

Xiaoshuang Li · Wenyao Liu · Cindy Q. Tang

The role of the soil seed and seedling bank in the regeneration of diverse plant communities in the subtropical Ailao Mountains, Southwest China

Received: 5 October 2009 / Accepted: 14 June 2010 / Published online: 16 July 2010
© The Ecological Society of Japan 2010

Abstract We compared species composition and diversity of the soil seed and seedling banks in three secondary vegetation types (shrubland, *Populus bonatii* forest, *Lithocarpus* regrowth forest) and a primary old-growth forest in the subtropical Ailao Mountains of southwestern China to clarify the importance of seed and seedling banks for forest dynamics. The average species richness was the highest in soil samples from the shrubland (26.80 ± 1.98), and the lowest from the primary forest (9.93 ± 0.50). The density of germinable tree seeds increased from the secondary vegetation to the primary forest, and the density of shrub, forb, and graminoid seeds decreased significantly. The most abundant seedlings recorded in soil samples were light-demanding species in the shrubland and *Populus bonatii* forest. For ground flora, the number of shrub seedlings strongly decreased with the increase in stand age, and shade-tolerant tree seedlings tended to increase. The species similarity between the seed bank and the aboveground vegetation in all sites was low (Sørensen's index = 0.11–0.33), however, the shrubland had higher similarity compared with the other three plant commu-

nities. In the primary forest, light-demanding woody species dominated in soil seed banks, while shade-tolerant species dominated in the overstory and the forest floor. In the primary forest, seedlings of dominant tree species were rare in the understory, and no seeds of the dominant species were found in the soil. Results indicated that the early stages of vegetation recovery should take into account the possibility of recovering soil seed bank processes. However, colonization and establishment of tree seedlings will be difficult once a primary forest is destroyed.

Keywords Seed bank · Seedling bank · Regeneration · Primary forest · Secondary vegetation

Introduction

Evergreen broad-leaved forests, dominated by the families Fagaceae, Lauraceae, and Hamamelidaceae, were once widely distributed in humid areas at mid-latitudes in the northern hemisphere (Kira 1991; Tagawa 1995). Of China's various vegetation types, the subtropical evergreen broad-leaved forest occupied the largest area. This type of forest was largely destroyed by human activities including deforestation, logging, fire, and unsustainable agricultural practices (Wu et al. 1987), after which regeneration requires several plant life cycles, including seed production and seedling or sapling establishment and survival (Harmer 1995). Seed banks are understood to be integral to many plant communities (James et al. 2007) and can be used to predict secondary succession (Pakeman and Hay 1996).

Previous studies concerning seed banks have mainly been concerned with temperate forests, heathlands, grasslands, and pastures, and largely confined to Europe and North America (Hopfensperger 2007). Studies also have been done on tropical ecosystems (Alvarez-Buylla and Martínez-Ramos 1990; Tang et al. 2006). Most of them have focused on the spatial distribution of seeds in soil (Pazos and Bertiller 2008), seed density, species

X. Li · W. Liu (✉)
Key Laboratory of Tropical Forest Ecology, Xishuangbanna
Tropical Botanical Garden, Chinese Academy of Sciences,
Kunming 650223, China
E-mail: liuw@xtbg.ac.cn
Tel.: +86-871-5153787
Fax: +86-871-5160916

X. Li
Graduate School of the Chinese Academy of Sciences,
Beijing 100039, China

W. Liu
School of Environmental Biology,
Curtin University of Technology, Perth, WA 6845, Australia

C. Q. Tang (✉)
Institute of Ecology and Geobotany, Yunnan University,
Kunming 650091, China
E-mail: cindytang@ynu.edu.cn
Tel.: +86-871-2263598
Fax: +86-871-5321702

richness, composition of the soil seed bank (Lemenih and Teketay 2006), effects of environmental factors on seed bank dynamics (Kitajima and Tilman 1996), and the similarities between species composition in the seed bank and the aboveground vegetation (Zobel et al. 2007). However, the seed bank characteristics of subtropical evergreen broad-leaved forests have not received adequate attention. The regenerative potential of seed banks in the subtropics is also little known.

The most reliable indicator of successful restoration of forest communities is likely to be the number, composition, and life form (tree vs. shrub) of the woody seedlings colonizing naturally (Hughes and Rood 2003). At the seedling stage, however, a high rate of mortality occurs (Burslen et al. 2000), mainly caused by factors including pathogenic fungi (Cruz-Rodríguez and López-Mata 2004), herbivores (Clark and Clark 1985), water stress (Poorter and Hayashida-Oliver 2000), and limitations on nutrients (McKinley and Van Auken 2005) and light (Benítez-Malvido et al. 2005). So, the seedling stage represents a demographic bottleneck for most populations, particularly those of species that do not have the ability to grow clonally (Messaoud and Houle 2006).

Nowadays, most studies on woody seedling regeneration, particularly of dominant species, have concentrated on the dynamics of seedlings or their contributions to regeneration in natural gaps (Walker 2000). Relatively few studies have elucidated the changes in the distribution of life forms for different ecological traits such as light requirements, and few have evaluated the regenerative potential of woody seedlings along a gradient of successional stages.

Thus, the objectives of this study were to (1) describe the species composition of the soil seed bank and the woody seedlings based on different light-demand levels in the sites; (2) evaluate the species richness, density, and life forms preserved in the soil seed bank and seedling bank in secondary and primary forests; (3) examine the relationship between the seed bank and aboveground vegetation and characterize the relationship among the seedling bank and saplings, poles, and trees; (4) evaluate the role of the seed bank and seedlings in the regeneration of the plant communities. We also hypothesized that the contribution of the seed bank to regeneration may be important in early stages of succession, and that with time the seedling bank gains in importance.

Materials and methods

Study area

The study area was in the Xujiaba region (2000–2650 m asl), a key area of the Ailao Mountain National Nature Reserve, covering 5100 ha on the northern crest of the Ailao Mountains in south-central Yunnan (23°35′–24°44′N, 100°54′–101°30′E). Meteorological observations (1982–1992) at the Forest Ecosystem Research

Station, Xujiaba (24°32′N, 101°01′E, 2450 m asl) show an annual mean precipitation of 1931.1 mm (85% in the rainy season from May to October). Annual evaporation is 1485.5 mm (23% less than precipitation). Annual mean air temperature is 11.3°C (from 5.4°C in January to 16.4°C in July). The mean active accumulated temperature above 10°C is about 3420°C, making this area similar to the warm temperate zone (Liu et al. 2002). Natural disturbances most commonly affecting forests in the Ailao Mountains are strong winds and the occasional cold spells that may be accompanied by snowfall. The soil under the evergreen broad-leaved forest is a typical yellow-brownish earth, with abundant organic matter (20–31%) and nitrogen content (0.7–1%). Parent rock is mainly schist, gneiss, and diorite. Soil texture is loamy, with acidic pH (4.2–4.6) (Tang et al. 2007). The thickness of the litter layer covering almost all the soil surface is about 3–7 cm.

In Yunnan, the evergreen broad-leaved forest is represented by trees of the genera *Lithocarpus* and *Castanopsis*. This forest is distributed mainly on subtropical mountains with an elevation of 2000–2600 m. With its abundance of rainfall, middle elevation, and high humidity, this forest type has been designated as “mid-montane humid evergreen broad-leaved forest” in Yunnan (Jin 1983; Wu et al. 1987; Bureau of Environment Conservation of Yunnan 1998; Tang et al. 2007; Tang and Ohsawa 2009) and represents the predominant vegetation of Xujiaba. As a result of deforestation, logging, fire, unsustainable agricultural practices, or grazing, only secondary patches are found around a reservoir or in the frontier zone of the Ailao Mountain National Nature Reserve.

