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REGULAR ARTICLE

Plant and soil seed bank diversity across a range of ages of *Eucalyptus grandis* plantations afforested on arable lands

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Abstract
Aims Plantation forests are often assumed to have reduced biodiversity relative to unmanaged forests. However, existing knowledge is based on studies of rotation-aged tree crops. We investigated how *Eucalyptus* afforestation of agricultural land affected plant species composition and biodiversity across a range of plantation ages (1–10 years). We also studied whether the soil seed bank could contribute to regeneration of existing vegetation in such plantations.
Methods We used a chronosequence approach to evaluate plant and seed species composition and diversity in forests and soil seed banks. We also quantified the similarity of seed banks and aboveground vegetation within plantation sites of a given age. Plantation sites were also compared to a nearby, mature pine forest.
Results Total plant species number, density and diversity in *Eucalyptus grandis* plantations increased for the first 3 years plantation establishment, then stabilized or decreased for the next 1–2 years and then increase significantly over the following years. Species number and density in soil seed bank increased significantly with plantation age only after an initial 6-year decrease. Shannon–Wiener index of total species diversity did not significantly differ with plantation age. The understory vegetation and soil seed bank were dominated by pioneer species in the first 3 years, but intermediate-successional and shade-tolerant species gradually invaded as plantations developed further. After 7 years, *E. grandis* plantation understories were composed of mainly shade-tolerant species. Nevertheless, the diversity of the diversity of intermediate-successional in soil seed banks were higher than that of shade-tolerant species in soil seed banks at this age range (7–10 year). Among species successfully germinated from soil seed banks, 48 % were not found in the aboveground plant community. Similarities between the species in the soil seed bank and the aboveground vegetation were low for both plantation and control forests and did not significantly change with plantation ages.
Conclusions *E. grandis* likely produces a changing microclimate during plantation development, which in turn drives composition and diversity dynamics in understory vegetation and soil seed banks after the afforestation of agricultural land. The first 4 years after plantation establishment is associated with lower plant and soil seed bank diversity, meriting a greater focus on biodiversity stabilization and possibly longer rotation periods.

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Introduction

Forest plantations, which occupy approximately 0.20 billion ha worldwide, support increasing local and global demands for wood (FAO 2007) and are considered rapid-response carbon sinks that may help mitigate increasing atmospheric CO_2. However, scientists increasingly recognise that the large-scale development of commercial plantations can have ecological consequences. Fast-growing trees can affect the establishment of natural vegetation and understorey ecology via resource competition (Smith et al. 2000; Bremer and Farley 2010), allelopathy (Ahmed et al. 2008; Zhang et al. 2010b) or degradation soil fertility (Wall and Heiskanen 2003; Sicardi et al. 2004; Zhang et al. 2010a, b). Therefore, understanding how plantations afforestation would affect the biodiversity is critical to understanding the ecological functions of plantations and improving their management.

Land use change has been recognised as the most important driver of changes in biodiversity in the current century (Brokerhoff et al. 2008). In recent decades, the afforestation of agricultural land has represented a major change in land use in some developing countries (e.g. Brazil, India and China). In particular, China, which has the largest area of plantation forests in the world, is engaging in massive ongoing afforestation programs, such as the project to return croplands to forests (FAO 2006), to mitigate environmental problems resulting from previous substantial losses of forests and forest biodiversity. Most previous studies have found that converting natural and semi-natural grasslands and shrublands or primary forest into plantations is likely to be detrimental for biodiversity (Barlow et al. 2007; Gibson et al. 2011). Furthermore, an expanding body of literature has found lower levels of biodiversity in plantations, especially when used for commercial production (Humphrey et al. 2000; Cao et al. 2010; Sang et al. 2013). Nevertheless, a few studies have shown that other types of plantations (restoration, wildlife conservation, etc.) can play important roles in biodiversity conservation and species restoration (Hartley 2002; Carnus et al. 2006; Brokerhoff et al. 2008; Cao et al 2008). This discrepancy has led to a lack of consensus as to whether or not plantations might be detrimental to biodiversity conservation. Numerous factors ultimately determine the likely effects of plantations on biodiversity, such as stand age, species grown, land use preceding the establishment of a plantation, the plantation species and whether plantation afforestation is for commercial, restoration, wildlife conservation or other purposes (Brokerhoff et al. 2008; Bremer and Farley 2010). We suggest that these factors known to influence biodiversity, along with others such as changes in understory microclimate after plantation establishment, position within the landscape matrix and whether the area is managed for conservation goals, should all be considered when determining the effects of a plantation forest on biodiversity conservation.

Plant diversity in the plantation understory plays important roles in improving soil fertility, stimulating the soil nutrient cycle and maintaining soil quality (Halpern 1995; Carnus et al. 2006; Wang et al. 2011). The maintenance of plant diversity in plantations depends on the soil seed bank and other propagules. Soil seed banks reflect past ecological conditions and offer important potential for regenerating current and past vegetation (Aparicio and Guisande 1997; Fenner 2000; Díaz-Villa et al. 2003; Macdonald and Fenniak 2007). However, little information regarding soil seed bank characteristics is available from plantations established on formerly arable lands. *Eucalyptus* is a fast-growing, commercially available tree that has been introduced in developing countries such as Brazil, India and China. In such countries, *Eucalyptus* plantations are generally managed with a short rotation period (5–7 years) for wood production (Zhang et al. 2010a, 2012). These plantations cover more than 200,000 ha in southwestern China (Zhang et al. 2010a), where *Eucalyptus grandis* Hill ex Maiden is one of the primary tree species used for afforestation of arable land. Previous studies have indicated that *Eucalyptus* plantations have impoverished floral, faunal and soil biodiversity (Pellen and Garay 1999; Behera and Sahani 2003; Cao et al. 2010; Calvino-Cancela et al. 2012). However, most of these studies were conducted in plantations of a particular age prior to the rotation period, providing little knowledge of biodiversity in well-established *Eucalyptus* plantations.

In order to help improve our current understanding about the effects of *Eucalyptus* plantations on biodiversity conservation, we measured changes in plant and soil seed bank diversity in *E. grandis* plantations converted from agricultural land. Using a chronosequence approach, we tested the hypotheses that (a) plant and soil seed bank diversity would increase with the development of *E. grandis* plantations and (b) plantation soil seed banks could offer the potential for the regenerating understory vegetation. The findings can help support the development of biodiversity management strategies for *Eucalyptus* stands in southwestern China.

Materials and methods

Study region and site locations

The study was conducted in the Danling region (102°57′–103°04′E, 29°55′–29°59′N, 570–592 m a.s.l) located to the western Sichuan Province of southwestern China. The study site has a subtropical climate, with a mean annual temperature, precipitation and relative humidity of the site are 17.5 °C, 1,397 mm and 82 %, respectively. The soil is classified as ferralsol derived from Pleistocene alluvium and has a yellow colour, loam texture and granular structure (Zhang et al. 2010a, b).Within the Danling region, *Eucalyptus* plantations, cultivated land and unmanaged forests formed a landscape mosaic in this region. The large, recently afforested plantations are located on former agricultural land and contain *E. grandis* ranging from 1 to 10 years old. *Pinus massoniana* lamb. trees dominate the unmanaged stands, along with a very few *Cyclobalanopsis glauca* (Thunb.) Oerst. trees. Although *P. massoniana* forests cannot be regarded as native or natural forests, these unmanaged forest areas represent stable, mature forest ecosystems and were treated as ecological controls for afforested sites.

Experimental site selection was based in part on consultations with forest survey personnel and landowners to confirm site suitability. The soils of all the sites were developed from the same parent material, and all sites had similar soil type, slope and land use history. In particular, all sites had been ploughed prior to afforestation, used agriculturally for at least 100 years prior, and previously managed with an intensity and cropping system typical for the region and similar to present agricultural sites. Management practices after afforestation had been similar across plantation sites, with no fertilization or weed control treatments applied. *E. grandis* trees had been planted no more than 2 years after tillage termination, and trees in the young stands had not been thinned. In summary, all study sites were larger than 10 ha, located on relatively flat terrain (<5°) and had been afforested from 1 to 10 years (Table 1, Fig. 1).

