Taiwan J For Sci 40(1): 1-20, 2025
https://doi.org/10.7075/TJFS.202503_40(1).0001


Research paper

# Small-Scale Spatial Patterns of Soil Seed Banks in a Subtropical Secondary Forest: Implications for Biodiversity Conservation and Management

Zhi-Ning Zhang[1], Wei Wang[1,2], Yen-Hsueh Tseng[1,2], and Hsy-Yu Tzeng[1]

## ABSTRACT

This study investigated the spatial distribution of seeds in the soil seed bank of a late-successional secondary forest at Huisun Forest Station, Taiwan. The primary objectives were to assess the influence of types of seed or fruit dispersal and to examine the compositional similarities between the soil seed bank and aboveground vegetation. A sample plot measuring 25 m × 25 m was selected and subdivided into 25 subplots, each measuring 5 m × 5 m. Thirty-six soil seed bank sampling sites were established at the intersections of these plots. Investigation of the aboveground vegetation identified 85 vascular plant species, including 11 Pteridophyta. The dominant trees were *Schima superba* Gardner & Champ., *Diospyros morrisiana* Hance *ex* Walp., and *Castanopsis kawakamii* Hayata, with *Blastus cochinchinensis* Lour. being the most common understory species. Using the seed germination method, the study produced 3,079 seedlings representing 56 species, for an approximate seed density of 3,801 seeds/m². The three species with the highest abundance of seeds in the soil were *Melastoma septemnervium* Lour., *Ilex ficoidea* Hemsl., and *Maesa perlaria* (Lour.) Merr., accounting for 48.55% of all seeds stored, revealing that the soil seed bank is dominated by a few species. A total of eight naturalized species were recorded, comprising only about 1% of the total seeds stored. Plant growth forms represented in the soil seed bank were, in descending order: trees, herbs, shrubs, and vines, while seed abundance followed in descending order: shrubs, trees, vines, and herbs. The study also found that the spatial distribution of dominant species in the soil seed bank was influenced by type of seed dispersal, vegetation history, and human disturbance. Species composition of the soil seed bank was weakly correlated with aboveground vegetation, with only two species (*Me. septemnervium* and *Bl. cochinchinensis*) being common to both. This indicates that most aboveground species do not rely on the soil seed bank for regeneration. Nevertheless, the soil seed bank plays a crucial role in species conservation, revealing that evaluations based solely on aboveground vegetation surveys may lead to significant underestimates of species diversity in subtropical late-successional secondary forests. This study highlights the importance of soil seed banks in maintaining species diversity in these forest ecosystems.

**Keywords:** soil seed bank, secondary forest, spatial distribution, seed dispersal, Huisun Forest Station

**Zhang ZN, Wang W, Tseng YH, Tzeng HY. 2025.** Small-scale spatial patterns of soil seed banks in a subtropical secondary forest: Implications for biodiversity conservation and management. Taiwan J For Sci 40(1):1-20.

[1] 國立中興大學森林學系，402202臺中市南區興大路145號 Department of Forestry, National Chung Hsing University. No. 145 Xingda Rd., Taichung City 40227, Taiwan.

[2] 林業試驗所，100051 臺北市中正區南海路53號 Taiwan Forestry Research Institute, No. 53 Nanhai Rd., Taipei 100051, Taiwan.

通訊作者：曾喜育 Corresponding author, Hsy-Yu Tzeng, Email: erecta@nchu.edu.tw

2024年9月送審，2025年3月通過。Received September 2024, Accepted March 2025.

## INTRODUCTION

The soil seed bank consists of the viable seeds present in the surface and sub-surface soil layers (Fenner and Thompson 2006) and represents an essential stage in the life cycle of seed plants. It is also an integral part of a plant community, reflecting to a certain extent the regenerative ability and seed dispersal characteristics of a species (Olano et al. 2002, Sakai et al. 2005, Wódkiewicz and Kwiatkowska-Falińska 2010, Tzeng et al. 2018). Studies of the soil seed bank can enhance our understanding of past and future development of aboveground vegetation, providing essential insights for maintaining biodiversity (Tang et al. 2011, Vandvik et al. 2016, Tzeng et al. 2018), regeneration and succession of vegetation (Sakai et al. 2005, Wu et al. 2014, Chang et al. 2019), and ecological restoration (Li et al. 2018, Lin et al. 2022).

