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Soil seed banks in four 22-year-old plantations in South China: Implications for restoration

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ABSTRACT

To better understand the potentials of the soil seed banks in facilitating succession towards a more natural forest of native tree species, we quantified the size and composition of the soil seed banks in established plantations in South China. The seed banks were from four typical 22-year-old plantations, i.e., legume, mixed-conifer, mixed-native, and *Eucalyptus* overstory species. Species diversity in the seed banks was low, and the vegetation species differed from those found in the seed bank in each plantation. A total of 1211 seedlings belonging to eight species emerged in a seedling germination assay, among which *Cyrtococcum patens* was most abundant. All species detected were shrubs and herbs, and no viable indigenous tree seeds were found in soil samples. Size and species composition of the seed banks might be related to the overstory species compositions of the established plantations. The seed bank density in soils was highest in the mixed-conifer plantation followed by *Eucalyptus*, mixed-native, and legume plantations. Species richness among the seed banks of plantations was ranked as follows: *Eucalyptus* > mixed-conifer > mixed-native = legume. The results indicated that the soil seed banks of the current plantations are ineffective in regenerating the former communities after human disturbances. Particularly, the absence of indigenous tree species seeds in the seed banks would limit regeneration and probably contribute to arrested succession at the pioneer community stage. It would appear from these data that the soil seed banks under the current plantations should not be considered as a useful tool leading the succession to more natural stages. Introduction of target indigenous species by artificial seeding or seedling planting should be considered to accelerate forest regeneration.

1. Introduction

Forest plantation is widely accepted as an effective approach to restore and rehabilitate degraded habitats (Haggar et al., 1997; Parrotta et al., 1997; Cusack and Montagnini, 2004). The plantations often provide timber products and ecological benefits, such as soil erosion control (Wishnie et al., 2007) and carbon sequestration (Guo, 2007; Redondo-Brenes and Montagnini, 2006). In addition, plantations can act as catalysts to facilitate forest succession in the understory, thus improving microclimate and attracting dispersal agents (Parrotta et al., 1997; Carnevale and Montagnini, 2002; Jones et al., 2004).

In China, plantations cover 53 million hectares and account for 30% of the total forested area, with the highest proportion located in South China (SFA, 2005). The provincial governments in South China have been heavily engaged in revegetating degraded lands (i.e., abandoned farming land) since 1985, and the forest coverage in Guangdong Province in South China has increased from 26.7% in 1985 to 56.9% in 2006 (Lin et al., 2008). Unfortunately, many species are introduced and belong to a few dominant groups such as *Pinus*, *Eucalyptus*, and *Acacia* (Ren et al., 2007). Although plantations with these pioneer species show fast recovery of degraded lands and sometimes support native species (particularly in the understory), they do not lead to natural forests which typically comprise *Cryptocarya concinna*, *Cryptocarya chinensis* and *Aporosa yunnanensis*. In other words, succession does not result in forests that resemble the native forests in the area. Instead, succession in artificial forests of *Pinus*, *Eucalyptus*, and *Acacia* is arrested at the pioneer stage, which is characterized by simple structure, reduced biodiversity, and ineffective ecosystem functioning and services (Ren et al., 2002).

For the reasons mentioned above, currently in South China, increased forest production is not the only objective of plantation, and sustainable "naturalness forestry" is receiving considerable attention (Li, 2004). Biodiversity conservation and carbon sequestration are among several environmental factors in consideration.

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Because of the perceived unnaturalness of current plantations, silviculture management that encourages acceleration of plantation succession to more natural stages is urgently needed (Ren et al., 2007).

Cost-effective forest regeneration, especially natural regeneration (i.e., regeneration of native tree species), is the keystone of sustainable forestry (Jonasova et al., 2006; Leinonen et al., 2008). Natural forest regeneration depends on the soil seed bank. The soil seed bank, and in particular the long-lived seed species, can buffer against environmental variability because it can provide new seedlings to re-establish the 'native' community after disturbances (Hyatt and Casper, 2000; Satterthwaite et al., 2007). Also, soil seed banks can be a source of colonizing species that can restore degraded ecosystems or accelerate forest succession (Augusto et al., 2001; Luzuriaga et al., 2005). The composition of the seed banks mainly depends on seed production and composition of the seed sources, which consist of current and previous vegetation. In managed forests, the quantitative and qualitative characteristics of the seed banks are often affected by the silvicultural management (Augusto et al., 2001; Godefroid et al., 2006).