Physiognomic attributes and information from local farmers were used to select the study sites. The three secondary plant communities and the primary evergreen broad-leaved forest were chosen as follows:

1. A shrubland (henceforth SL), mainly distributed in the frontier zone of the reserve. The shrubland is a consequence of severe damage to the evergreen broad-leaved forests from agriculture and repeated burning/grazing. The most abundant species are *Eupatorium adenophorum*, *Lyonia ovalifolia*, *Hypericum uralum*, *Gaultheria forrestii*, and *Osbeckia opi-para*. Until 1987, this site was used to grow corn, potatoes (*Solanum tuberosum* L.), and buckwheat (*Fagopyrum esculentum* Moench.).
2. A *Populus bonatii* secondary forest (henceforth PBF) resulting from cutting during reconstruction of the Xujiaba reservoir in the middle of the last century (Sheng and Xie 1991). The dominant tree species are *P. bonatii*, *L. xylocarpus*, and *Vaccinium duclouxii*.
3. A *Lithocarpus* regrowth forest (henceforth LRF). The many regenerated trees indicate that *Lithocarpus* was probably cut for timber and/or grazing but not for cultivation. When the reservoir was initially constructed about 100 years ago, some surrounding forest was cut; it is now regenerating into a secondary evergreen broad-leaved forest having mostly the same

- dominant species as the primary forest (Young et al. 1992).
4. Primary forest (henceforth PF). The primary moist evergreen broad-leaved forest has two tree layers and subordinate shrub layers, as well as abundant epiphytes. The upper canopy of the forest is 18–25 m high and contains a number of tree species including *L. chitungensis*, *L. xylocarpus*, *Manglietia insignis*, *Machilus bombycina*, *Illicium macranthum*. Shrub, bamboo, and ground cover herbs occur in localized patches (Tang et al. 2007). Various epiphytes, climbing plants, ferns, and mosses grow on tree trunks and branches, exposed rock, and dead wood (Young and Herwitz 1995).

Vegetation and seed-bank sampling

Vegetation and seed-bank samples were taken at the same locations for each site studied. Vegetation composition of each site was sampled in sixteen 40 × 5 m transects (with at least 5 m between transects). We subdivided each transect into four 5 × 5 m plots (5 m between plots). We identified and measured the height and diameter of all live woody plants 1.3 m or greater in height. All woody individuals < 1.3 m tall were identified and counted in the 5 × 5 m plots. Within each plot, we characterized all woody plants into the following size classes: (1) stage 1 (S1) ≥ 0.2 m tall and < 1.3 m tall for tree species, and ≥ 0.2 m tall and < 0.5 m tall for shrub species, (2) stage 2 (S2) ≥ 1.3 m tall and < 5 cm DBH for tree species, and ≥ 0.5 m tall and < 1 m tall for shrub species, (3) stage 3 (S3) ≥ 5 cm DBH and < 10 cm DBH for tree species, and ≥ 1 m tall for shrub species, (4) stage 4 (S4) (stems ≥ 10 cm DBH). In this paper, seedlings belong to S1, saplings to S2, poles to S3 for both shrub and tree species, and trees to S4.

Seed bank data were collected by a seedling germination method. Soil sampling for investigation of the seed bank was done in late April 2008, just prior to natural germination of seeds. One soil core (10 × 10 × 10 cm) was taken from the center of each 5 × 5 m plot in each stand site. A total of 256 samples were collected. After removing gravel, litter, and roots, the soil samples from each soil core were placed separately in cloth bags and transported to a glasshouse and were then spread out into a thin layer (about 2 cm) on plastic trays for germination. Before the soil was put into trays, the bottom of each tray was pierced and a gravel layer installed in order to prevent the soil from becoming water-saturated. The trays were kept in a glasshouse at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Science, Kunming, Yunnan, and watered every 1–2 days to keep the soil continually moist. Seedling emergence in the trays was checked weekly from early May 2008 to late June 2009.

Identified individuals were removed from the trays. Individuals of unknown species were transplanted to bigger trays to allow for later growth and identification. When emergence was zero for several days, soils were allowed to dry, stirred by hand, and rewetted. Emerging seedlings were again identified and removed. This was repeated until no seedlings emerged. We did not take into consideration fern species, except for noting their presence, since they cannot be identified at the prothallus stage. The species were identified according to the International Code of Botanical Nomenclature (Greuter et al. 2000) and the Flora of China.

Species were classified according to life form as trees, shrubs, lianas, forbs, and graminoids. We further categorized species according to their light requirements as light-demanding, intermediate, and shade-tolerant, as suggested by Comita and Hubbell (2009). Designation of species attributes was based on (1) field observation and (2) the information from published authorities (e.g., You 1983; Lin and Cao 2009) and (3) the Chinese Virtual Herbarium (<http://www.cvh.org.cn/>).

Data analysis

Species basal area (BA, m²) and the relative proportion of each species's basal area (relative basal area, RBA) were calculated from the DBH data of woody species individuals. We used dominance analysis to determine dominant species in different plant communities (Ohsawa 1984). According to this scheme, in a community dominated by a single species, the relative dominance may be stated as 1. When two species share dominance, the relative abundance of each should ideally be 0.5, and if there are three codominants it should be 0.33, and so on. The number of dominant species is that which shows the least deviation between the actual relative dominance values and the expected percent share of the corresponding codominant-number model. The deviation (d) is calculated by the following equation:

$$d = 1/N \left[\sum (x_i - x')^2 + \sum x_j^2 \right], \quad i \in T, j \in U$$

where x_i is the actual percent share (here, RBA is adopted) of the top species (T), i.e., of the top dominant in the one-dominant model, the two top dominants in the two-dominant model, and so on; x' is the ideal percent share based on the model as mentioned above; x_j is the percent share of the remaining species (U); and N is the total number of the species (Kikvidze and Ohsawa 2002).

Seedling density was computed for each plot and the four vegetation types and expressed as the number of seedlings per square meter. Shannon's index in the four vegetation classes was calculated using $H' = -\sum P_i \ln P_i$

(Magurran 1991), where P_i is the proportion of individuals of the i th species out of the total individuals in the sample, i.e., $P_i = (N_i/N)$, where N is the total number of individuals recorded in the sample and N_i is the number of the individuals of the i th species in the sample; S is the number of species recorded in the sample.

Similarity between pairs of plots was calculated using Sørensen's coefficient of community CC (Schoener 1970): $CC = 2c/(a + b + 2c)$, where a is the number of species unique to plot A , b the number of species unique to plot B , and c the number of species shared by plots A and B .

The similarity among the species composition in the seed bank and that of different components of the forest (seedlings, saplings, poles, and trees) was calculated using Sørensen's similarity index. Differences in the mean number among the four vegetation classes, species richness, and diversity of germinated seedlings in the soil seed bank as well as the average abundance and Shannon's index of woody seedlings (shrub and tree) were analyzed using one-way ANOVA followed by the Tukey-Kramer test. Level of significance was set at $P < 0.05$. The difference in the number of shrub and tree seedlings among communities was tested by the chi-squared test. All statistical analyses were done using the SPSS (version 13) statistical software (SPSS, Chicago, IL, USA) and SigmaPlot 10.0 software (Aspire Software International, Leesburg, VA, USA).