The above site selection criteria are consistent with the assumption that the study sites had similar soil characteristics prior to afforestation and that an adjacent agricultural site could be considered as another control. At all agricultural sites selected, crop rotations were similar and had remained the same for several decades. Rice, potatoes, white gourd and broccoli were grown during the sampling year (2008), although oat and sweet potato had also been planted in the past 5 years. Fertilisation rates were generally low and comparable at all sites, with yard manure applied every year at a rate of 15 t ha^{-1} and occasional applications of mineral fertilizers. None of these sites had been limed during the past 6 years. Seeds in previous agricultural use were always harvested with the crop.

Plant survey and soil sampling

A chronosequence approach was used to evaluate changes in plant diversity and soil seed banks following afforestation. We divided plantation sites into three age categories: (1) prior to rotation period (1–4 years), (2) during rotation period (5–7 years) and (3) after rotation period (8–10 years). Three sites of each age were selected for sampling. Soil physicochemical properties for each plantation age were shown in Table 2. One agricultural site and three *P. massoniana* forests within approximately 1 km of the plantation sites were chosen as control sites (Fig. 1). At each site, one 20×20 m plot was established in October 2008, and vegetation surveys were conducted in these plots. Within each plot, five quadrats of 5×5 m, each containing a 1×1 m subquadrat at its centre, were designated to quantify the shrub layer and herbaceous layer (Fig. 1). For both shrubs (tree seedlings and woody climbing plants with <2.5 cm stem diameter) and herbaceous plants (perennial and annual herbs, herbaceous climbing plants and ferns), the number of stems and plant heights were tallied for each species. The coverage of each seed plant species was estimated visually, and species were classified into pioneer species, intermediate-successional and shade-tolerant species (Flora Republicae Popularis 2004)

After manually removing stones, roots and plant fragments, six soil samples of 10×10×10 cm were

Table 1 Characteristics of study sites and *E. grandis* tree across a range of forest ages

Site (years)	Altitude (m)	Slope aspect	Slope (°)	Density (ind ha^{-1})	Canopy closure (ratio)	Mean DBH (cm)	Mean height (m)
1	556.2	NE27	4.1	1,665	0.40 (0.11)	6.0 (0.7)	3.0 (0.5)
2	557.1	NE36	3.6	1,665	0.50 (0.12)	7.5 (0.8)	6.5 (0.5)
3	558.3	NE38	4.3	1,700	0.65 (0.09)	9.0 (0.9)	9.6 (0.5)
4	556.5	NE30	3.9	1,700	0.70 (0.06)	12.0 (1.1)	13.5 (0.2)
5	557.3	NE30	3.4	1,700	0.60 (0.03)	13.0 (1.2)	14.0 (0.5)
6	556.4	NE32	0.38	1,700	0.65 (0.13)	13.5 (1.8)	15.0 (0.7)
7	557.7	NE29	3.7	1,700	0.60 (0.22)	14.5 (1.6)	17.8 (0.9)
8	556.1	NE28	3.9	1,665	0.65 (0.12)	16.7 (1.0)	18.5 (0.2)
9	555.7	NE27	4.8	1,665	0.70 (0.08)	21.8 (1.1)	22.0 (0.3)
10	556.8	NE29	4.9	1,665	0.75 (0.12)	23.6 (0.5)	25.0 (0.6)

Parentheses indicate±standard deviation

randomly excavated from each 20×20 m plot with enough care to keep the litter intact. The soil samples were split into three depth classes (litter layer, 0–5 cm and 5–10 cm), then these subsamples were placed in plastic bags, mixed thoroughly, and taken to the laboratory for seed bank analysis.

Laboratory analyses

To assess seed abundance (density) and species composition in the seed banks at each site, we conducted seed germination trials. Each soil sample was first passed through a 2-mm sieve to remove coarse debris; then

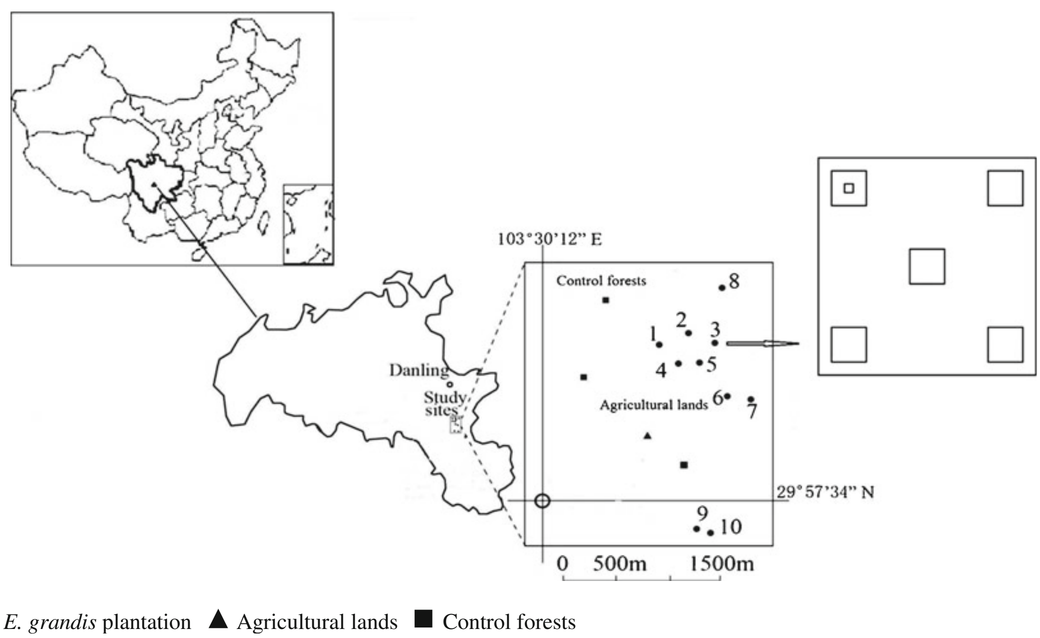


Fig. 1 Study region in southwest China, sites, plots and sampling regimes. *Inset* shows the plantation, unmanaged forest and agricultural sites near Hechang Township. *Arrow* indicates the sampling setup of 5×5 m quadrats within a single 20×20 m plot and shows an example 1×1 m sub-quadrat

Table 2 Soil physicochemical properties across a range of *E. grandis* plantation ages

Plantation age (years)	Bulk density (mg m^{-2})	Water content (kg kg^{-1})	Organic matter (g C kg^{-1})	N tot (g N kg^{-1})	P tot (mg P kg^{-1})	MBC (mg kg^{-1})	MBN (mg kg^{-1})
1	1.56 (0.02)	0.24 (0.05)	10.3 (1.29)	0.165 (0.02)	342.0 (14.0)	202.16 (24.60)	6.24 (1.35)
2	1.44 (0.07)	0.26 (0.03)	8.69 (1.66)	0.166 (0.01)	339.2 (8.30)	247.75 (19.76)	5.83 (1.67)
3	1.39 (0.04)	0.27 (0.01)	8.48 (1.35)	0.153 (0.01)	335.2 (32.70)	256.78 (7.13)	5.15 (1.87)
4	1.31 (0.06)	0.26 (0.03)	7.33 (1.10)	0.149 (0.02)	320.2 (28.70)	200.85 (17.99)	4.26 (0.96)
5	1.25 (0.02)	0.29 (0.01)	8.33 (1.21)	0.167 (0.03)	319.4 (51.5)	257.48 (19.82)	5.61 (1.06)
6	1.22 (0.01)	0.32 (0.03)	10.26 (1.22)	0.168 (0.01)	315.2 (17.20)	319.36 (13.27)	7.45 (1.65)
7	1.21 (0.02)	0.32 (0.01)	12.21 (1.23)	0.165 (0.03)	312.7 (21.80)	390.15 (21.28)	9.51 (2.19)
8	1.22 (0.01)	0.32 (0.06)	15.26 (1.15)	0.166 (0.01)	311.1 (21.70)	488.10 (20.92)	10.75 (1.44)
9	1.17 (0.01)	0.33 (0.01)	16.37 (1.28)	0.168 (0.03)	308.1 (16.50)	518.23 (17.89)	12.11 (1.93)
10	1.13 (0.02)	0.34 (0.05)	18.29 (1.31)	0.171 (0.04)	306.5 (18.00)	538.17 (21.233)	12.38 (1.78)

Values in parentheses indicate±standard deviation

N tot total nitrogen, *P tot* total phosphorus, *MBC* microbial carbon biomass, *MBN* microbial nitrogen biomass

seeds with a diameter larger than 2 mm were retrieved and returned to their respective sieved samples. Each sieved soil sample was spread on a layer of heat-sterilised (100 °C, 10 h) sand in a seed germination tray. All the germination trays were covered with nylon nets to prevent seed intrusion from or within the glasshouse and were placed in an experimental greenhouse, watered daily to keep the soil moist. Newly germinated seedlings were identified at the species level, 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. The germination assay continued until no new seedlings emerged for 4 weeks (Wang et al. 2009). The greenhouse had a mean temperature of 25 °C and mean relative humidity of 65 %.