Both lack of seeds of desirable species in the seed banks and unfavorable environmental conditions for seed germination and seedling establishment (Shono et al., 2006) can substantially limit colonization by indigenous tree species and thus hamper succession. Therefore, to better understand regeneration in artificial forests, we need to analyze the size and species composition of soil seed banks in plantations and to identify factors contributing to succession. Yet, to date, there is little knowledge about the soil seed banks in the plantations in South China.

In this study, we investigate the composition of the soil seed banks in four typical plantations in South China, i.e., a mixed-native plantation, a mixed-conifer plantation, a *Eucalyptus* plantation, and a legume plantation. Specifically, we address the following questions: (1) are there differences in size and species composition of the soil seed banks among the four plantations? (2) What is the relation between the soil seed bank and aboveground vegetation? (3) How does overstory community composition affect the size and species composition of the soil seed banks? (4) Does the soil seed bank have the potential in forest regeneration? Finally, we test the hypotheses that the inhibited succession of established plantations is due to lack of seeds of indigenous tree species.

2. Methods

2.1. Study site

The study site is located at Heshan National Field Research Station of Forest Ecosystem, Chinese Academy of Science (112°54′E, 22°41′N), Heshan City, Guangdong, South China. This site is characterized by a typical subtropical monsoon climate with a mean annual temperature of 21.7 °C. The mean annual rainfall is 1700 mm, which is concentrated between May and September. The mean annual evaporation is approximately 1600 mm, and the elevation ranges from 0 to 90 m. The soil is acrisols. The zonal climax vegetation is lower subtropical monsoon evergreen broad-leaved forest (typically comprise *C. concinna*, *C. chinensis* and *A. yunnanensis*), the closest remnant is located at Dinghushan Mountain, about 70 km north of the research station. The closest Fengshui forests (i.e., secondary forest, generally, it is close to village and consists of native tree species) are approximately 3 km from the experimental plantations. In 1984, experimental plantations were established by native and introduced species on similar degraded hilly land (such as topography, soil properties, vegetation composition) in order to restore the degraded systems and to study the restoration process. The dominant species before experimental plantation species were established were shrub and herbaceous species, such as *Ischaemum indicum*, *Eriachne pallescens*, and *Baeckea frutescens*. The experimental plantations were as follows: mixed-conifer species plantation (3.17 ha), the main established species were *Pinus massoniana* and *Cunninghamia lanceolata*, which were native pioneer species; legume plantation (4.58 ha), the main established species was *Acacia mangium*, which was exotic species; *Eucalyptus* plantation (1.79 ha), the main established species was *Eucalyptus exserta*, which was exotic species; mixed-native plantation (2.68 ha), the main established species were *Schima superba* and *Cinnamomum burmanii*, which were native and late-successional stage species. Generally, those tree species can produce seeds after 10 years old and the seeds are not dormant (Yu and Peng, 1996). After trees were planted at 2.5 m × 2.5 m spacing, all four plantations were left to develop naturally without anthropogenic disturbance.

2.2. Seed bank sampling and vegetation survey

In September 2006, two parallel transects (5 m × 25 m) with the same slope were established 10 m apart in each plantation. Each transect was divided into five quadrants (5 m × 5 m) with a subplot (1 m × 1 m) located at the centre of each quadrant. Six soil samples of 10 cm × 10 cm × 10 cm with litter intact were randomly and carefully excavated from each subplot. The soil samples were split into two depth classes: 0–5 cm and 5–10 cm, and the six soil samples were pooled for each subplot and depth class, as suggested by Bossuyt et al. (2002).

To assess the seed abundance (density) and species composition in the seed banks, we conducted seed germination experiment. Germination assays were performed following the procedures by Grime (1989). Each soil sample was first passed through a 2-mm sieve to remove coarse debris. Seeds with diameter >2 mm were retrieved and returned to soil samples. Each soil sample was spread on a layer of heat-sterilized (120 °C for 10 h) sand (2 cm thick) in a seed germination tray. All germination trays were placed in an experimental greenhouse and watered daily to keep the soil moist. Newly germinated seedlings that were identified at the species level were counted and then removed from the seed trays every 2–5 days. Unidentified seedlings were transplanted into additional germination trays for further growth until the species could be identified. Five seed trays filled with sterilized sand only were used as a control for seed contamination of the sand; no seedlings were found in these control trays. The germination assay continued until no new seedlings emerged for 4 weeks (Wang et al., 2009). The mean temperature in the greenhouse was 28 °C, and the mean relative humidity was 65.9%.