Results

Species composition of the overstory ($H \geq 1.3$ m high) in the four plant communities

Forty-five woody species that had relative basal areas $\geq 0.01\%$ were found in the four plant communities (Table 1). The shrubland (SL), representing the early pioneer stage of the secondary succession, was dominated by light-demanding *L. ovalifolia* and *H. uralum*, with participation of *P. bonatii*, *Ilex corallina*, *Ternstroemia gymnanthera*, and *V. duclouxii*. The *Populus bonatii* secondary forest (PBF), representing the late pioneer stage of the secondary succession, was dominated by light-demanding *P. bonatii*, intermediate *V. duclouxii*, and shade-tolerant *L. chintungensis* and included 23 other species. The *Lithocarpus* regrowth forest (LRF), representing the seral stage of the secondary succession, had 26 species. LRF was dominated by shade-tolerant *L. chintungensis*. In the primary forest (PF), representing the late stage of the succession, 28 species were found. It was dominated by shade-tolerant trees *L. chintungensis*, *L. xylocarpus*, *M. bombycina*, and *M. insignis*. In PF, more shade-tolerant species were found including *I. macranthum*, *Neolitsea chuii*, *M. yunnanensis* among others. The RBA of shade-tolerant

species increased while the light-demanding species decreased in the overstory as succession progressed from SL, to PBF and LRF, and finally to PF (Fig. 1).

Seedling banks

Fifty-five woody species (tree and shrub) and 8256 individual plants were collected (Appendix). The number of individuals of woody plant seedlings showed a sharp decrease along the succession gradient. The average abundance differed significantly among communities ($F_{3,252} = 55.26$, $P < 0.05$), being highest in SL. Richness also differed among the forest stages, with PBF having the most, and SL the least. There was a significant difference in Shannon's index among vegetation types ($F_{3,252} = 88.47$, $P < 0.05$). The values were higher in PBF and LRF than in SL and PF (Table 2). The most common species were *H. uralum*, *Viburnum erubescens*, *O. opipara*, and *G. forrestii* in SL; *H. uralum* in PBF; *I. corallina* and *L. chintungensis* in LRF; and *M. bombycina* in PF (Appendix).

The difference in the number of shrub seedlings among communities was significant ($\chi^2 = 10812.93$, $df = 3$, $P < 0.001$), being highest in SL, followed by PBF, LRF, and PF. The number of tree seedlings also differed significantly among vegetation types ($\chi^2 = 38.69$, $df = 3$, $P < 0.001$) (Fig. 2). SL was dominated by light-demanding species whereas the intermediate and shade-tolerant species were rare. With the progress of the succession, the number of shade-tolerant seedlings for shrubs and trees increased, and no seedlings of light-demanding plants were found in PF.

Seed banks

A total of 35077 seedlings (5965 in PF, 3869 in LRF, 7672 in PBF, 17571 in SL) representing 94 species germinated in the greenhouse experiment from the soil samples collected in 2008. Of the 94 species, there were 14 trees, 8 shrubs, 10 lianas, 45 forbs, and 17 graminoids. The most abundant three species were *L. ovalifolia* (55.9%), *V. duclouxii* (24.2%), and *I. szechuanensis* (4.4%) in PF. In LRF, the species with the greatest numbers of individuals were *Carex teinogyna* (31.0%), *Spiraea japonica* (30.8%), and *V. duclouxii* (10.6%). PBF was dominated by *C. nubigena* (28.8%), *O. opipara* (14.3%), and *Mimulus tenellus* (10.0%); and SL by *H. uralum* (18.4%), *E. adenophorum* (17.2%), and *O. opipara* (6.9%) (Appendix).

The differences in average soil seed density among communities were significant ($F_{3,252} = 67.24$, $P < 0.05$), being the highest in the soil of SL, followed by PBF, PF, and LRF. The average species richness for all the life forms also differed significantly among communities ($F_{3,252} = 180.05$, $P < 0.05$), being highest

Table 1 Composition of the woody species ($H \geq 1.3$ m tall) for different plant communities

Successional stage Community type	Early pioneer SL	Late pioneer PBF	Seral LRF	Late PF
<i>Lyonia ovalifolia</i>	69.83*	0.07	3.88	
<i>Hypericum uralum</i>	24.37*			
<i>Populus bonatii</i>	2.14	41.76*	4.51	
<i>Ilex corallina</i>	1.87	4.63	6.19	
<i>Ternstroemia gymnanthera</i>	1.68	3.63	4.93	
<i>Vaccinium duclouxii</i>	0.11	13.91*	6.3	
<i>Lithocarpus chintungensis</i>		24.36*	41.77*	32.33*
<i>Salix pseudotangii</i>		3.64	0.35	
<i>Camellia forrestii</i>		2.09		
<i>Lithocarpus xylocarpus</i>		1.69	0.06	13.02*
<i>Ilex szechuanensis</i>		0.79	0.97	0.73
<i>Rhododendron irroratum</i>		0.51	0.09	
<i>Gaultheria forrestii</i>		0.47		
<i>Illicium macranthum</i>		0.41		5.48
<i>Symplocos ramosissima</i>		0.38	6.47	2.31
<i>Lithocarpus hypoglauca</i>		0.34	3.24	0.59
<i>Styrax perkinsiae</i>		0.34	2.45	0.28
<i>Eriobotrya bengalensis</i>		0.28		0.47
<i>Schima noronhae</i>		0.17	4.41	0.04
<i>Litsea elongata</i>		0.15	0.09	0.65
<i>Docynia delavayi</i>		0.15	0.56	
<i>Symplocos dryophila</i>		0.08		0.14
<i>Stranvaesia davidiana</i>		0.07	2.9	
<i>Schefflera shweliensis</i>		0.05		
<i>Symplocos anomala</i>		0.02		1.97
<i>Machilus yunnanensis</i>		0.01		2.01
<i>Cotoneaster pannosus</i>		0.01		
<i>Lithocarpus pachyphylloides</i>			3.95	
<i>Ligustrum delavayanum</i>			3	0.06
<i>Acanthopanax evodiaefolius</i>			0.99	
<i>Machilus bombycina</i>			0.78	9.76*
<i>Neolitsea polycarpa</i>			0.53	1.49
<i>Lindera thomsonii</i>			0.47	0.08
<i>Castanopsis wattii</i>			0.41	0.13
<i>Rhododendron leptothrium</i>			0.39	2.08
<i>Viburnum coreaceum</i>			0.32	
<i>Manglietia insignis</i>				10.54*
<i>Neolitsea chunii</i>				4.13
<i>Meliosma kirkii</i>				3.81
<i>Prunus pilosiuscula</i>				2.06
<i>Eurya yunnanensis</i>				1.97
<i>Symplocos sumuntia</i>				1.7
<i>Hartia sinensis</i>				1.08
<i>Laurocerasus undulata</i>				0.81
<i>Symplocos poilanei</i>				0.25

Values are relative basal area of each species (Ohsawa 1984). Those species that had relative basal areas $\geq 0.01\%$ are included. Asterisks indicate dominant species
 SL Shrubland, PBF *Populus bonatii* secondary forest, LRF *Lithocarpus* regrowth forest, PF primary forest

in soil samples from SL. The number of trees species was significantly higher in PF and LRF than in SL and PBF ($F_{3,252} = 148.86$, $P < 0.05$), and the number of graminoid species was significantly lower in PF and LRF than in SL and PBF ($F_{3,252} = 285.23$, $P < 0.05$). Trees dominated in the soil seed bank of PF. Forbs were the most numerous in the soil seed bank of SL. The diversity indices decreased significantly with the age of the plant communities ($F_{3,252} = 105.04$, $P < 0.05$) (Table 3). The number of germinable tree seeds increased throughout succession, and the number of shrubs and forbs decreased with the increasing age of the plant communities (Fig. 3). Light-demanding tree species contributed the highest proportion of germinable seeds in PF. Light-demanding shrub species dominated

the germinable seed bank in SL, PBF, LRF, but not PF (Fig. 4).

Relationships between the seed bank and aboveground vegetation

The similarity between the composition of seedlings (or woody seedlings germinated from the seed bank) and that of trees, poles, and saplings was highest in LRF, followed by PF, PBF, and SL (Fig. 5a–f). The similarity between woody seedlings germinated from the seed bank and woody species or seedlings recorded in aboveground vegetation tended to decrease as the successional stage advanced from SL, to PBF and

LRF, and finally to PF (0.33 in shrubland to 0.11 in primary forest) (Fig. 5g, h).