Data analysis

Seed density was calculated from the number of emerged seedlings per square metre. Shannon–Wiener (H′) values were selected to determine the diversity of plants and of the soil seed bank (Halpern 1995). Similarities in species composition between the soil seed banks and the aboveground vegetation in *E. grandis* plantation and control forests were analysed using the Sorensen index (SI), $SI = c/(a+b-c)$, where a is the number of species present in site A, b is the number of species present in site B and c is the number of species that site A and site B have in common (Du et al. 2007).

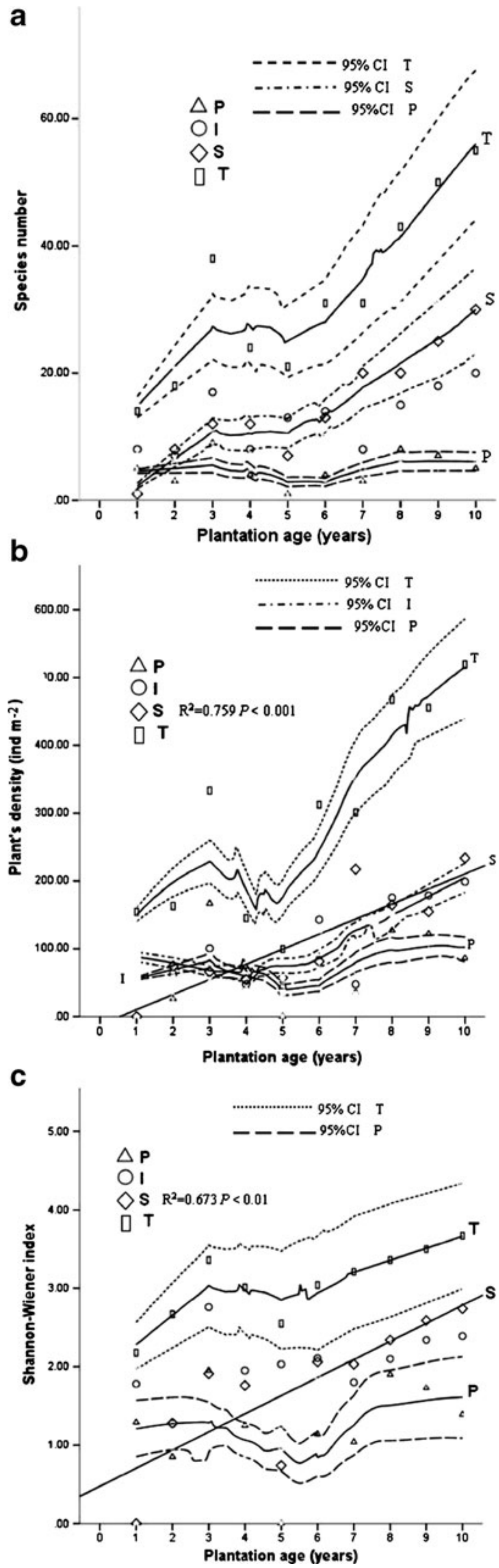
All data were statistically analysed using SPSS v.21.0. After the pairwise comparisons tests made upon the MANOVA, the responses of the abundance and diversity of the vegetation and the soil seed bank properties to age were evaluated by liner and non-parametric LOESS regression with the 95 % confidence intervals (95 % CI). After verifying the general ANOVA hypothesis, detailed post hoc mean comparisons for the study stands and the control sites were performed using Tukey's HSD. The homogeneity of the variances was tested by the Levene's test. Any data sets failing this test were log-transformed before further analysis to help satisfy the requirement of variance homogeneity. Differences among means were considered statistically significant if $p<0.05$, with levels of significance denoted as follows: ***$p<0.001$, significant at **$p<0.01$, significant at *$p<0.05$, *ns*=not significant.

Results

Composition and diversity of understorey plant species

Seventy-eight species in 44 vascular plant families were observed in 1- to 10-year-old *E. grandis* plantation sites (Table 5 in Appendix). Herbs, followed by woody plant, dominated the composition of the understorey

Fig. 2 Species number (**a**), species density (**b**) and Shannon–Wiener index (**c**) for understory plants sampled in a chronosequence of *E. grandis* plantations. *T* = total plant species, *P* = pioneer species, *I* = intermediate-successional species and *S* = shade-tolerant species



vegetation in terms of species richness. Among the total herbaceous species across all sampled plantation ages, perennial herbs were dominant (55–73 %), followed by annual herbs (15–27 %) and climbing herbaceous plants (7–21 %) plants. For total species (T), plant species number, density and Shannon–Wiener index, all increased significantly in the first 3 years exhibited a decrease or no change during the fourth and fifth years, and increased again with additional years (Fig. 2). The pioneer species (P) remained at low richness and density through the chronosequence (Fig. 2a, b). The Shannon–Wiener index of pioneer species decreased during the first 5 years, then increased during following years (Fig. 2c). The number and density of intermediate-successional species (I) also tracked the corresponding trends for total species, while the Shannon–Wiener index for this group increased significantly with plantation age (Fig. 2c). Finally, while the number of shade-tolerant species (S) followed the same trend as seen for total species (Fig. 2a), species density and Shannon–Wiener index for this group both increased significantly with plantation age (Fig. 2b, c).

Composition, size and diversity of the soil seed bank

The seeds of 58 species in 38 vascular plant families were observed in the soil seed banks of 1- to 10-year-old *E. grandis* plantations sites (Table 6 in the Appendix). Herbaceous species again dominated, both in terms of species number and seed density. Most seeds were found in 0–5 cm soil subsample, with fewer in the leaf litter and the fewest in the 5–10-cm soil layer (F= 561.165, p<0.001). The species number of total species increased significantly with plantation age (Fig. 3a), while the total seed density decreased significantly for the first 6 years before increasing with additional plantation age (Fig. 3b). No significant responses to age were found for the Shannon–Wiener index of total species of seeds (Fig.3c). While the number of pioneer species decreased during the first 4 years before beginning to increase with age (Fig. 3a), the density and Shannon–Wiener index of this group decreased during the first 6 years before increasing (Fig. 3b, c). The