For comparisons between the seed banks and aboveground vegetation, in each quadrant, the species name and its coverage of each seed plant was estimated visually. All vegetation surveys were done just after soil sampling finished. The naming of the seed plant followed a modified Englerian system (Wu and Raven, 1994). Meanwhile, we selected a 1 m × 1 m subplot randomly in each quadrant and collected the standing leaf litter on the ground. The collected leaf litter was oven dried at 65 °C for 72 h and then weighed.

2.3. Data analysis

Seed density, measured by the number of seedlings per square meter, was calculated from the number of emerged seedlings. Differences in the numbers of germinated seedlings, the number of species in the soil seed banks, standing leaf litter biomass among different communities and between the two soil layers were analyzed using one-way ANOVA tests followed by LSD tests when ANOVAs were significant. Statistical analyses were performed with

SPSS 11.5 for Windows (Li and Luo, 2005). Similarities in species composition between the soil seed banks and corresponding vegetation were analyzed using Sorensen similarity index (SI), $SI = 2a/(b + c)$, where a refers to the number of species common to both the seed bank and the aboveground vegetation, and b and c represent total number of species detected in the seed bank and the corresponding aboveground vegetation, respectively (Cox, 1985; Arroyo et al., 1999).

3. Results

3.1. Standing leaf litter biomass

The standing leaf litter biomass on forest floors of the four plantations was as follows: legume (1124 ± 134 g m^{-2}) > mixed-native (877 ± 107 g m^{-2}) > mixed-conifer (741 ± 134 g m^{-2}) > *Euca-Eucalyptus* (362 ± 38 g m^{-2}). Significant differences in the standing leaf litter biomass were found among the four plantations ($F = 7.009$, $P = 0.001$).

3.2. Seed density

Table 1 shows the number and spatial distribution of viable seeds in the seed banks in the four plantations. A total of 1211 seedlings were recorded from all soil samples with an overall seed density of 503 seeds m^{-2}. The size of the soil seed banks significantly differed among the four plantations ($F = 6.255$, $P < 0.01$). The seed bank density was ranked as follows: mixed-conifer > *Eucalyptus* > mixed-native > legume. The overall vertical distribution of viable seeds in the soil samples from all the communities was similar. Seed abundance was significantly higher in the 0–5 cm soil layer than in the 5–10 cm layer. There were significant differences in the numbers of seedlings germinated in the two soil layers from all communities except the mixed-conifer (Table 1).

Table 1
Spatial distribution and seed density (mean ± SE) of the soil seed banks in the four plantations and the results from LSD test after one-way ANOVA.

Plantation type	Seedlings germinated		Seed density (seeds m^{-2})
	0–5 cm	5–10 cm	
Mixed-conifer	432	147	$967 \pm 461^{a,NS}$
Legume	74	28	$170 \pm 28^{b,**}$
Mixed-native	179	74	$422 \pm 92^{a,*}$
Eucalyptus	211	66	$455 \pm 115^{a,*}$

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{NS}P > 0.05$. Seed densities marked with a and b indicate that they were significantly different from each other.

3.3. Species composition

Species composition of the four soil seed banks is shown in Table 2. In total, eight species (four shrubs and four herbs) were detected. Two species (*Cyrtococcum patens* and *Trema tomentosa*)

Table 2
The mean cover of seed plant species (%) in the aboveground vegetation (av) and mean seed density (seeds m^{-2}) in the soil seed bank (sb).