Discussion

Our study has recorded higher seed density and species richness as compared to similar studies conducted in East Asian forests. For instance, Naka and Yoda (1984) found seeds of a single species (*Eurya japonica*) to be abundant in different aged stands of the Kasugayama Forest Reserve, whilst in our study we found differing species to dominate in stands of different ages.

Previous studies have shown that the species richness of a seed bank often decreases during secondary succession (Roberts and Vankat 1991; Bakker et al. 1996). This is usually associated with a decline in the density of seeds (Kalamees and Zobel 1998). The higher seed bank densities found in earlier forest successional stages may be due to the higher fecundity, earlier reproduction, and longer dormancy associated with the higher seed longevity of pioneer species that predominate in these sites (Janzen and Vázquez-Yanes 1990). In our study, the density of germinated seedlings and species richness in the soil seed banks also decreased with

the increasing age of plant communities from SL to PF. The higher seed density in SL can be explained by a larger number of early successional pioneer species (e.g., *H. uralum*, *E. adenophorum*, *O. opipara*, and *Anaphalis margaritacea*) in the seed bank, which produce persistent seeds (Leary and Howes-Keiffer 2004). Herb species were rare in the late-successional PF; Naka and Yoda (1984) also reported that most herb species were rarely found in mature forest stands. The microclimatic conditions beneath the mature stage do not favor establishment of pioneer species. Further, dispersal of seeds of pioneer species from the margins toward the inner forest may be severely limited (Devlaeminck et al. 2005). Higher species richness was observed in SL, where the seeds of more forb species may remain dormant within the soil (Meiners and Gorchoff 1994). In our study, 37 forb species were recorded in the seed bank of SL versus only 10 in PF (Appendix).

Some studies have shown that seeds of tree species, especially those adapted to later successional stages, were relatively scarce in the soil seed banks of most ecosystems, including natural forests (Senbeta and Teketay 2001; Bossuyt and Hermy 2001). In our investigation sites, the dominant canopy tree species of *Castanopsis*, *Lithocarpus*, *Machillus*, and *Schima* were

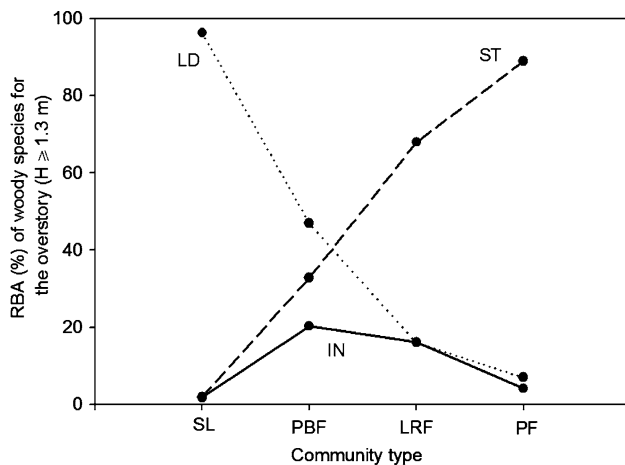


Fig. 1 The relative basal area (RBA) of woody species for the overstory ($H \geq 1.3$ m high) of the four plant communities. *SL* Shrubland, *PBF* *Populus bonatii* secondary forest, *LRF* *Lithocarpus* regrowth forest, *PF* primary forest, *LD* light-demanding, *IN* intermediate light demand, *ST* shade-tolerant

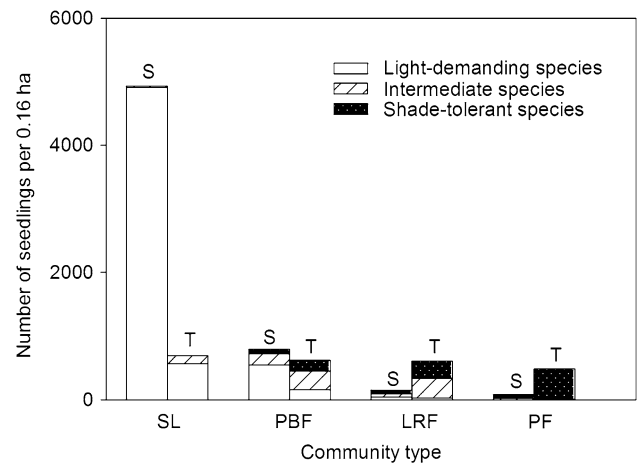


Fig. 2 The number of shrub and tree seedlings in different plant communities in the Ailao Mountains (mean \pm SE). *SL* Shrubland, *PBF* *Populus bonatii* secondary forest, *LRF* *Lithocarpus* regrowth forest, *PF* primary forest, *T* trees, *S* shrubs

Table 2 Structural parameters of the regeneration strata (woody plants < 1.3 m tall) of different plant communities (sampling area = 1600 m² each) in the Ailao Mountains

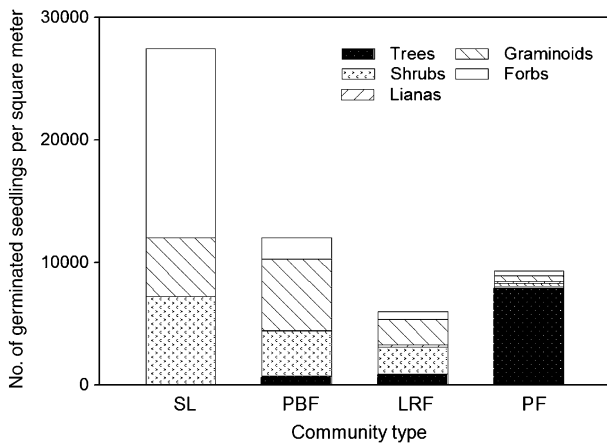
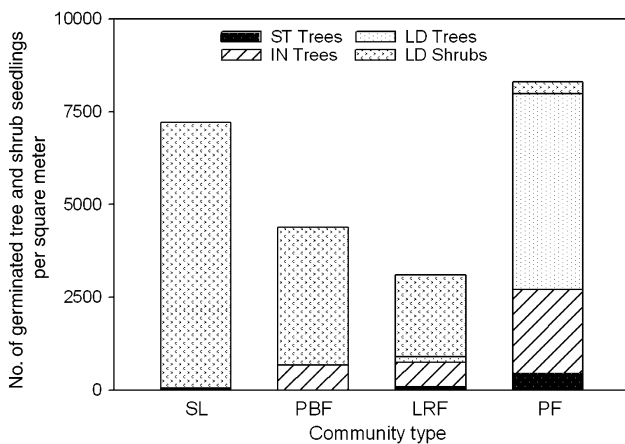
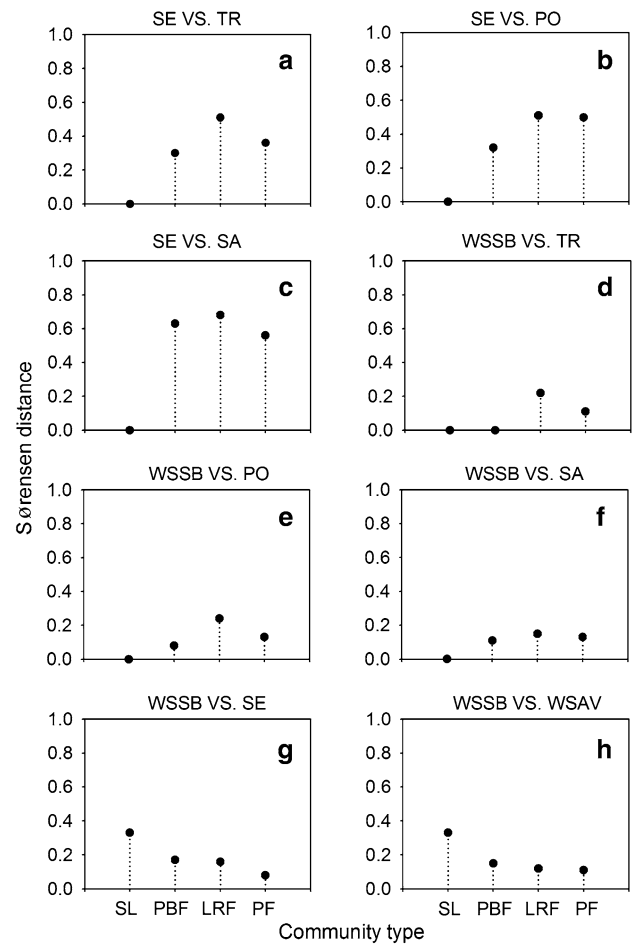
Community type	SL	PBF	LRF	PF
Total abundance (n)	5625	1310	757	564
Average (\pm SE) abundance (plants per plot)	87.9 \pm 9.2 ^a	20.5 \pm 3.3 ^b	11.8 \pm 2.6 ^b	8.8 \pm 1.4 ^b
Total species richness (n)	9	50	32	31
Shannon's index (H')	1.4 \pm 0.0 ^a	2.6 \pm 0.0 ^b	2.4 \pm 0.1 ^b	1.4 \pm 0.2 ^a