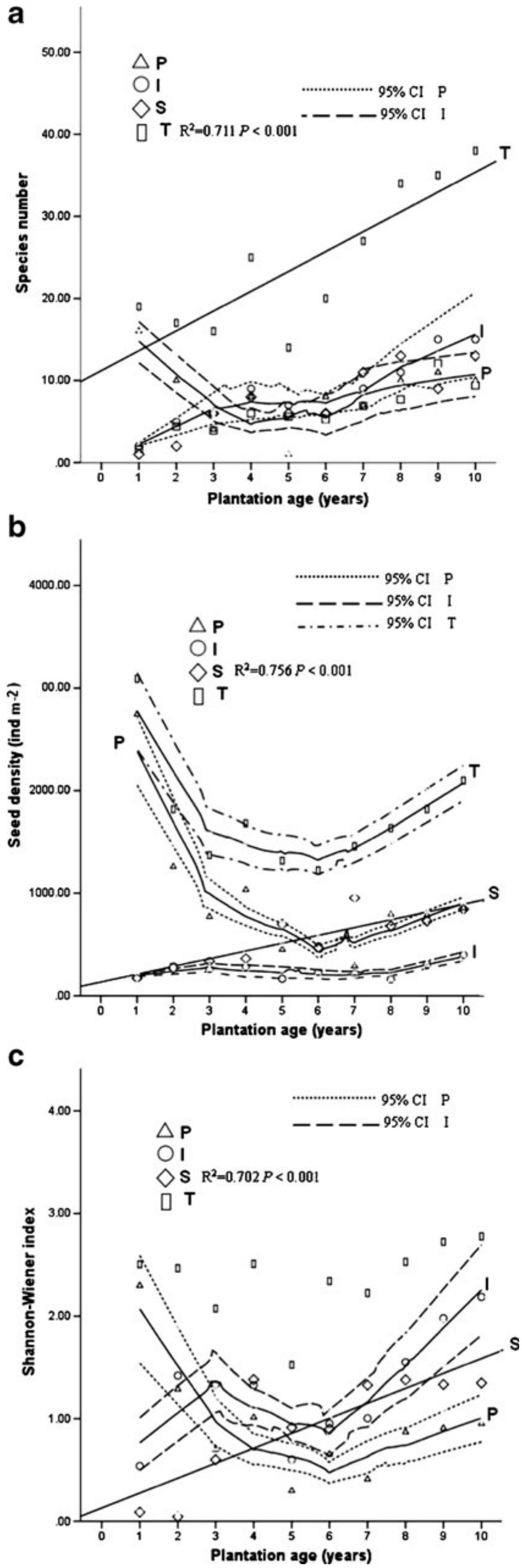


Fig. 3 Species number (**a**), species density (**b**) and Shannon–Wiener index (**c**) for seedlings germinated from soil seed bank samples from a chronosequence of *E. grandis* plantations. *T* = total plant species, *P* = pioneer species, *I* = intermediate-successional species and *S* = shade-tolerant species

species number, density and Shannon–Wiener index of intermediate-successional species increased during the first 3 years, then stabilized during years 4 through 6 before increasing with age (Fig. 3).This pattern was also seen for the number of shade-tolerant species' seed, while the density and Shannon–Wiener index for this type of seed showed a continuous, significant increase with plantation age (Fig. 3b, c).

Across 10-year range of plantation ages, 75 % of species in the extant vegetation were present in the soil seed bank and 62 % of the species in the soil seed bank were present in the extant vegetation. The species composition similarity of herb (0.08–0.14) and total (0.06–0.32) between the soil seed bank and the aboveground vegetation in the study sites was low. The species composition similarity of shrub species in 2–10-year-old stands was low (0.18–0.47), with the exception of the shrub species in 1-year-old plantation (0.80). Despite this observation, plantation age did not significantly influence species composition similarity (Table 3).

Comparison with the control sites

Eight weed species, belonging to 6 families, were found in the agricultural sites; 16 weed species, belonging to 10 families, germinated from the soil samples of these sites (data not shown). Multiple comparisons test indicated that species richness, density and diversity for both the vegetation and soil seed bank of the *E. grandis* study sites were significantly higher ($p<0.001$) than the corresponding measurements in the agricultural land (data not shown).

One hundred and sixty-four understorey plant species, belonging to 75 families, were found in the forest sites (*P. massoniana*) (Table 7 in the Appendix), while 95 plant species, belonging to 74 families, germinated from the soil samples of these sites (Table 8 in the Appendix). Herbaceous species dominated the composition of both the understory plants and soil seed bank. As seen for the plantations, the species composition similarity (0.32) of the species between the soil seed bank and aboveground vegetation were relatively low (Table 3). Species found in aboveground vegetation at

Table 3 Species composition similarity (SI) between understory plants and soil seed banks in a chronosequence of *E. grandis* plantations and control forests (*P. massoniana*)

	Plantation age (years)										Control
	1	2	3	4	5	6	7	8	9	10	
Herb layer	0.08 (0.02)	0.15 (0.03)	0.20 (0.04)	0.08 (0.01)	0.11 (0.02)	0.23 (0.06)	0.21 (0.05)	0.24 (0.06)	0.25 (0.04)	0.14 (0.06)	0.21 (0.02)
Woody layer	0.80 (0.02)	0.18 (0.03)	0.24 (0.02)	0.17 (0.01)	0.00 (0.00)	0.42 (0.01)	0.26 (0.03)	0.43 (0.06)	0.32 (0.04)	0.47 (0.05)	0.32 (0.04)
Community	0.19 (0.01)	0.16 (0.02)	0.22 (0.04)	0.12 (0.01)	0.06 (0.02)	0.32 (0.11)	0.23 (0.08)	0.35 (0.03)	0.29 (0.05)	0.32 (0.04)	0.28 (0.04)

Values in parentheses indicate+standard deviation

these control sites accounted for 87 % of those found in the soil seed banks of plantation sites overall. Multiple comparisons test (Table 4) indicated that species richness and density for both the vegetation and soil seed bank of the *E. grandis* study sites were significantly lower than the corresponding measurements in the control forests. The Shannon–Wiener indices for all understorey vegetation in the 1-, 2- and 5-year-old *E. grandis* plantations were significantly lower than that found for the control forests; however, the indices for 3-, 4-, and 6–10-year-old *E. grandis* plantation were similar to those in the control forests. The Shannon–Wiener indices for herbaceous species in the soil seed bank of *E. grandis* plantations 1–8 years old were significantly lower than that of the control forests; in the 9- and 10-year-old plantations, they were similar to that for the control forests. In plantation sites of 1–2 years old, the Shannon–Wiener indices for all plant seeds and for woody species' seeds in the soil seed bank were significantly lower than that of the control forests. However, *E. grandis* plantations in the mid- to post-rotation phase (6–10 years) showed no significant differences in Shannon–Wiener indices compared to control forests.

Discussion

Understorey vegetation

Our hypotheses that plant would increase with the development of *E. grandis* plantations were supported by the findings in this study. However, our results showed that plant abundance and diversity in *E. grandis* plantations increased for the first 3 years plantation establishment, then stabilized or decreased for the next 1–2 years and then increase significantly over the following years.

Table 4 Tukey's HSD tests separating mean plant and soil seed bank species richness, density and diversity indices for a chronosequence of *E. grandis* plantations and a control site (*P. massoniana*)

	Species richness	Density (ind m^{-2})	Shannon–Wiener index
Plants			
Herb	(1–10)[a] ***	(1–10)***	(1)**; (2, 5)*; (3, 4, 6–10) ns
Shrub	(1–10)***	(1–10)***	(1)**; (2, 5)**; (3, 4, 6–10) ns
Community	(1–10)***	(1–10)***	(1)**; (2, 5)**; (3, 4, 6–10)ns
Soil seed banks			
Herb	(1–10)***	(1–10)***	(1, 2, 4, 5)***; (3, 8)*; (6, 7)**; (8)*; (9–10)ns
Shrub	(1–10)***	(1–10)***	(1, 5)**; (2)*; (3, 4, 6–10)ns
Community	(1–10)***	(1–10)***	(1)***; (2, 5)**; (4)*; (3, 6–10)ns

Levels of significance are indicated as described in "Materials and methods"

[a] Plantation age

A few weed species were found in previous agricultural site because the tillage weeding was applied and seeds were always harvested with the crop. Although the plantations in this study were afforested on the former cropland many, plant propagates (e.g. root stumps, soil seed banks in deeper soil layers) remained (Egler 1954). Furthermore, plant regeneration during the initial stage of *E. grandis* afforestation (the first 3 years) most likely resulted from the cessation of agricultural management and the closure of the lower canopy, which facilitated the germination and dispersal of seeds from the pioneer, shade-intolerant herbaceous species, a few intermediate-successional species and the growth of younger seedlings (Sem and Enright 1995; Garay et al. 2004; Wang et al. 2009). A previous study of the sites investigated here indicated that the growth rate of *E. grandis* increased and reached a maximum rate before the rotation period began, approximately 4 years after initial afforestation, and then decreased with plantation age (Zhang et al. 2012). At a plantation age of about 4–5 years, fast-growing *E. grandis* could likely still compete for soil resources with other plants. Soil organic matter has previously been shown to exhibit an initial decline over the first 4 years of *E. grandis* plantation establishment, but it increases significantly over time in the upper soil layers thereafter (Zhang et al. 2012). At this stage, higher concentrations of allelochemicals and more severe allelopathic effects from roots and soil in *E. grandis* plantations are known to inhibit seed germination and growth of younger seedlings, reducing the abundance of other species (Zhang et al. 2010a, b). Canopy cover has been found to support the occurrence and growth of shade-tolerant and reduce intolerant species (Parrotta et al. 1997; Plue et al 2010). The rapid growth rate of the *Eucalyptus* trees in plantations creates a closed canopy prior to the rotation period, and subsequent limited light conditions did not facilitate the input of shade-intolerant seeds or the regeneration of younger seedlings. Microclimatic changes of limited light availability, severe competition for water and nutrients, and allelopathy could help account for the relative stability or decrease in understory plant biodiversity during the fourth and fifth years after plantation establishment. As *E. grandis* stands aged (6–10 years), the understory vegetation was gradually replaced by shade-adapted species. This may be due to a gradual increase in facilitative effects of the planted trees for shade-adapted species based on increased lateral and vertical heterogeneity, better development of soil organic layers and associated fungal flora, increased deadfall and a better light environment over time (Allen et al. 1995; Brockerhoff et al. 2003; Bremer and Farley 2010; Zhang et al 2012). Furthermore, the abundant availability of precipitation in this region could weaken any allelopathic effects associated with greater plantation ages (Moline 1991; Zhang et al. 2010a). As a whole, changing microclimatic conditions across the *E. grandis* chronosequence was a likely driving factor in plant species composition and diversity dynamics after afforestation.