Species	Mixed-conifer		Legume		Mixed-native		*Eucalyptus*	
	av	sb	av	sb	av	sb	av	sb
Trees and shrubs								
Pinus massoniana	37.5	0	0	0	0	0	0	0
Cunninghamia lanceolata	28.3	0	0	0	0	0	0	0
Acacia mangium	0	0	26.5	0	0	0	0	0
Schima superba	0	0	0	0	43.2	0	0	0
Cinnamomum burmanii	0	0	0	0	38.5	0	0	0
Eucalyptus exserta	0	0	0	0	0	0	34.7	0
Mallotus apelta	0.2	0	0	0	0	0	0	0
Trema tomentosa	1.5	120	6	38	3.7	85	0.1	67
Clerodendrum fortunatum	9.5	0	0.9	0	2.4	0	1.4	0
Gardenia sootepensis	1.6	0	0.6	0	0.7	0	0.4	0
Wikstroemia indica	0.1	0	0	0	0	0	0	0
Ilex asprella	21.9	0	4	0	4.5	0	9	0
Eurya chinensis	5.3	0	0.2	0	0.7	0	2.6	0
Evodia lepta	9.9	75	4.8	25	4.4	0	30.2	40
Litsea cubeba	3	0	0.7	0	2.1	0	4.8	3
Rhodomyrtus tomentosa	0.8	0	9.6	0	0	0	0.2	0
Rubus alceaefolius	1	0	0	0	0	0	6.8	0
Melastoma candidum	0.5	0	0	0	0.6	0	0	0
Toxicodendron succedaneum	1	0	0	0	0	0	0	0
Mussaenda pubescens	2.2	0	0.1	0	6	0	1.7	0
Smilax china	0	0	0.1	0	0.2	0	0.1	0
Embelia burmanii	0	0	3.9	0	7	0	2.9	0
Psychotria rubra	0	0	0	0	1	0	0	0
Schefflera octophylla	0	0	0	0	0.1	0	0	0
Ficus hirta	0	0	0	0	0.1	0	0	0
Rhaphiolepis indica	0	0	0	0	0	0	0.4	0
Rhus chinensis	0	0	0	0	0	0	0.3	2
Herbs								
Lophatherum gracile	0.5	0	0	0	2.5	0	0	0
Polygonum chinense	1.2	0	0	0	0	0	0	0
Dianella ensifolia	1.1	0	0	0	0.3	0	0.1	0
Cyrtococcum patens	30.7	630	1.3	100	10.7	267	11.5	322
Melastoma dodecandrum	8.5	127	0	0	1	70	4.5	23
Eupatorium odoratum	0	0	0	0	0	0	0	5
Centella asiatica	0	13	0	0	0	0	0	0
Vine								
Ampelopsis cantoniensis	0.1	0	0	0	0	0	0	0
Total number of species	22	5	13	3	19	3	18	7

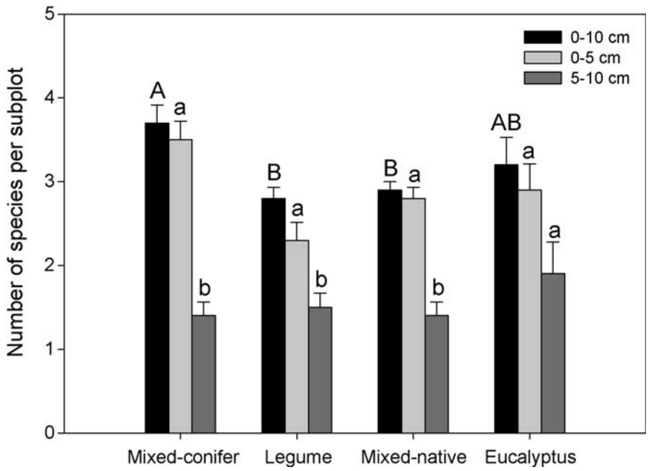

Fig. 1. Number of species per subplot in the seed banks of the four plantations (mean ± SE). A and B indicate the differences ($P < 0.05$) between 0 and 10 cm soil layers of different plantations, whereas a and b indicate the differences ($P < 0.05$) between the upper and lower soil layers in the same plantation, based on the LSD test after one-way ANOVA.