Different letters within a row denote significantly different means as determined by Tukey-Kramer tests ($P < 0.05$)
SL Shrubland, *PBF* *Populus bonatii* secondary forest, *LRF* *Lithocarpus* regrowth forest, *PF* primary forest

Table 3 Mean density, species richness, and species diversity (H') of the samples in different plant communities of the soil seed bank in the Ailao Mountains

Community type	SL	PBF	LRF	PF
Mean number of germinated seedlings/m ² (n)	22760 ± 3233 ^a	11980 ± 1092 ^b	6160 ± 1271 ^c	9333 ± 1066 ^b
Mean number of species ± SD				
T	0.47 ± 0.17 ^a	0.73 ± 0.12 ^a	2.93 ± 0.41 ^b	3.53 ± 0.27 ^b
S	3.13 ± 0.29 ^{ab}	3.93 ± 0.43 ^a	2.33 ± 0.35 ^b	2.20 ± 0.28 ^b
L	0.20 ± 0.14 ^a	0.53 ± 0.29 ^{ab}	1.33 ± 0.27 ^c	1.13 ± 0.24 ^{bc}
F	15.33 ± 1.32 ^a	3.60 ± 0.49 ^b	3.47 ± 0.052 ^b	1.80 ± 0.28 ^b
G	7.13 ± 0.58 ^a	6.27 ± 0.34 ^a	1.73 ± 0.30 ^b	1.27 ± 0.21 ^b
Total	26.80 ± 1.98 ^a	14.80 ± 0.81 ^b	11.87 ± 0.94 ^c	9.93 ± 0.50 ^c
Shannon's index (H')	2.53 ± 0.08 ^a	1.90 ± 0.09 ^b	1.77 ± 0.11 ^b	1.40 ± 0.09 ^c

Data are mean ± SD. Different letters within a row denote significantly different means as determined by Tukey-Kramer tests ($P < 0.05$) SL Shrubland, PBF *Populus bonatii* secondary forest, LRF *Lithocarpus* regrowth forest, PF primary forest, TR trees, S shrubs, L lianas, F forbs, G graminoids

**Fig. 3** Number of germinated seedlings of different life forms recorded in soil samples in different plant communities in the Ailao Mountains. SL Shrubland, PBF *Populus bonatii* secondary forest, LRF *Lithocarpus* regrowth forest, PF primary forest**Fig. 4** Number of tree and shrub seedlings germinated in soil samples in different plant communities in the Ailao Mountains. SL Shrubland, PBF *Populus bonatii* secondary forest, LRF *Lithocarpus* regrowth forest, PF primary forest, ST shade-tolerant, IN intermediate light demand, LD light-demanding**Fig. 5** Sørensen's index for the species composition of soil seed banks and different components of the forest (a–h) in different plant communities in the Ailao Mountains. SL Shrubland, PBF *Populus bonatii* secondary forest, LRF *Lithocarpus* regrowth forest, PF primary forest, TR trees, PO poles, SA saplings, SE seedlings, WSAV woody species recorded in aboveground vegetation, WSSB woody seedlings germinated from the seed bank

absent from the seed bank, while a relatively high density of shade-intolerant *V. duclouxii* and *L. ovalifolia* was found in the soil seed bank of PF (Appendix). Our study

found the number of tree species to be relatively low in the soil seed banks of early successional communities of SL and PBF. This scarcity could be attributed to several factors. First, tree seeds may not be dormant. Second, trees usually have large seeds that cannot be dispersed easily over long distances (Hermy et al. 1999). Thus, inputs of seed rain from adjacent natural forests to the soil seed bank of the early successional stage may be minimal (Mengistua et al. 2005). Third, seeds may be lost through predation (Teketay 1998). Finally, such environmental factors as high temperature and direct solar radiation on the bare soils may reduce seed viability (Lemenih and Teketay 2006).

As in other tropical and temperate forests (Olano et al. 2002) and grasslands (Funes et al. 2001), seed bank composition and the established aboveground vegetation were dissimilar, especially in late successional stages. Only 11–33% of the total species are common to the vegetation and the seed bank. This can be explained by the fact that (1) the seed bank composition may be derived from a former successional stage (Thompson et al. 1997); (2) the vegetation may be partly derived from seeds dispersed from outside the site or through seed rain from adjacent natural forest; (3) seeds may germinate immediately once they fall into a moist soil. Another reason for the low similarity is that late succession forest species have larger seeds that are targeted for predation by small mammals on the forest floor (Gross-Camp and Kaplin 2005).

The similarities between woody seedlings and saplings, seedlings and poles, and seedlings and trees were higher in PF, LRF, and PBF as compared with the similarity between the seed bank and standing vegetation. These results imply that the woody seedling bank may contribute to regeneration at the later successional stages of the montane moist evergreen broad-leaved forest, and that the seed rain, not the seed bank,

appears to determine the structure of the forest during the later stages, with birds being especially important dispersing agents (Purves et al. 2007). Naka and Yoda (1984) also found a few seeds of evergreen broad-leaved species in the soils, with these species tending to recruit instead from seedling banks. Therefore, rapid vegetation restoration from the soil seed banks of degraded abandoned farm fields may not be possible in this area.

The soil seed bank (especially, in the cases of shrubs and forbs *E. adenophorum*, *G. forrestii*, *O. opipara*, *V. erubescens*, and *H. uralum*) plays a significant role in the restoration of vegetation following clear-cutting in the forest. On the other hand, the dense exotic species *E. adenophorum*, as well as shrub species that may grow quickly from the soil bank, may result in strong competition for the tree species. Therefore, the colonization and establishment of tree seedlings may be very slow now that this forest has been destroyed.

Acknowledgments This work was supported by the Natural Science Foundation of China (no. 30771705), the Knowledge Innovation Program (no. KSCX2-YW-N066-03), and the Program of Hundreds of Talent Scientists of the Chinese Academy of Sciences (BRJH2002098). The Management Authority of the Ailao Mountain Nature Reserve is thanked for granting permission to undertake the research reported. Messer Li Dawen, Yang Wenzheng, Yang Guoping, Qi Jinhua, and other staff members of the Ailao Mountain Forest Ecosystem Research Station are thanked for their help in the field work. Professor Lu Shugang is thanked for species identification.

Appendix

Table 4 presents information on germinated seedlings from the seed bank and from the seedling banks of the different communities.