Seed banks

We did not find support for our hypothesis that soil seed bank diversity would increase with the development of *E. grandis* plantations. The present results showed that Shannon–Wiener index of total species diversity of soil seed bank did not significantly differ with plantation age. However, species number and density in soil seed bank increased significantly with plantation age only after an initial 6-year decrease. Seed bank density at all study sites were relatively higher compared with those found in some previous studies of the effects of plantations afforestation (Wang et al. 2009; Li et al. 2012). Seed bank density in plantations afforested on grasslands or shrublands has often been found to peak early (initial 1–2 years) after afforestation, then slowly decline (Sem and Enright 1995; Huang et al. 1996; Thompson 2000; Plue et al. 2010). In the present study, species abundance and diversity was greatest at the initial stage of *E. grandis* afforestation of former agricultural land. This was associated with high number of pioneer annual and perennial herbs, suggesting a high seed input for these species upon cessation of agricultural management. Seeds in previous agricultural use were always harvested with the crop. Later in the chronosequence, pioneer species' seed densities and diversity decreased, while abundance and diversity of intermediate-successional and shade-tolerant species became relatively stable. This might be attributable to microclimatic changes associated with the development of the plantations, such as canopy closure, reduced light availability, greater allelopathy, germination of the pioneer seeds without survival to the reproductive phase and seed death caused by factors such as higher soil moisture or invertebrate predation. After 7 years, the composition of soil seed bank was increasingly composed of intermediate-successional and shade-tolerant species, which might be attributed to continuing changes in microclimatic conditions resulting from the plantations' succession. The aboveground structural complexity developed after the rotation period (7–10 years) is known to be more conducive to seed input and dispersal for intermediate-successional and shade-tolerant species (Li et al. 2012; Bremer and Farley 2010). The diversity of intermediate-successional species in soil seed banks was higher than that of shade-tolerant species. Furthermore, among the 58 plant species observed in plantation the soil seed banks, herbaceous species accounted for 40.5–83.3 %, with annuals comprising 24.3–50 % and perennials comprising herbs comprising 16.2–33.3 %, suggesting that the plant community was at a comparatively early successional stage (Thompson 2000). We also found that soil seed bank density was significantly higher in 0–5-cm soil layer than in leaf litter or 5–10 cm layer, inconsistent with previous results in which seeds in the litter layer accounted for the highest proportion of the total number of seeds (Du et al. 2007). Such a result might be attributable to a looser litter layer, greater turnover of leaf litter or greater seed dispersal by birds, vertebrates and soil fauna in *E. grandis* plantations (Appleby 1991; Yan et al. 2010; Zhang et al. 2010a, b). Despite observed changes in species number and abundance, species diversity (Shannon–Wiener index) of the soil seed bank did not change across the chronosequence, possibly indicating changes in species evenness related to the dominance of species such as *Polygonum hydropiper*, *Digitaria sanguinalis* or *Oplismenus undulatifolius* under *E. grandis* plantations.

Under natural conditions, seeds in the soil seed bank are both derived from the local aboveground vegetation and contribute to the regeneration of that aboveground vegetation through germination and seedling growth. Significant differences between the composition of the seed bank and the actual vegetation are not uncommon (Thompson 2000; Díaz-Villa et al. 2003; Vilà and Gimeno 2007) and may be attributed to the environmental variability that affects seed dispersal and the effect of dormancy, which buffers against rapid changes in species composition (Thompson and Grime 1979; Thompson 1992; Yan et al. 2010; Plue et al. 2010). A few studies have indicated that the species number in common between soil seed bank and aboveground vegetation decreases with forest succession (Bremer and Farley 2010; Hu et al. 2013). Across a range of *E. grandis* plantation ages (1–10 years), 75 % of species in the extant vegetation were present in the soil seed bank, indicating that the succession of *E. grandis* plantations facilitated seed input and seedling regeneration, likely in conjunction with changes in understory microclimate. Our hypothesis that plantation soil seed banks could offer the potential for the regenerating understory vegetation was supported by the findings in this study. At the same time, 48 % of the species germinated in soil seed bank samples were not found in the aboveground plant community. Meanwhile, 87 % of the species in the soil seed bank of *E. grandis* plantations were identified located in the aboveground vegetation of the control sites (*P. massoniana*). The planted trees therefore affected the makeup of understory vegetation both during plantation development and relative to the control site. Such observations may be related to changing understory microclimates or the greater development of litter and humus layers in *Eucalyptus* plantations over time. These changes may have led to increased seed inputs from the neighbour forests by seed-dispersing wildlife attracted to the plantations (Thompson 2000; Brockerhoff et al. 2008). However, factors such as the closed canopy, more severe allelopathy and relatively thicker litter layer during or prior to the rotation period (starting about 4–6 years after establishment) may account for a stabilization in seed species number, density or diversity index in soil seed banks of the *E. grandis* plantations.

Conservation implications

Most of the studies on plantations biodiversity have compared species measures to those in natural forests without considering whether such comparisons are appropriate (Brokerhoff et al. 2008). *Eucalyptus* plantation forests are often assumed to support lower species abundance and diversity compared to natural forests (Nsabimana et al. 2004; Stephen and Wagner 2007; Bremer and Farley 2010). However, most of these studies focused on young *Eucalyptus* plantations prior to the rotation period. The short rotation period of 5–7 years generally used for wood production in developing countries can inhibit a clear, comprehensive understanding of the effects of *Eucalyptus* plantations on understory plant diversity. In the present study, the species abundance and diversity of plants and soil seed banks exhibited dynamic changes after the afforestation of agricultural land with *E. grandis*. Plant and soil seed bank diversity in *E. grandis* plantations were not significantly different from those measures in control forests once the plantations have surpassed the rotation period. Although the control forests, consisting mainly of *P. massoniana*, do represent stable, mature forest ecosystems common in this region, they were not native forests, but forests dominated by an exotic species. Furthermore, similarity indices between seed banks and vegetation at these sites were relatively low, and the indices for plantation sites did not significantly change with succession. Therefore, the recovery of plant diversity in the study plantations is likely to last a longer period of time than that before which *E. grandis* plantations are typically harvested (<5–7 years).

Such findings overall support the use of scientific management measures to support biodiversity conservation in *E. grandis* plantations, especially for the relatively lower plant diversity found in *E. grandis* plantations prior to the rotation period (~4 years). Although *Eucalyptus* plantations of different ages are found in study region, they are typically composed of the single tree species. The establishment of plantations with diverse tree species would provide more habitat types for native species (Lamb 1998; Norton 1998; Hartley 2002; Hu et al. 2013). Furthermore, avoiding intensive site preparation of plantations may help limit the destruction of existing herbaceous vegetation and woody debris (Hartley 2002; Lindenmayer and Franklin 2002; Carnus et al. 2006). Wider tree spacing during plantation establishment support better maintenance of understorey vegetation (Brokerhoff et al. 2008). Although the afforestation of agricultural land in China aims to mitigate environmental problems, the majority of plantation forests are managed primarily for production purposes and have a short rotation period. An increase in rotation length has been advocated as a means to enhance the native biodiversity in plantations (Rosoman 1994; Humphrey et al. 2006; Bremer and Farley 2010). This approach is also supported by the results of our chronosequence study of plant and seed bank biodiversity. Scientific thinning, fertilising, watering and soil burrowing for the first 4 years after establishment while forbidding litter collection may lessen competition for resources and increase the environmental heterogeneity, by facilitating the regeneration of understorey vegetation.