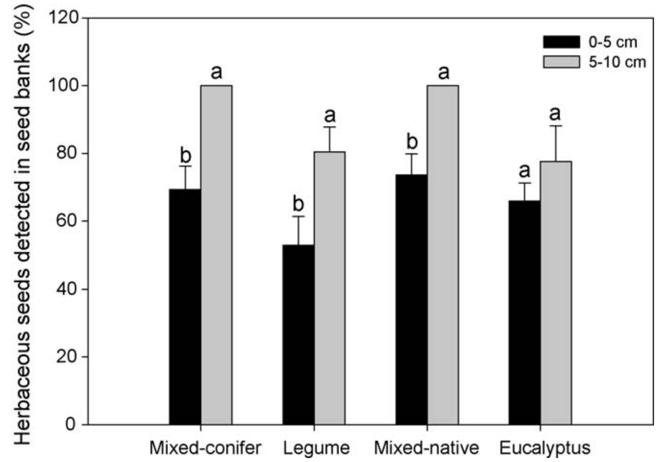

Fig. 2. Percentage of herbaceous seeds detected in each sampling subplot of the four plantations (mean ± SE). a and b indicate differences ($P < 0.05$) between the upper and lower soil layers in the same plantation, based on the LSD test after one-way ANOVA.

were common in all seed banks. Species richness was generally low in each plantation and the number of species detected from soil samples in each subplot differed significantly among the four plantations ($F = 3.63$, $P < 0.05$). The mean number of species per subplot of plantations was ranked as follows: (mixed-conifer = *Eucalyptus*) > (mixed-native = legume) (Fig. 1). However, the total number of species in the soil seed banks was ranked as follows: *Eucalyptus* > mixed-conifer > legume = mixed-native (Table 2). In all plantations, species richness was significantly less in the deep soil layer than in the upper soil layer, except in the *Eucalyptus* plantation (Fig. 1).

The most frequently detected species was *C. patens*, which was found in all sampling subplots in each plantation. In addition, the seed density of *C. patens* was much higher than that of other species in each plantation's seed bank, accounting for 65.2, 58.8, 44.8, and 63.2% of germinated seedlings in the seed banks from the mixed-conifer, legume, mixed-native, and *Eucalyptus* plantations, respectively. Many species were found only in the upper soil layer, such as *Rhus chinensis* and *Evodia lepta* in the *Eucalyptus* plantation.

There were approximately equal numbers of herbaceous and woody species detected in the seed banks in the four different plantations (Table 2). However, the numbers of seeds of herbaceous species were much higher than those of woody species in all the soil seed banks (Fig. 2). In the soil samples from each plantation, more than 50% of germinated seedlings were herbaceous. More herbaceous seeds were found in the lower than in the upper soil depth; the abundance of herbaceous seeds differed significantly between the 0–5 cm and 5–10 cm soil layers in all plantations except *Eucalyptus*. The 5–10 cm soil layer from the mixed-conifer and mixed-native species plantations had only seeds of herbaceous species.

3.4. Correlations between seed bank and aboveground vegetation

A total of 33 seed plant species were found in the aboveground vegetation, six of which were also detected in the soil seed banks (Table 2). The mixed-conifer plantation contained relatively more understory species than the other plantations. In the understory of the conifer and mixed-native plantations, there was relatively high grass coverage, and the vegetation was dominated by shade-tolerant shrubs, such as *Litsea cubeba*. The understory vegetation of the legume plantation was similar to that of the *Eucalyptus* plantation, consisting of tall shrubs in both cases.

In all four plantations, species richness of the standing vegetation was much higher than that of the seed bank. Many species conspicuous in the vegetation, such as *Mussaenda pubescens*, *Eurya chinensis*, and *Ilex asprella*, were absent from the seed banks. However, a range of 80–100% of the species in the seed banks were also present in aboveground vegetation, including the most abundant species (*C. patens*) and other species such as *R. chinensis*, *T. tomentosa*, and *L. cubeba*. The Sorensen similarity index indicated that the similarity between vegetation and soil seed banks was not high. The values of the Sorensen similarity index for the four plantations ranged from 0.261 to 0.48, with the highest value in the *Eucalyptus* plantation (Table 3).

4. Discussion

4.1. Seed bank composition

The seed densities recorded in our study are within the range previously reported for established plantations elsewhere in China, i.e., 67–1088 seeds m^{-2} in subalpine spruce forests (Yin and Liu, 2005), 220 seeds m^{-2} in a conifer plantation (Zheng et al., 2004), 649 seeds m^{-2} in a *Larix principis-rupprechtii* plantation, and 839 seeds m^{-2} in a *Robinia pseudoacacia* plantation (Wang and

Table 3
A comparison between standing vegetation and the soil seed banks in the four plantations.