Table 4 Species, total number, and life forms of germinated seedlings in the samples of seed bank collected and of woody plant seedlings in primary forest and different secondary communities in the Ailao Mountains

Species	Traits	Seed bank				Seedling bank				
		SL	PBF	LRF	PF	SL	PBF	LRF	PF	
Trees										
<i>Vaccinium duclouxii</i> (Levl.) Hand.-Mazz.	IN	17	431	410	1442	–	92	81	–	
<i>Aralia chinensis</i> L.	LD	10	–	–	2	–	–	–	–	
<i>Lyonia ovalifolia</i> (Wall.) Drude	LD	4	–	36	3332	224	8	14	–	
<i>Acanthopanax evodiaefolius</i> Franch.	LD	3	–	–	–	–	–	–	–	
<i>Ternstroemia gymnanthera</i> (Wight et Arn.) Beddome	IN	–	3	–	–	18	24	67	–	
<i>Ilex szechuanensis</i> Loes.	ST	–	–	51	265	–	6	7	4	
<i>Prunus conradinae</i> Koehne	LD	–	–	21	4	–	–	–	–	
<i>Symplocos ramosissima</i> Wall. ex G. Don	ST	–	–	21	26	–	51	44	47	
<i>Viburnum coreaceum</i> Blume.	LD	–	–	17	13	–	3	2	–	
<i>Betula alnoides</i> Buch Ham.	LD	–	–	13	6	–	–	–	–	
<i>Meliosma kirkii</i> Hemsl. et Wils.	LD	–	–	7	13	–	–	–	–	
<i>Lithocarpus chintungensis</i> Hsu et qian sp. Nov.	ST	–	–	2	–	–	26	107	17	
<i>Litsea cubeba</i> (Lour.) Pers.	LD	–	–	1	–	–	–	–	–	
<i>Litsea elongata</i> (Wall. ex Nees) Benth. et Hook. f.	ST	–	–	–	5	–	7	4	9	
<i>Salix pseudotangii</i> C. Wang et C. Y. Yu	LD	–	–	–	–	281	1	–	–	

Table 4 continued

Species	Traits	Seed bank				Seedling bank				
		SL	PBF	LRF	PF	SL	PBF	LRF	PF	
<i>Ilex corallina</i> Franch.	IN	–	–	–	–	108	87	123	5	
<i>Populus bonatii</i> Levl.	LD	–	–	–	–	62	42	–	–	
<i>Schefflera shweliensis</i> W. W. Smith	IN	–	–	–	–	–	37	23	5	
<i>Machilus bombycina</i> King ex Hook. f.	ST	–	–	–	–	–	22	44	283	
<i>Schima noronhae</i> Reinw. ex Bl. Bijdr.	IN	–	–	–	–	–	16	8	–	
<i>Eriobotrya bengalensis</i> Hook. f.	IN	–	–	–	–	–	14	–	–	
<i>Symplocos sumuntia</i> Buch.-Ham. ex D. Don	ST	–	–	–	–	–	14	–	4	
<i>Neolitsea polycarpa</i> Liou	ST	–	–	–	–	–	13	11	8	
<i>Ilex mannei</i> S. Y. Hu	IN	–	–	–	–	–	11	–	–	
<i>Illicium macranthum</i> A. C. Smith	ST	–	–	–	–	–	9	6	38	
<i>Polygala arillata</i> Buch.-Ham. ex D. Don	IN	–	–	–	–	–	8	7	–	
<i>Symplocos anomala</i> Brand	ST	–	–	–	–	–	7	–	–	
<i>Ligustrum delavayanum</i> Hariot.	ST	–	–	–	–	–	4	17	8	
<i>Schefflera fengii</i> Tseng & Hoo	IN	–	–	–	–	–	3	1	–	
<i>Daphniphyllum macropodum</i> Miq.	ST	–	–	–	–	–	2	–	–	
<i>Symplocos dryophila</i> Clarke	ST	–	–	–	–	–	2	–	8	
<i>Skimmia arborescens</i> T. Anders. ex Gamble	ST	–	–	–	–	–	2	2	6	
<i>Lindera thomsonii</i> Allen	ST	–	–	–	–	–	1	9	2	
<i>Lithocarpus xylocarpus</i> Markg.	ST	–	–	–	–	–	1	7	2	
<i>Manglietia insignis</i> (Wall.) Bl.	ST	–	–	–	–	–	1	3	13	
<i>Docynia delavayi</i> (Franch.) Schneid	LD	–	–	–	–	–	1	1	–	
<i>Neolitsea chunii</i> Merr.	ST	–	–	–	–	–	1	–	7	
<i>Machilus yunnanensis</i> Lec.	ST	–	–	–	–	–	1	–	1	
<i>Michelia floribunda</i> Finet et Gagnep.	ST	–	–	–	–	–	1	–	–	
<i>Rhododendron leptothrium</i> Balf.f.et Forrest	IN	–	–	–	–	–	1	–	–	
<i>Styrax perkinsiae</i> Rehd.	LD	–	–	–	–	–	–	9	–	
<i>Castanopsis wattii</i> A. Camus	ST	–	–	–	–	–	–	6	8	
<i>Hartia sinensis</i> Dunn	ST	–	–	–	–	–	–	2	6	
Shrubs										
<i>Hypericum uralum</i> Buch.	LD	3226	350	51	11	3089	262	–	–	
<i>Osbeckia opipara</i> C. Y. Wu et C. Chen	LD	1220	1096	–	5	604	93	–	–	
<i>Hypericum elodeoides</i> Choisy	LD	47	204	–	1	–	–	–	–	
<i>Spiraea japonica</i> Linn.	LD	47	81	1190	3	–	7	5	–	
<i>Gaultheria forrestii</i> Diels	LD	26	563	137	179	508	84	–	–	
<i>Hypericum japonicum</i> Thunb.	LD	13	60	–	–	–	–	–	–	
<i>Lycycteria formosa</i> Wall.	LD	–	13	21	7	–	–	–	–	
<i>Buddleja asiatica</i> Lour.	LD	–	6	2	–	–	–	–	–	
<i>Viburnum erubescens</i> Wall.	LD	–	–	–	–	710	92	27	–	
<i>Berberis wuliangshanensis</i> C. Y. Wu ex S. Y. Bao	IN	–	–	–	–	21	95	28	4	
<i>Camellia forrestii</i> (Diels) Coh. St.	IN	–	–	–	–	–	73	2	–	
<i>Daphne papyracea</i> Wall. ex Steud.	ST	–	–	–	–	–	42	54	29	
<i>Ardisia crenata</i> Sims	ST	–	–	–	–	–	18	–	–	
<i>Myrsine semiserrata</i> Wall.	ST	–	–	–	–	–	7	5	1	
<i>Mahonia mairei</i> Takeda	IN	–	–	–	–	–	7	4	9	
<i>Rhamnus heterophylla</i> Oliv.	LD	–	–	–	–	–	4	11	–	
<i>Aucuba chinensis</i> Benth.	ST	–	–	–	–	–	2	–	15	
<i>Zanthoxylum alpinum</i> Huang	LD	–	–	–	–	–	2	–	1	
<i>Cotoneaster pannosus</i> Franch.	LD	–	–	–	–	–	2	–	–	
<i>Symplocos poilanei</i> Guill.	ST	–	–	–	–	–	1	–	17	
<i>Helwingia himalaica</i> Hook.	IN	–	–	–	–	–	–	16	3	
<i>Eurya yunnanensis</i> Hsu	IN	–	–	–	–	–	–	–	4	
Lianas										
<i>Rubus biflorus</i> Buch.-Ham. ex Smith		9	13	17	7					
<i>Rubus corchorifolius</i> Linn. f.		4	–	–	16					
<i>Rosa longicuspis</i> A. Bertoloni		4	–	21	10					
<i>Rubus foliolosus</i> D. Don		–	26	–	–					
<i>Celastrus angulatus</i> Maxim.		–	6	11	17					
<i>Rubus lineatus</i> var. <i>linetus</i>		–	2	–	–					
<i>Rubus multibracteatus</i> Lévl. et Vant.		–	–	43	1					
<i>Actinidia chinensis</i> Planch		–	–	17	27					
<i>Amphicarpaea trisperma</i> Baker		–	–	7	–					
<i>Rubus pinfaensis</i> Levl. Et Vant.		–	–	–	13					
Forbs										
<i>Eupatorium adenophorum</i> Spreng		3019	11	38	–					
<i>Leontopodium sinense</i> Hemsl.		1062	17	37	13					