Conclusions

In conclusion, the present chronosequence study of biodiversity in *E. grandis* plantations partly supports the hypothesis that plant's abundance and diversity in such plantations can increase given a more comprehensive time frame. In particular, the plant species abundance and diversity increased with plantation age for the first 3 years, then stabilized or slightly decreased during years 4 and 5. Our hypothesis that plantation soil seed banks could offer the potential for the regenerating understory vegetation was supported by the findings in this study. Seed species number and density of plantation soil seed banks increased significantly with plantation age, only after an initial 6-year decline in total seed species density. Contrary to our initial hypothesis, the diversity index of total species of soil seed bank did not respond significantly to plantation age. Some evidence of succession was seen in this study, as the understory vegetation and soil seed bank were dominated by pioneer species in the first 3 years, with intermediate-successional and shade-tolerant species gradually invading as plantations aged. After 7 years, the understory vegetation in *E. grandis* plantations was primarily made up of shade-tolerant species; however, the diversity of intermediate-successional seeds in soil seed banks was higher than that of shade-tolerant species. Overall, our results suggest the use of scientific management measures may help support greater biodiversity in *E. grandis* plantations, especially for plantations prior to the rotation period (~4 years), which exhibited relatively low plant diversity.

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Appendix

Table 5 Understory shrub and herbaceous species names, the individual number, important value and habit along a chronosequence of *E. grandis* plantations

Species name, and habit	Abundance									
	1 Plantation age (years)	2	3	4	5	6	7	8	9	10
Shrub species										
1 *Symplocos laurina* (I)		1[a] (9.32)[b]	6 (5.13)				5 (6.46)	7 (5.40)	5 (4.07)	6 (3.60)
2 *Gordonia acuminate* (S)					1 (8.10)	3 (5.25)	6 (6.77)	6 (5.12)	7 (4.63)	6 (3.62)
3 *Ficus henryi Warb* (S)				1 (7.24)	1 (8.20)			2 (3.90)	3 (3.48)	2 (2.79)
4 *Broussonetia papyifera* (S)									1 (2.90)	2 (2.78)
5 *Castanopsis spach* (S)								3 (4.22)	2 (3.20)	6 (3.61)
6 *Symplocos botryatha* (I)			13 (6.84)		7 (13.10)	9 (7.55)	10 (8.13)		7 (4.62)	5 (3.41)
7 *Cinnamomum camphora* (S)								2 (3.92)	1(2.93)	4 (3.26)
8 *Melia azedarac* (I)					1 (8.1)			2 (3.91)	1 (2.92)	4 (3.25)
9 *Rhododendron* sp. (I)				7 (10.88)	6 (12.27)	10 (7.93)		9 (6.02)	5 (4.06)	4 (3.20)
10 *Cornus officinalis* (S)						4 (5.63)				11 (4.66)
11 *Mallotus hookerianus* (S)		2 (10.47)				6 (6.40)	8 (7.48)	9 (6.12)	6 (4.34)	4 (3.27)
12 *Phoebe sheareri* (S)							1 (5.08)		2 (3.20)	3 (3.00)
13 *Trema cannabina* (S)			8 (5.62)	3 (8.47)		7 (6.78)	8 (7.48)	7 (5.40)	3 (3.49)	3 (3.01)
14 *Melastoma candidum* (I)		4 (12.76)	10 (6.11)					5 (4.80)	6 (4.34)	9 (4.24)
15 *Rhus chinensis* (S)		2 (10.47)	7 (5.39)			2 (4.87)	4 (6.12)	5 (4.82)	6 (4.35)	5 (3.41)
16 *Evodia lepta* (I)			8 (5.63)	6 (10.27)		5 (6.02)	10 (6.81)	7 (5.42)	7 (4.64)	6 (3.61)
17 *Myrsine Africana* (S)			5 (4.90)	3 (8.45)			12 (8.84)	7 (5.40)	6 (4.33)	5 (3.42)
18 *Rhodomyrtus tomentosa* (S)			9 (5.87)		5 (11.43)					
19 *Symplocos stellaris* (S)			7 (5.39)			5 (6.03)		3 (4.22)	5 (4.06)	4 (3.25)
20 *Eurya japonica* (S)						2 (4.87)	3 (5.78)		4 (3.77)	4 (3.20)
21 *Acanthopanax wilsonii* (S)						1 (4.48)		2 (3.91)	1 (2.92)	4 (3.19)
22 *Mallotus apelta* (S)				9 (12.09)	6 (12.25)	6 (6.40)			6 (4.33)	12 (4.86)
23 *Symplocos setchuensis* (S)			11 (6.35)	10 (12.69)				11 (6.63)	8 (4.91)	12 (4.85)
24 *Vitex negundo* (S)		4 (12.76)	5 (4.92)	4 (9.06)			4 (6.12)			3 (3.00)
25 *Lespedeza bicolor* (S)		6 (15.06)	9 (5.67)	7 (10.88)			12 (8.84)	7 (5.42)	9 (5.20)	8 (4.04)
26 *Lonicera szechuanica* (I)			9 (5.99)		9 (14.77)	13 (9.08)	11 (7.50)	5 (4.82)	6 (4.34)	9 (4.25)
27 *Smilax china* (P)	1 (27.12)		6 (5.15)							
28 *Broussonetia kaempferi* (I)	4 (39.13)	7 (16.21)	6 (5.17)		4 (10.60)	5 (6.02)	4 (6.12)		5 (4.06)	
29 *Rosa multiflora* (P)		3 (12.18)	9 (5.87)					9 (6.02)	5 (4.06)	6 (3.62)
30 *Millettia nitida* (I)			6 (5.16)	5 (9.66)		5 (6.12)		3 (4.22)		6 (3.62)
31 *Streptocaalon Griffith* (P)	3 (33.75)		4 (4.66)			4 (5.64)				7 (3.83)
Herb species										
32 *Cyerus szechuanensis* (P)			44 (8.12)			46 (9.97)		36 (3.48)	44 (5.88)	45 (5.16)
33 *Taraxacum mongolocum* (P)			8 (4.20)				7 (4.38))	4 (5.85)	6 (3.16)	7 (2.84)
34 *Oxalis corniculata* (P)				13 (7.12)		15 (6.41)			22 (4.31)	30 (4.24)
35 *Setaria allidifusca* (P)	21 (15.61)		36 (7.25)					15 (4.30)	19 (4.09)	
36 *Duchesnea indica* (I)	11 (11.01)	19 (9.61)			15 (14.79)	13 (6.18)		9 (3.85)	10 (3.45)	18 (3.51)
37 *Iris lacteal* (P)						27 (7.80)		29 (5.33)	12 (3.60)	

Table 5 (continued)

