | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.125 |
| *Garuga pinnata* | Burseraceae | Shade-tolerant | Others | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0.125 |
| *Alangium barbatum* | Alangiaceae | Shade-tolerant | Others | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.125 |
| *Canthium parvifolium* | Apocynaceae | Shade-tolerant | Others | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0.125 |

Others = gravity, ballistic and water; RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard

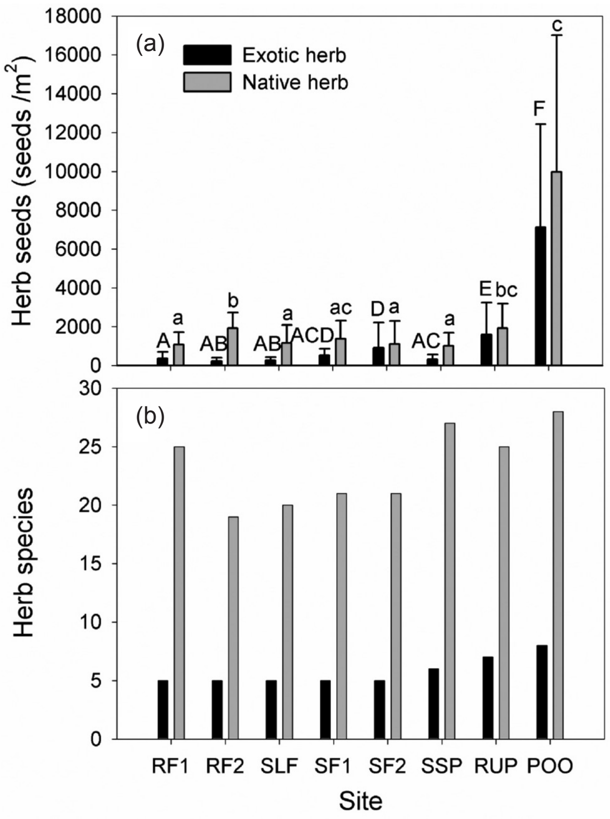


**Figure 3** Herb seed storage as determined by (a) seeds and (b) species in the eight sites (mean ± SD); different letters indicate significantly different sites at $p < 0.05$; RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard

compared with other forest sites in South-East Asia (Metcalfe & Turner 1998, Singhakumara et al. 2000), our results were comparable with other studies on soil seed bank in Xishuangbanna (Cao et al. 2000, Tang et al. 2006). The abundant seed storage of rainforest 1 and rainforest 2 might be attributed to the highly fragmented distribution of local seasonal rainforests. However, the soil seed banks of rainforest sites had fewer seeds than the soil seed banks of secondary forests and plantations surveyed in this study. A study on soil seed bank at different stages of succession in Xishuangbanna also found higher seed density and greater number of pioneer tree seeds in the secondary forest than in the rainforest (Cao et al. 2000).

Higher soil seed storage densities found in earlier phases of forest succession are due to higher fecundity and early reproduction associated with greater seed longevity of pioneer species than primary species, which predominate in secondary forest sites (Dalling & Brown 2009). Sites that were surrounded by extensively disturbed areas such as plantations and pastures had high soil seed storage densities and contained large numbers of seeds of light-demanding shrubs and herbaceous species because of the seed inputs of pioneer species (Quintana-Ascencio et al. 1996). The secondary forest 1 and secondary forest 2 in present study were naturally regenerated after slash-and-burn cultivation. Many pioneer species then germinated from the soil seed bank and newly dispersed seeds from nearby forest because no more farming practice took place in the sites since they were abandoned.

## Conversion of natural forest to plantation

Our study showed significant differences between the soil seed bank compositions of the rubber plantation and pomelo orchard with the soil seed bank compositions of other sites. Seeds of herbaceous species dominated the soil seed banks of the rubber plantation and pomelo orchard in terms of seed density and species number. These sites were intensively affected by human activities which eliminated tree seeds (Tables 2 and 3), although they significantly increased the seed abundance of herbs (Tables 2 and 4). Large soil seed banks of herbs were also observed in other studies. In Nigeria, herbaceous species made up 98% of the total seeds stored in citrus, oil palm, cashew and cocoa plantations; in contrast, only three woody species emerged from the soil seed bank of four plantations (Oke et al. 2007). In Mexico, only a few seeds of late successional tree species (< 2% of the species) were observed in the diverse soil samples that ranged from milpa fields to tropical rainforests (Quintana-Ascencio et al. 1996). Tree seedlings were continuously removed by repeated weeding in agricultural ecosystems. Thus, herbs and herbaceous seeds quickly dominated the seedling and soil seed bank respectively because of the short life cycle and high reproductive capacity of herbs. These changes eventually alter the soil seed banks composition, resulting in an abundance of herb seeds rather than seeds of successional woody species. These findings seem to suggest a deterministic role of intensive management in shaping soil seed banks in agricultural farming systems.