Table 4 continued

Species	Traits	Seed bank				Seedling bank			
		SL	PBF	LRF	PF	SL	PBF	LRF	PF
<i>Lysimachia christinae</i> Hance		879	–	–	–				
<i>Mimulus tenellus</i> var. <i>nepalensis</i> (Benth.) Tsoong		649	764	137	–				
<i>Dichrocephala integrifolia</i> (L. f.) Kuntze		516	–	–	4				
<i>Cardamine hirsuta</i> L.		478	21	1	124				
<i>Stachys kouyangensis</i> (Vaniot) Dunn		337	4	5	–				
<i>Galium aparine</i> Linn. var. <i>tenerum</i> (Gren. et Godr.) Rebb.		316	–	–	–				
<i>Plantago asiatica</i> Linn.		299	–	–	–				
<i>Fragaria moupinensis</i> (Franch.) Card.		299	–	94	94				
<i>Impatiens rubro-striata</i> Hook. f.		235	–	–	–				
<i>Polygonum nepalense</i> Meisn.		230	–	2	–				
<i>Epilobium royleanum</i> Hausskn.		218	–	–	–				
<i>Primula denticulata</i> Smith		145	9	1	–				
<i>Stellaria vestita</i> Kurz		145	7	–	–				
<i>Spergularia salina</i> J. et C. Presl		141	–	6	–				
<i>Elsholtzia rugulosa</i> Hems I.		94	–	–	4				
<i>Ainsliaea latifolia</i> (D. Don) Sch.		94	–	–	–				
<i>Circaea alpina</i> Linn.		90	–	–	–				
<i>Gnaphalium affine</i> D. Don		90	9	13	7				
<i>Hemiphragma heterophyllum</i> Wall.		73	–	7	–				
<i>Potentilla fragarioides</i> L.		64	–	12	–				
<i>Galinsoga parviflora</i> Cav.		60	–	–	–				
<i>Gentiana cephalantha</i> Franch. ex Hemsl.		60	107	–	–				
<i>Impatiens cyathiflora</i> Hook. f.		55	–	–	–				
<i>Veronica laxa</i> Benth.		55	–	–	–				
<i>Viola pilosa</i> Blume		43	–	–	13				
<i>Blumea martiniana</i> Van.		26	–	–	–				
<i>Picris hieracioides</i> Linn.		26	–	–	–				
<i>Valeriana hardwickii</i> Wall.		26	–	–	–				
<i>Galium asperuloides</i> Edgew. subsp. <i>hoffmeisteri</i> (Klotzsch) Hara		13	–	–	–				
<i>Hedyotis auricularia</i> L.		13	81	–	–				
<i>Artemisia apiacea</i> Hance		9	–	–	14				
<i>Geranium wilfordii</i> Maxim.		4	–	–	–				
<i>Viola japonica</i> Langsd.		4	–	–	–				
<i>Myriactis nepalensis</i> Less.		4	30	38	4				
<i>Girardinia diversifolia</i> (Link) Friis		2	–	–	–				
<i>Pratia nummularia</i> (Lam.) A. Br. et Aschers.		–	26	–	–				
<i>Laggera pterodonta</i> Benth.		–	6	2	–				
<i>Anaphalis contorta</i> (D. Don) Hook. f.		–	5	–	–				
<i>Crassocephalum crepidioides</i> (Benth.) S. Moore		–	4	–	–				
<i>Conyza canadensis</i> (L.) Cronq.		–	2	–	–				
<i>Chamabainia cuspidata</i> Wight		–	–	3	–				
<i>Youngia japonica</i> (Linn.) DC.		–	–	1	–				
<i>Ainsliaea henryi</i> Diels		–	–	–	4				
Graminoids									
<i>Carex teinogyna</i> Boott		563	602	1199	209				
<i>Agrostis myriantha</i> Hook. f.		516	115	4	21				
<i>Brachypodium sylvaticum</i> P. Beauv.		337	60	–	–				
<i>Fimbristylis miliacea</i> (L.) Vahl [<i>Scirpus miliaceus</i> L.]		273	294	23	3				
<i>Fimbristylis dichotoma</i> (L.) Vahl.		269	–	–	–				
<i>Carex perakensis</i> C. B. Clarke		265	90	132	11				
<i>Bulbostylis barbata</i> (Rottb.) C. B. Clarke		201	34	–	–				
<i>Digitaria sanguinalis</i> (Linn.) Scop.		166	–	–	–				
<i>Arthraxon hispidus</i> (Trin.) Makino		137	55	–	–				
<i>Juncus effusus</i> L.		128	85	9	–				
<i>Spatholirion volubile</i> Edgew.		77	–	–	–				
<i>Eriocaulon buergerianum</i> Körn		47	–	–	–				
<i>Carex nubigena</i> D. Don ex Tilloch & Taylor		38	2210	9	18				
<i>Kyllinga brevifolia</i> Rottb.		21	162	–	–				
<i>Isachne dispar</i> Trin		17	–	–	–				
<i>Scirpus asiaticus</i> Beetle		13	4	–	17				
<i>Carex miyabei</i> var. <i>maopengensis</i>		–	4	–	–				
Total		17571	7672	3869	5965	5625	1310	757	564

SL Shrubland, PBF *Populus bonatii* secondary forest, LRF *Lithocarpus* regrowth forest, PF primary forest, LD light-demanding, IN intermediate light demand, ST shade-tolerant