Species name, and habit	Abundance									
	1 Plantation age (years)	2	3	4	5	6	7	8	9	10
38 *Paspalum paspaloides* (P)							12 (4.89)			4 (2.66)
39 *Cayratia japoni* (I)	9 (11.43)		9 (4.34)							14 (3.27)
40 *Lygodiumjaponicum* (S)			23 (5.85)			28 (7.90)			21 (4.24)	
41 *Imerata cylindrical* (P)		7 (7.18)		6 (5.73)						
42 *Beautiful hyllodium* (P)	21 (14.96)	19 (9.61)	21 (5.63)	19 (8.47)				20 (5.63)		
43 *Dicranoteris linearis* (S)				11 (6.78)	14 (14.13)		10 (4.69		2 (2.88)	
44 *Prunella vulgaris* (I)			19 (5.40)			32 (8.36)		33 (4.67)	34 (5.17)	35 (4.55)
45 *Bothriochloa ischaemum* (P)			21 (5.63)				17 (5.40)			
46 *Paederia scandens* (I)			6 (4.01)			5 (5.26)	4 (4.07)			5 (2.72)
47 *Rubus corchorifolius* (I)	10 (10.72)		9 (4.34)	5 (5.52)				11 (4.00)	9 (3.38)	7 (2.84)
48 *Pteris semipinnata* (S)				13 (7.21)						22 (3.76)
49 *Arundinella hirta* (S)						11 (5.95)		20 (4.67)		
50 *Pedicularia* sp. (S)						33 (8.48)	44 (8.17)	38 (6.01)	36 (5.31)	30 (4.24)
51 *Deyeuxia arundinacea* (S)		19 (9.61)	23 (5.85)		17 (15.50)			10 (3.93)		5 (2.72)
52 *Stellaria alsine Grimm* (S)							17 (5.40)		21 (4.24)	40 (4.86)
53 *Sorghum nitidum* (I)		13 (8.39)							9 (3.38)	
54 *Duchesnea indica* (I)	11 (11.01)	19 (9.61)			15 (14.79)	13 (6.18)		9 (3.85)	10 (3.45)	18 (3.51)
55 *Pteris vittata* (I)				6 (5.73)	11 (13.37)		8 (4.48)			
56 *Iris lacteal* (I)						27 (7.80)		29 (5.33)	12 (3.60)	
57 *Centipeda minima* (P)				5 (5.52)				8 (3.78)		
58 *Senecio scandens* (S)							22 (5.91)			29 (4.18)
59 *Bothriochloa intermedia* (S)				22 (9.10)				19 (4.59)		10 (3.02)
60 *Cyperus rotundus* (S)						8 (5.60)	23 (6.01)			
61 *Geum aleppicum* (S)									11 (3.52)	
62 *Cuscuta chinensis* (I)			5 (3.91)	6 (5.73)		8 (5.60)		12 (4.08)	10 (3.45)	6 (2.78)
63 *Eragrostis pilosa* (S)							22 (5.19)	31 (5.48)		20 (3.63)
64 *Plantago asiatica* (S)							24 (6.11)	30 (5.41)	12 (3.59)	9 (2.96)
65 *Lophatherum gracile* (I)	13 (11.60)		18 (5.31)							
66 *Paspalum paspaloides* (S)							12 (4.89)			4 (2.66)
67 *Ficus tikoua* (I)	7 (9.83)	11 (7.99)	12 (4.66)	10 (6.57)		10 (5.83)			31 (4.95)	25 (3.94)
68 *Cayratia japoni* (I)	9 (11.43)		9 (4.34)							14 (3.27)
69 *Adiantum flabellalatum* (S)				6 (5.73)			9 (4.58)			
70 *Panax seudo-ginseng* (S)			1 (3.47)	1 (4.57)				1 (3.26)	1 (2.80)	
71 *Setaria allidifusca* (P)	21 (15.61)		36 (7.25)					15 (4.30)	19 (4.09)	
72 *Tribulus terrestris* (S)		8 (7.38)	6 (4.01)		9 (12.66)					3 (2.60)
73 *Commelina communis* (I)				20 (8.68)			34 (7.13)	40 (6.15)	22 (4.31)	
74 *Veronica didyma* (S)		30 (11.83)					20 (5.71)		33 (5.09)	
75 *Apluda mutioa* (S)					17 (15.49)			13 (4.15)		28 (4.12)
76 *Erlgeron Canadensis* (I)			11 (4.55)							15 (3.33)
77 *Ageratum conyzoides* (I)	21 (13.96)					33 (8.44)		31 (5.48)	30 (4.88)	40 (4.86)
78 *Erigeron sonchifol* (S)		17 (9.20)	11 (4.55)				12 (4.89)		15 (3.81)	30 (4.24)

P pioneer species, *I* intermediate-successional species, *S* shade-tolerant species

[a] The number of stems

[b] Important value

Table 6 Species, habit and density of seeds germinated from the soil seed bank across a range of *E. grandis* plantation ages

Species name and habit	Soil seed bank density (ind. m^{-2})									
	1 Plantation age (years)	2	3	4	5	6	7	8	9	10
Annual herb										
Rostellularia procumbens (P)	165							35	27	
Gnaphaliumoffined.Don (P)	67	64				27	34		29	37
Impatiens balsamina (P)	354	207		129		67		46	82	
Polygonum hydropiper (S)	169	267	32	137	432	334	558		337	498
Digitaria sanguinalis (P)	285	166	353	267		158	100	298	292	285
Oplismenus undulatifolius (P)	671	234	224	287	452	115		185		124
Viola diffusa (S)					206			334	235	184
Dichrocephala (I)				133	145					
Hypericum japonicum Thunb (S)			287				178	105		
Phyllanthus urinaria (I)		89	100						78	89
Stellaria media (P)	435	275							87	112
Asteracea *Tagetes patula* L (P)		145	133	31						
Eleusine indica (P)	59						35			
Commelina communis (I)	40								39	46
Mazus japonicus (I)		67								
Cyperus szechuanensis (S)				69	52	75	97	185	97	45
Perennial herb										
Cyperus rotundus (P)	85	68								
Cardamine leucantha (P)	37									
Setaria plicata (P)	101	65							107	117
Oxalis corniculata (P)	265		61				32		75	78
Stellaria vestita (P)						67	71	98		
Viola philippica (P)	49			134						
Plantago asiatica (P)	104			166						
Murdannia malabaricum (I)	133			103						
Begonia palmata (I)		61	80						67	87
Rhynchospermum verticillatum (I)		71	62			147	164			
Taraxacum mongolocum (P)	31					36		37		
Sorghum nitidum (P)								67	63	73
Phytolacca americana (P)						48		15		
Shrub species										
Smilax sp. (P)	2	2		8			8	9	11	15
Melastoma candidum (I)		3	9	11	3	4	7	8	2	11
Evodia lepta (I)					5	6	5	8	9	10
Acanthopanax wilsonii (S)			5	3	2	8	18	5		8
Castanopsis Spach (S)				7		4		9	7	5
Broussonetia kaempferi (I)				2		5	8	9		11
Symplocos setchuensis (I)					4	3	7	8	6	6
Cornus officinalis (S)							15	7	8	4

Table 6 (continued)

Species name and habit	Soil seed bank density (ind. m^{-2})									
	1	2	3	4	5	6	7	8	9	10
	Plantation age (years)									
Millettia nitida (I)			8	10	2		1	2	2	8
Phoebe sheareri (S)			5	9				3		14
Cinnamomum camphora (S)	3	2			4		8	7	7	9
Trema cannabina (S)			5				11	9	9	11
Melia azedarac (P)				11		1			9	4
Vitex negundo (S)				3		2		8	7	5
Symplocos stellaris (S)			4	8	2		7	7		
Mallotus barbatus (I)			2		3			5	6	8
Ficus gasparriniana (I)							6	6	9	9
Lonicera japonica (I)				5			5	9	6	10
Melastoma normale (I)				11	4			7	6	10
Liquidambar formosana (I)				9					5	
Philadelphus pekinensis (I)				1				2	2	11
Camellia oleifera (P)							8	3	4	9
Urena lobata (I)							11		1	8
Citrus sinensis (S)							3	1		7
Fatsia japonica (S)							2	1		9

P pioneer species, *I* intermediate-successional species, *S* shade-tolerant species

Table 7 Plant species, the number of stems (ind), density of individuals and Shannon–Wiener index for control forests (*P. massoniana*)

Species	Ind	Species	Ind	Species	Ind
Shrub species					
Broussonetia papyifera	7	*Symplocos stellaris*	4	*Melastoma candidum*	2
S. botryatha	4	*Smilax* sp.	5	*Melastoma normale*	4
Evodia lepta	3	*Castanopsis spach*	5	*Philadelphus pekinensis*	5
Phoebe sheareri	4	*Cornus officinalis*	7	*Camellia oleifera*	7
Rhus chinensis	2	*Cinnamomum camphora*	5	*Urena lobata*	2
Vitex negundo	3	*Millettia nitida*	4	*Rhus chinensis*	5
Myrsine africana	4	*Trema cannabina*	2	*Mallotus barbatus*	7
Lespedeza bicolor	5	*Ficus gasparriniana*	3	*Liquidambar formosana*	4
Acacia farnesiana	3	*Lithocarpus megalophyllus*	3	*Elaeagnus pungens*	4
Broussonetia papyifera	8	*Rhus succedaneal*	1	*Mahonia fortune*	2
Ficus henryi Warb	2	*Clerodendrum tibetanum*	2	*Daphniphllum macnpodum*	3
Rhus hypoleuca Champ	*3*	*Acer sinense*	3	*Symplocos setchuensis*	1
Schima uperba	3	*Machilus lichuanensis*	2	*Aucuba japonica*	3
Machilus pingii	4	*Melastoma* sp.	2	*Camellia* sp.	1
Evrya sp.	3	*Viburnum foetidum*	2	*Corylopsis sinensis*	1
Acer davidii	2	*Ficus neteromorpha*	4		
Lithocarpus megalophyllus	3	*Euonymus* sp.	5		