Plantation type	Number of species found in the seed banks	Number of species found in vegetation	Number of species both in vegetation and the seed banks	Similarity between vegetation and the seed banks (Sorensen similarity index)
Mixed-conifer	1	18	4	0.296
Legume	0	12	3	0.375
Mixed-native	0	25	3	0.261
Eucalyptus	1	17	6	0.48

Ren, 2004). Compared to the natural forests in the same region (Wei et al., 2005), greater seed density and fewer species are found in soils of plantations. Because the soil seed banks to some degree reflect vegetation (Pugnaire and Lazaro, 2000; Ren et al., 2007), the generally low species richness in the soil seed banks may be related to the relatively low species richness in the vegetation.

Consistent with observations from the seed banks of plantations established on degraded hilly land elsewhere in South China (Zheng et al., 2004), herbaceous species also dominate the soil seed banks at our study sites. Nearly 78% of seeds in the soil seed banks are herbaceous. Moreover, there are more herbaceous seeds in the 5–10 cm soil layer than in the 0–5 cm soil layer. The high density of herbaceous seeds in the seed bank may be related to species traits. An early study reports that herbaceous seeds in the soil remain viable for longer than other seed types (Ghersa and Martinez-Ghersa, 2000). Seed persistence in soil is also related to microsite conditions that partially regulate seed germination or dormancy (Reuss et al., 2001). As plantations mature, the increasingly shaded conditions of the understory would inhibit germination of light-requiring herbs.

Our results show lower species richness and seed density in the lower soil layer than in the upper soil layer in all plantations. This pattern may be attributed to seed size (Decocq et al., 2004) and the vertical movement of seeds (Guo et al., 1998), an explanation supported by the current study's finding that large-seeded species such as *L. cubeba* only appear in the upper soil layer while the smaller seeds of herbaceous species dominate in the lower soil layer.

Although aboveground and belowground species compositions are often related, the relationship is not as strong as expected. This is especially the case in artificial forests (Augusto et al., 2001; Sakai et al., 2005; Godefroid et al., 2006). Many dominant species, including some overstory species, are absent from the soil seed banks. Previous research has shown that existence and persistence of seeds in the soils are partially influenced by seed production and intrinsic attributes of seeds (Luzuriaga et al., 2005). Ren et al. (1996) finds that *A. mangium* in this region does not produce seeds. Thus, it is not surprising that *A. mangium* seeds are very rare in the soil seed banks in the legume plantation. The scarcity of coniferous species in the seed banks probably reflects the short persistence of their seeds in the soils (Hill and Stevens, 1981). The relative abundance of seeds of *P. massoniana* in the mixed-conifer seed banks probably reflects the production of many seeds with short persistence; i.e., these seeds are relatively transient. Seed size may be another factor responsible for the scarcity of many aboveground species in the seed banks, because seed size and seed longevity are often negatively correlated (Bossuyt et al., 2002). In our study, the large-seeded *L. cubeba* is among the least abundant species in the seed banks, while the small-seeded herbaceous species, *C. patens*, is the most abundant species in the seed banks. However, the results of our study cannot fully explain why the soil seed banks contain very few seeds of some species with high seed production. Further studies are clearly required to clarify this.

4.2. Comparison of soil seed banks among different plantations

Despite the differences in species richness in the soil seed banks, the plantations shared many common species. In this instance, species compositions of the soil seed banks in our study are similar among the four plantations. Our results are in contrast with previous studies that the characteristics of seed banks are largely affected by established plantation species (Augusto et al., 2001; Godefroid et al., 2006). All the four plantations studied here are established on previously similar degraded land (Yu and Peng, 1996). Furthermore, the absence of natural vegetation nearby leads to limited seed input into those four plantations. Although the light availability in the understory of those plantations is different (light transmittance varied from 29.9 to 38.3%) (Yu and Peng, 1996), such differences are not sufficient to result in intrinsic distinction in seed bank composition among the plantations.