Seed dispersal is a critical process in the expansion of the distribution range of seed plants, and plays a key role in determining the probability of plant recruitment in new habitats (Howe and Smallwood 1982). Seeds dispersed via biotic or abiotic vectors enter the soil and accumulate in the soil seed bank, serving as prerequisites for vegetation regeneration. The spatial distribution of seeds in the soil after their dispersal represents the initial spatial distribution of vegetation and affects subsequent ecological processes (Lin et al. 2010). Spatial pattern analysis is crucial when studying the characteristics of vegetation, interaction, and the relationship between vegetation and its environment (Haase 1995). Spatial patterns of soil seed banks can facilitate understanding of the compositional characteristics of succession and regeneration after forest disturbance (Olano et al. 2002, Wódkiewicz and Kwiatkowska-Falińska 2010). At a fine spatial scale, the distribution of a species within a community may be a random, uniform, or clustered. The spatial distribution of species also indicates their ecological characteristics and adaptability to habitats (Molles 2017).

To understand the composition of the soil seed bank and small-scale spatial pattern characteristics of the subtropical late-successional secondary forests in the *Schima superba* Gardner & Champ. Protected Area of Huisun Forest Station, the soil seed bank and aboveground vegetation were investigated; followed by analysis of the spatial distribution patterns of the soil seed bank. The aim was to generate baseline data on the relationship between aboveground vegetation composition and the soil seed bank, providing a reference for plant ecology research and forest management.

## MATERIALS AND METHODS

### Site description

Huisun Forest Station (惠蓀林場) is one of four forest stations of National Chung-Hsing University in central Taiwan, and ranges in altitude from 454 to 2,419 m (Figure 1). The bedrock in the area is primarily composed of Takken sandstone and Gayang slate layers (Ho 2006). Annual average rainfall is 2,470 mm, and the average temperature is 17.9℃ (Chiu et al. 2012). The climate is seasonal, with most rainfall occurring during the warm-wet season from May to October, which includes the rainy and typhoon seasons. There is a brief period of relative drought in November (Figure 1b). According to Thornthwaite climate classification, this study area falls under the AB'wa' category, indicating a wet but warm winter climate (Yu 2001). The study site is located in the *S. superba* Protected Area of Huisun Forest Station (121°02'12.0" E, 24°04'28.0" N)

at an altitude of approximately 1,175 m, with a slope of 35° and an aspect of 172°. The soil pH of the plot ranges from 4 to 5. The vegetation at the site is typical of a warm forest, characterized by a *Machilus-Castanopsis* vegetation zone predominantly dominated by species from the Lauraceae and Fagaceae families (Lu and Ou 1996).

**Plot setting and sampling method**

**Investigation of aboveground vegetation**

The study was conducted July 16-17, 2018. The sample plot (25 m × 25 m) was established and subdivided into 25 subplots of 5 m × 5 m each (Figure 1c). Tree species, number, and diameter at breast height (DBH) of the overstory of trees (with a DBH > 1 cm) in each subplot were surveyed; meanwhile, the relative positions of trees were plotted. The coverage of the understory for ferns, herbs, vines and trees with DBH < 1 cm in each subplot was surveyed.

**Soil seed bank sampling**

The soil seed bank was sampled concurrently with the investigation of aboveground vegetation. Soil samples were collected at the intersections and borders of each subplot using a 15 cm × 15 cm metal frame. Upper-soil-layer samples (0-5 cm; including litter) and lower-soil-layer samples (5-10 cm) were collected and labeled separately. A total of 72 packs of soil samples were acquired from 36 sample sites representing a total surface area of 0.81 $m^2$ and a total volume of 0.081 $m^3$.