References

- Alvarez-Buylla ER, Martínez-Ramos M (1990) Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84:314–325
- Bakker JP, Bakker ES, Rosen E, Verweij GL, Bekker RM (1996) Soil seed bank composition along a gradient from dry *alvar* grassland to *Juniperus* shrubland. *J Veg Sci* 7:165–176
- Benítez-Malvido J, Martínez-Ramos M, Camargo JLC, Ferraz IDK (2005) Responses of seedling transplants to environmental variations in contrasting habitats of Central Amazonia. *J Trop Ecol* 21:397–406
- Bossuyt B, Hermy M (2001) Influence of land use history on seed banks in European temperate forest ecosystems: a review. *Ecography* 24:225–238
- Bureau of Environment Conservation of Yunnan (1998) Bulletin of environment of status of Yunnan Province in 1997 (in Chinese). Yunnan Technology and Sciences Press, Kunming
- Burslen DFRP, Whitmore TC, Brown GC (2000) Short-term effects of cyclone impact, and long term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J Ecol* 88:1063–1078
- Clark DB, Clark DA (1985) Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66:1884–1892
- Comita LS, Hubbell SP (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* 90:328–334
- Cruz-Rodríguez JA, López-Mata L (2004) Demography of the seedling bank of *Manilkara zapota* (L.) Royen, in a subtropical rain forest of Mexico. *Plant Ecol* 172:227–235
- Devlaeminck R, Bossuyt B, Hermy M (2005) Inflow of seeds through the forest edge: evidence from seed bank and vegetation patterns. *Plant Ecol* 176:1–17
- Funes G, Basconcelo S, Diaz S, Cabido M (2001) Edaphic patchiness influences grassland regeneration from the soil seed-bank in mountain grasslands of central Argentina. *Austral Ecol* 26:205–212
- Greuter W, McNeill J, Barrie FR, Burdet HM, Demoulin V, Filgueiras TS, Nicolson DH, Silva PC, Skog JE, Trehane P, Turland NJ, Hawksworth DL (eds) (2000) International code of botanical nomenclature (St. Louis Code). Koeltz, Königstein
- Gross-Camp N, Kaplin BA (2005) Chimpanzee (*Pan troglodytes*) seed dispersal in an Afrotropical forest: microhabitat influences on the postdispersal fate of large seeds. *Biotropica* 37:641–649
- Harmer R (1995) Natural regeneration of broadleaved trees in Britain: III. Germination and establishment. *Forestry* 68:1–9
- Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson J (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol Conserv* 91:9–22
- Hopfensperger KN (2007) A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* 116:1438–1448
- Hughes FMR, Rood SB (2003) Allocation of river flows for restoration of floodplain forest ecosystems: a review of approaches and their applicability in Europe. *Environ Manag* 32:12–33
- James CS, Capon SJ, White MG, Rayburg SC, Thoms MC (2007) Spatial variability of the soil seed bank in a heterogeneous ephemeral wetland system in semi-arid Australia. *Plant Ecol* 190:205–217
- Janzen DH, Vázquez-Yanes C (1990) Aspects of tropical seed ecology of relevance to management of tropical forested wildlands. In: Gómez-Pompa A, Whitmore TH, Hadley M (eds) Rain forest regeneration and management. MAB Series. UNESCO, Paris, pp 137–154
- Jin ZZ (1983) On the characteristics and nature of the evergreen broad-leaved forest in Xujiaba region, Ailao Mountains (in Chinese with English abstract). In: Wu CY (ed) Research of forest ecosystems of Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, pp 204–214
- Kalamees R, Zobel M (1998) Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, western Estonia. *Acta Oecol* 19:175–180
- Kikvidze Z, Ohsawa M (2002) Measuring the number of co-dominants in ecological communities. *Ecol Res* 17:519–525
- Kira T (1991) Forest ecosystems of east and southeast Asia in global perspective. *Ecol Res* 6:185–200
- Kitajima K, Tilman D (1996) Seed banks and seedling establishment on an experimental productivity gradient. *Oikos* 76:381–391
- Leary CI, Howes-Keiffer C (2004) Comparison of standing vegetation and seed bank composition one year following hardwood reforestation in southwestern Ohio. *Ohio J Sci* 104:20–28
- Lemenih M, Teketay D (2006) Changes in soil seed bank composition and density following deforestation and subsequent cultivation of a tropical dry Afrotropical forest in Ethiopia. *Trop Ecol* 47:1–12
- Lin L, Cao M (2009) Edge effects on soil seed banks and understory vegetation in subtropical and tropical forests in Yunnan, SW China. *For Ecol Manag* 257:1344–1352
- Liu WY, Fox JED, Xu ZF (2002) Litterfall and nutrient dynamics in a montane moist evergreen broad-leaved forest in Ailao Mountains, SW China. *Plant Ecol* 164:157–170
- Magurran A (1991) Ecological diversity and its measurement. Chapman and Hall, London
- McKinley DC, Van Auken OW (2005) Influence of interacting factors on the growth and mortality of *Juniperus* seedlings. *Am Midl Nat* 154:320–330
- Meiners SJ, Gorchov DL (1994) The soil seed pool of Huffman Prairie, a degraded Ohio prairie, and its potential in restoration. *Ohio J Sci* 94:82–86
- Mengistua T, Teketayb D, Hultenc D, Yemshaw Y (2005) The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. *J Arid Environ* 60:25–281
- Messaoud Y, Houle G (2006) Spatial patterns of tree seedling establishment and their relationship to environmental variables in a cold-temperate deciduous forest of eastern North America. *Plant Ecol* 185:319–331
- Naka K, Yoda K (1984) Community dynamics of evergreen broadleaf forests in southwestern Japan II. Species composition and density of seeds buried in the soil of a climax evergreen oak forest. *Bot Mag Tokyo* 97:61–79
- Ohsawa M (1984) Differentiation of vegetation zones and species strategies in the subalpine region of Mt. Fuji. *Vegetatio* 57:15–52
- Olano JM, Caballero I, Laskurain NA, Loidi J, Escudero A (2002) Seed bank spatial pattern in a temperate secondary forest. *J Veg Sci* 13:775–784
- Pakeman RJ, Hay E (1996) Heathland seed banks under recreation *Pteridium aquilinum* L. Kuhn and their importance for revegetation after bracken control. *J Environ Manag* 4:329–339
- Pazos GE, Bertiller MB (2008) Spatial patterns of the germinable soil seed bank of coexisting perennial-grass species in grazed shrublands of the Patagonian Monte. *Plant Ecol* 198:111–120
- Poorter L, Hayashida-Oliver I (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *J Trop Ecol* 16:481–498
- Purves DW, Zavala MA, Ogle K, Prieto F, Benayas JMR (2007) Environmental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in Mediterranean Spain. *Ecol Monogr* 77:77–97
- Roberts TL, Vankat JL (1991) Floristics of a chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. II. Seed banks. *Bull Torrey Bot Club* 118:377–384
- Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418
- Senbeta F, Teketay D (2001) Regeneration of indigenous woody species under the canopy of tree plantations in Central Ethiopia. *Trop Ecol* 42:175–185
- Sheng CY, Xie SC (1991) Studies on the growth regularity and the successional status of *Populus bonatii* in the Ailao Mountains (in Chinese with English abstract). *J Southwest For Coll* 11:33–40

- Tagawa H (1995) Distribution of lucidophyll oak-laurel forest formation in Asia and other areas. *Tropics* 5:1–40
- Tang CQ, Ohsawa M (2009) Ecology of subtropical evergreen broad-leaved forests of Yunnan, southwestern China as compared to those of southwestern Japan. *J Plant Res* 122:335–350
- Tang CQ, Li TX, Zhu XH (2007) Structure and regeneration dynamics of three subtropical midmontane moist evergreen broadleaved forests in southwestern China, with special reference to bamboo in the forest understories. *Can J Res* 37:2701–2714
- Tang Y, Cao M, Fu XH (2006) Soil seedbank in a dipterocarp rainforest in Xishuangbanna, southwest China. *Biotropica* 38:328–333
- Teketay D (1998) Soil seed banks at an abandoned Afromontane arable site. *Feddes Repert* 109:161–174
- Thompson K, Bakker JP, Bekker RM (1997) The soil seed banks of northwest Europe: methodology, density and longevity. Cambridge University Press, Cambridge
- Walker LR (2000) Seedling and sapling dynamics of treefall pits in Puerto Rico I. *Biotropica* 32:262–275
- Wu ZY, Zhu CY, Jiang HQ (eds) (1987) The vegetation of Yunnan (in Chinese). Science Press, Beijing
- You CX (1983) Classification vegetation in Xujiaba region of the Ailaoshans (in Chinese with English abstract). In: Wu CY (ed) Research on forest ecosystems of Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, pp 74–117
- Young SS, Herwitz SR (1995) Floristic diversity and co-occurrences in a subtropical broad-leaved forest and two contrasting regrowth stands in central-west Yunnan Province, China. *Vegetatio* 119:1–13
- Young SS, Carpenter C, Wang ZJ (1992) A study of the structure and composition of an old growth and secondary broad-leaved forest in the Ailao Mountains of Yunnan, China. *Mt Res Dev* 12:269–284
- Zobel M, Kalamees R, Püssa K, Roosaluuste E, Moora M (2007) Soil seed bank and vegetation in mixed coniferous forest stands with different disturbance regimes. *For Ecol Manag* 250:71–76