However, species richness of the seed bank is relatively low in legume and mixed-native plantations compared with other two plantations. Environmental conditions clearly play important roles in forming the soil seed banks (Arevalo and Fernandez-Palacios, 2000; Godefroid et al., 2006). For example, the plantation cover substantially affects the light penetrating into the understory and thereby modifies soil moisture and temperature (Lin et al., 2003). Seeds in the soil of mixed-native plantation tend to rot under the conditions of high soil moisture (Duan et al., 2008). Also, as reported elsewhere (Igarashi and Kiyono, 2008), leaf litter accumulation on the ground and leaf characteristics of the overstory species can greatly affect the size and composition of soil seed banks. In our study, the broad-leaved species *S. superba* and *A. mangium* have larger leaf area than *P. massoniana* and *E. exserta*. The standing leaf litter biomass on forest floors of the legume and mixed-native plantations is relatively high. When leaf litter is dense, as is in the broad-leaved plantations, seeds that drop onto the forest floor from parent plants in the community or that are dispersed from forest areas outside the plantation have less chance of penetrating the soil layer and become part of the seed banks.

Prolonged periods of high moisture could also result in loss of seeds through increased mortality (Sester et al., 2006). The climate of South China is usually characterized by humid and wet conditions throughout the first half of the year. Under such conditions, loss of seeds on the soil surface could occur, leading to formation of a seed bank that does not reflect the diversity of the aboveground vegetation. This may explain the low species richness of the soil seed banks in spite of the relatively high species richness of the aboveground vegetation in the mixed-native plantation. In this respect, plantations established with native species such as *S. superba* and *C. burmanii* do not necessarily form the soil seed banks that can facilitate forest regeneration. Because of the better performance in ameliorating soil properties and microclimate conditions, plantations established by indigenous tree species are receiving considerable attention in South China (Yu and Peng, 1996). However, the characteristics of the soil seed banks under plantations established by other indigenous tree species commonly appeared in the climax vegetation still need further studies.

4.3. Contribution of seed banks to forest regeneration

One of the main objectives of this study is to evaluate the potential of the soil seed bank in plantation regeneration. The soil seed banks of the plantations in the current study contain relatively few species and are dominated by herbaceous species. In addition, seed density and species richness significantly decrease with soil depth, indicating a transient soil seed bank under these established, 22-year-old plantations. These findings suggest that the previous communities on the sites of these plantations make only a small contribution to the seed banks. Moreover, all woody species detected in the seed banks are also found in the aboveground vegetation, and no viable seeds of indigenous tree species are detected. These results indicate that the soil seed banks of current plantations play a minor role in forest regeneration and yet vegetation outside the plantations makes minimum contribution to the composition of seed banks. Under the new government regulations, local foresters and forest managers are maintaining the plantations to develop naturally, so that those plantations can eventually succession into natural forests with more native species. However, the lack of native seeds in the soil seed bank will restrict the natural succession of established plantations to more diverse communities and to a more natural state. Therefore, as also previously noted by Decocq et al. (2004), sustainable forestry should not rely on such existing soil seed banks. Silvicultural managements such as thinning or soil disturbance which can stimulate forest regeneration from soil seed banks (Luzuriaga et al., 2005; Sakai et al., 2005) would not be effective in this case. As a result, the lack of seed availability is the main factor limiting the succession of current plantations in South China. Introduction of indigenous species may be an effective method in facilitating the plantation succeeding to a more natural stage (Hardwick et al., 1997).

Undisturbed primary forests may serve as major seed sources for indigenous tree species, and seed dispersal from adjacent natural forests plays a major role in the recolonization of native species (Lee et al., 2005; Lemenih and Teketay, 2005). Because of intensive human activities at our experimental sites, the original or virgin forests are scarce or patchy. For example, the nearest well-protected forests are approximately 3-km from the experimental plantations. Therefore, native tree species are rarely found in both understory vegetation and the soil seed banks. At the same time, bird and mammal communities in the plantations are small and low in species diversity (Zou and Yang, 2005), thus the limited seed dispersal agents may also have contributed to the lack of natural regeneration (Carnevale and Montagnini, 2002; Shono et al., 2006).

5. Conclusion

In general, species compositions of the soil seed banks are similar among the four plantations. The characteristics of the soil seed banks at the study sites reflect the overstory compositions of the established plantations as the soil seed banks include common shrub and herbaceous species found in the aboveground vegetation. The soil seed banks in the 22-year-old plantations are unlikely to be an important seed source for diversifying the vegetation and to facilitate the regeneration of native vegetation. For this reason, it would be necessary to introduce target indigenous species by artificial seeding or planting at least initially so that the native species seed banks may be developed in the future. To better understand the mechanisms limiting the succession of plantations, further studies linking soil seed banks with seed rain and seedling recruitments are required.

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