Table 7 (continued)

Species	Ind	Species	Ind	Species	Ind
Rhus succedaneal	1	*Ardisia crenata*	2		
Clerodendrum tibetanum	2	*Padus grayana*	2		
Gordonia acuminata	1	*Beilschmiedia robusta*	1		
Comus officinalis	3	*Lindera setcbuenensis*	1		
Species richness	69	Individual density (ind m^{-2})	8.25	Shannon–Wiener index	4.08
Herb species					
Imerata cylindrical	6	*Centipeda minima*	6	*Hypericum japonicum* Thunb	12
Beautiful hyllodium	4	*Senecio scandens*	12	*Phyllanthus urinaria*	5
Dicranoteris linearis	15	*Bothriochloa intermedia*	4	*Stellaria media*	23
Prunella vulgaris	12	*Cyperus rotundus*	4	*Cyperus orthostachyus* Franch	8
Bothriochloa ischaemum	6	*Geum aleppicum*	12	*Achyranthes aspera*	12
Paederia scandens	4	*Cuscuta chinensis*	12	*Commelina communis*	8
Rubus corchorifolius	9	*Eragrostis pilosa*	23	*Mazus japonicus*	9
Pteris semipinnata	10	*Plantago asiatica*	34	*Cyperus szechuanensis*	14
Arundinella hirta	12	*Lophatherum gracile*	12	*Youngia japonica*	2
Pedicularia sp.	14	*Rostellularia procumbens*	15	*Cardamine leucantha*	5
Deyeuxia arundinacea	24	*Gnaphaliumoffined.Don*	8	*Setaria plicata*	23
Stellaria alsine Grimm	12	*Viola diffusa*	9	*Oxalis corniculata*	16
Sorghum nitidum	12	*Polygonum hydropiper*	40	*Stellaria vestita*	12
Duchesnea indica	6	*Oplismenus undulatifolius*	12	*Viola philippica*	7
Erlgeron Canadensis	15	*Eragrostis pilosa*	12	*Plantago asiatica*	20
Iris lacteal	5	*Dichrocephala*	9	*Murdannia malabaricum*	3
Phytolacca americana	10	*Cayratia japonica*	5	*Begonia palmata*	4
Eleusine indica	5	*Capillipedium parviflorum*	9	*Rhynchospermum verticillatum*	8
Lygodium japonicum	4	*Ageratum conyzoides*	32	*Duchesnea indica*	4
Arthraxon hispidus	8	*Lyonia villosa*	16	*Gonostegia neurocarpa*	3
Curculigo orchioides	9	*Sanicula astrantiifolia*	13	*Taraxacum mongolocum*	10
Veronica serpyllifolia	8	*Ilex jinyunensis*	5	*Paspalum scrobiculatum*	12
Schizonepeta tenuifolia	2	*Heteropogon contortus*	6	*Prunella vulgaris*	14
Centella asiatica	3	*Anaphalis sinica*	9	*Sorghum nitidum*	4
Mimosa pudica	12	*Clintonia udensis*	4	*Artemisia argyi* Levl	8
Crotalaria mairei	8	*Helwingia japonica*	6	*Ficus tikoua*	15
Ophiopogon platyphyllum	12	*Calamagrostis epigeios*	8	*Senecio scandens*	13
Tribulus terrestris	24	*Hemerocallis fulva*	12	*Polygonum hydropiper*	34
Hypolepis punctata	10	*Woodwardia unigemmata*	6	*Rubia cordifolia*	23
Dicranopteris dichotoma	9	*Fragaria vescal*	9	*Pilea notate*	6
Eupatorium japonicum	3	*Impatiens balsamina*	10	*Hedyotis auricularia*	12
Buddleja lindleyana	5				
Species richness	95	Individual density (ind m^{-2})	1,044	Shannon–Wiener index	4.36
Community					
Species richness	164	Individual density (ind m^{-2})	1,052	Shannon–Wiener index	4.76

Table 8 Seed species, species richness, number of individuals germinated (ind), density of individuals and Shannon–Wiener index for soil seed banks of control forests (*P. massoniana*)

Species	Ind	Species	Ind	Species	Ind
Herb species					
Dicranoteris linearis	2	*Erlgeron canadensis*	12	*Cyperus orthostachyus* Franch	3
Prunella vulgaris	1	*Cyperus rotundus*	6	*Achyranthes aspera*	1
Bothriochloa ischaemum	1	*Geum aleppicum*	3	*Commelina communis*	3
Paederia scandens	2	*Cuscuta chinensis*	10	*Mazus japonicus*	3
Rubus corchorifolius	3	*Eragrostis pilosa*	7	*Cyperus szechuanensis*	2
Pteris semipinnata	1	*Plantago asiatica*	5	*Youngia japonica*	3
Arundinella hirta	2	*Lophatherum gracile*	5	*Adiantum flabellalatum*	3
Pedicularia sp.	1	*Rostellularia procumbens*	1	*Panax seudo-ginseng*	2
Deyeuxia arundinacea	5	*Gnaphaliumoffined.Don*	8	*Setaria allidifusca*	9
Stellaria alsine Grimm	7	*Viola diffusa*	2	*Tribulus terrestris*	3
Sorghum nitidum	8	*Polygonum hydropiper*	9	*Commelina bengalensis*	2
Duchesnea indica	3	*Digitaria sanguinalis*	1	*Veronica didyma*	4
Eragrostis pilosa	4	*Oplismenus undulatifolius*	3	*Apluda mutioa*	3
Dichrocephala	4	*Phyllanthus urinaria*	8	*Erlgeron canadensis*	2
Hypericum japonicum Thunb	7	*Stellaria media*	3	*Ageratum conyzoides*	5
Carex manbertiana	2	*Artemisia argyi*	1	*Erigeron sonchifol*	4
Polygonum capitatum	3	*Cerastium glomeratum*	2	*Aster panduratus*	3
Roripa cantoniensis	3	*Portulaca*	2	*Arthraxon hispidus*	2
Species richness	54	Individual density (ind m^{-2})	3,400	Shannon–Wiener index	3.78
Shrub species					
Vitex negundo	5	*Elaeagnus pungens*	6	*Schima sinensis*	8
Myrsine Africana	7	*Mahonia fortunei*	7	*Camellia oleifera*	8
Lespedeza bicolor	9	*Daphniphllum macnpodum*	9	*Liquidambar formosana*	7
Symplocos stellaris	11	*Symplocos setchuensis*	12	*Acer cinnamomifolium*	2
Smilax s	17	*Machilus lichuanensis*	8	*Sapium sebiferum*	3
Castanopsis spach	18	*Symplocos aenea*	9	*Celtis cerasifera*	4
Acer davidii	19	*Fargesia demissa*	4	*Glochidion lutes*	1
Acer sinense	5	*Zelkova serrata*	5	*Gordonia acuminate*	4
Evrya sp.	6	*Rhus chinensis*	8	*Bothrocaryum controversum*	5
Lithocarpus confinis	7	*Eurya loquaiana*	10	*Quercus myrsinaefolia*	8
Castanopsis jucunda Hance	9	*Neolitsea sutchuanensis*	7	*Castanopsis platyacantha*	9
Machilus chinensis	12	*Gordonia acuminata*	5	*Mallotus tanuifolia*	5
Lithocarpus megalophyllus	8	*Lithocarpus fangii*	8	*Ficus henryi*	9
Castanopsis carlesii	12	*Ficus heteromorpha*	6		
Species richness	41	Individual density (ind m^{-2})	322	Shannon–Wiener index	3.60
Community					
Species richness	95	Individual density (ind m^{-2})	3,722	Shannon–Wiener index	4.06

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