**Table 4** The 24 most abundant species of herb seeds stored in the soil seed banks of the eight sites

| Species | Family | Functional group | Seed dispersal | RF1 | RF2 | LSF | SF1 | SF2 | SSP | RUP | POO | Total | Frequency |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ageratum conyzoides* | Asteraceae | Exotic | Others | 2 | 4 | 0 | 7 | 5 | 9 | 169 | 845 | 1041 | 0.875 |
| *Torenia flava* | Scrophulariaceae | Native | Others | 18 | 0 | 19 | 19 | 2 | 6 | 4 | 720 | 788 | 0.875 |
| *Lindernia stricta* | Scrophulariaceae | Native | Others | 53 | 226 | 109 | 19 | 55 | 18 | 14 | 11 | 505 | 1 |
| *Saxifraga atolonifera* | Saxifragaceae | Native | Others | 0 | 0 | 0 | 37 | 44 | 2 | 5 | 226 | 314 | 0.625 |
| *Gonostegia hirta* | Urticaceae | Native | Animal | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 290 | 296 | 0.375 |
| *Crassocephalum crepidioides* | Asteraceae | Exotic | Wind | 20 | 21 | 17 | 26 | 25 | 18 | 42 | 54 | 223 | 1 |
| *Thysanolaena maxima* | Poaceae | Native | Others | 39 | 42 | 7 | 50 | 28 | 38 | 4 | 5 | 213 | 1 |
| *Isachne globosa* | Poaceae | Native | Others | 4 | 0 | 0 | 49 | 9 | 6 | 132 | 4 | 204 | 0.75 |
| *Spermacoce latifolia* | Rubiaceae | Exotic | Animal | 0 | 0 | 0 | 29 | 8 | 4 | 6 | 143 | 190 | 0.625 |
| *Conyza sumatrensis* | Asteraceae | Exotic | Wind | 9 | 5 | 13 | 12 | 10 | 9 | 26 | 71 | 155 | 1 |
| *Chromolaena odorata* | Asteraceae | Exotic | Wind | 3 | 5 | 9 | 11 | 98 | 11 | 1 | 5 | 143 | 1 |
| *Hedyotis corymbosa* | Rubiaceae | Native | Others | 1 | 3 | 0 | 1 | 7 | 8 | 35 | 58 | 113 | 0.875 |
| *Vernonia cinerea* | Asteraceae | Native | Wind | 9 | 11 | 12 | 6 | 10 | 23 | 27 | 5 | 103 | 1 |
| *Kyllinga monocephala* | Cyperaceae | Native | Others | 0 | 1 | 1 | 6 | 2 | 1 | 6 | 61 | 78 | 0.875 |
| *Euphorbia hirta* | Euphorbiaceae | Exotic | Others | 25 | 3 | 5 | 0 | 0 | 0 | 2 | 31 | 66 | 0.625 |
| Poaceae sp. 1 | Poaceae | Native | Others | 0 | 4 | 0 | 0 | 0 | 15 | 1 | 46 | 66 | 0.5 |
| *Cardamine flexuosa* var. *debilis* | Brassicaceae | Native | Others | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 49 | 49 | 0.125 |
| *Phyllanthus urinaria* | Euphorbiaceae | Native | Animal | 1 | 0 | 0 | 0 | 2 | 0 | 4 | 35 | 42 | 0.5 |
| Poaceae sp. 2 | Poaceae | Native | Others | 0 | 0 | 1 | 7 | 0 | 9 | 21 | 1 | 39 | 0.625 |
| *Cynoglossum amabile* | Boraginaceae | Native | Others | 16 | 0 | 0 | 9 | 0 | 11 | 2 | 0 | 38 | 0.5 |
| *Dichondra repens* | Convolvulaceae | Native | Others | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 34 | 35 | 0.25 |
| *Stevia rebaudiana* | Asteraceae | Exotic | Wind | 0 | 0 | 2 | 0 | 0 | 1 | 8 | 24 | 35 | 0.5 |
| *Digitaria chinensis* | Poaceae | Native | Others | 0 | 0 | 3 | 0 | 3 | 12 | 2 | 11 | 31 | 0.625 |
| *Ludwigia prostrata* | Onagraceae | Native | Others | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 25 | 27 | 0.375 |

Others = gravity, ballistic and water; RF1 = rainforest 1, RF2 = rainforest 2, SLF = selectively logged rainforest, SF1 = secondary forest 1, SF2 = secondary forest 2, SSP = *Senna siamea* plantation, RUP = rubber plantation, POO = pomelo orchard

## Pioneer tree species

Rapid growth and copious widely-dispersed seeds increase the probability of pioneer species reaching and settling in high light habitats. However, seedlings of shade-tolerant species experience rapid and high mortality because of reduced canopy shade (Swaine & Whitmore 1988). Forests with intermediate levels of disturbance have large soil seed banks dominated by pioneer tree species (Alvarez-Aquino et al. 2005). One of the most important tree species in the soil seed banks of secondary forest 1 and secondary forest 2 was *T. orientalis*. It is a short-lived pioneer tree species in the tropical Asia (Whitmore 1990). This tree species might even establish mono-dominant stands in abandoned, slash-and-burn fields (Cao & Zhang 1996). *Trema* seeds require disturbance of the soil surface and low canopy cover to increase light transmittance and stimulate germination respectively (Dalling et al. 1998). Therefore, *Trema* seeds may be stored in the soil seed bank under tropical forest canopies. Furthermore, dormant seeds lead to prolonged seed persistence of *Trema* in the soil (Dalling & Brown 2009). The most abundant tree group recorded in our study was fig with 9 species and 396 seeds. Fig seeds are photoblastic (Vázquez-Yanes et al. 1996).Therefore, these seeds may be stored in the soil seed bank because of poor light filtration through superficial soil (Bliss & Smith 1985).

## Exotic herbs

Exotic herbs are thought to be super competitors because of their lack of enemies, high resource-use efficiency and allelopathy (Callaway & Maron 2006, Funk & Vitousek 2007). Although herbs may not inhibit the settlement of tree seedlings (Aide & Cavelier 1994), several studies have shown that tree seedlings perform better after the clearance of herbs (Holl et al. 2000, Hooper et al. 2005). One of the most competitive exotic herbs observed in the present study was *C. odorata*. It is a perennial herb capable of forming dense canopy in degraded areas of the pan tropical region (Derouw 1991). Invasion of *C. odorata* was suggested as the primary factor responsible for poor regeneration of degraded forests in Ghana (Honu & Dang 2000).

Exotic herbs commonly occur in farmland and pastures. Exotic herbs need light for seed germination and seedling growth and can be excluded from the understorey by a closed forest canopy (Hooper et al. 2005). Most of the seeds stored in soil seed bank are dispersed on-site (Young et al. 1987). Thus, the seed inputs of exotic herbs were much higher in the rubber plantation and pomelo orchard than in the other forest sites, resulting in the soil seed banks of the rubber plantation and pomelo orchard containing more seeds of exotic herbs (Table 4).

## Seed availability and restoration potential

High seed storage of pioneer tree species represents higher restoration potential. The enrichment of pioneer species in the soil seed banks may accelerate the rate of secondary succession (Zimmerman et al. 2000). Pioneer trees are adapted to degraded environments and their seed germination can be induced by high light or fluctuating temperature created by disturbance in forests (Pearson et al. 2002). In contrast, seeds of weeds dominating soil seed banks in intensively-managed agricultural fields showed low restoration potential (Wijdeven & Kuzee 2000, Zimmerman et al. 2000). Low seed availability is one of the main barriers to tropical rainforest restoration after intensive disturbance (Standish et al. 2007). Therefore, we recommend that quantitative assessment on restoration potential be conducted by examining seed availability of pioneer tree species and competitive herb seeds in soil seed banks.

The numbers of pioneer tree and exotic herb seeds in in the soil seed bank were higher in secondary forests than in primary forests. Furthermore, there were roughly equal numbers of pioneer tree and exotic herb seeds in primary forests. Nevertheless, the seed storage of pioneer trees was higher than that of exotic herbs in secondary forests, especially in secondary forest 2. Thus, the soil seed banks of secondary forests might promote early forest restoration. Many exotic herbs and few pioneer trees emerged from the soil seed banks of the rubber plantation and pomelo orchard, suggesting that natural regeneration might be arrested in these areas.

## CONCLUSIONS

Soils from secondary forests had larger numbers and more species of pioneer tree seeds than rainforests. The conversion of natural forest into rubber plantations and pomelo orchards had exhausted stored seeds of tree species in the soil and increased the seed density of exotic herbs in the soil seed bank. Thus, there was low seed availability for forest restoration in the intensively-managed plantations and orchards. However, the addition of soil seed banks from secondary forests, which contained abundant seeds of pioneer tree species in abandoned plantations and orchards might promote natural regeneration of these sites.

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