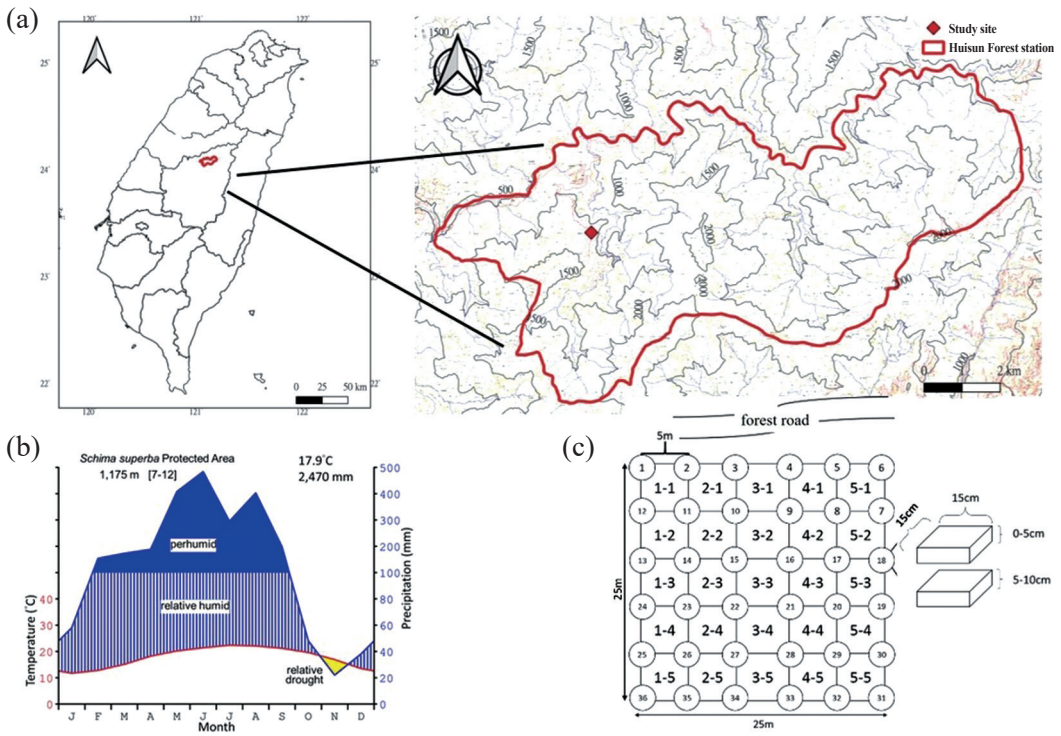


**Figure 1. Location of the study site (a) ecoclimate diagram (b) and sampling setup schematic (c). The number in the circle is the sampling number of the soil seed bank, and the number in the box is the cell number.**

**Investigation of soil seed bank**

Seed germination was conducted in the Beigou Nursery Greenhouse of the Department of Forestry, National Chung Hsing University. The greenhouse provided a full-daylight environment and prevented contamination from alien seeds (Tang et al. 2011). Plastic germination containers with dimensions of 60 cm × 40 cm × 10 cm were utilized for the experiment. White nonwoven fabric was placed at the bottom of the containers, followed by a layer of perlite to maintain moisture while preventing the loss of seeds and soil through drainage holes. Soil samples were then spread evenly over the perlite layer with a thickness of less than 1 cm. The germination experiment began on July 17, 2018, and ended on May 15, 2019, with weekly observations and records. Seedlings of confirmed species were removed from the germination containers, and seedlings of unidentified species were transplanted until they had grown sufficiently to be identified. The scientific names of plant species were determined using the *Flora of Taiwan*, 2nd ed. (Boufford et al. 2003). Rare plants were classified in accordance with *The Red List of Vascular Plants of Taiwan, 2017* (Editorial Committee of the Red List of Taiwan Plants 2017), and naturalized plants were identified by referring to Wu et al. (2004), Chang et al. (2008), and Chang-Yang et al. (2022).

**Data analysis**

Vegetation data were categorized into overstory and understory layers. The density, frequency, and coverage of various plant species were calculated and converted into relative values. The sum of these relative values was used as a parameter to indicate the importance of a particular plant species within the sample plot, as well as to identify the dominant species in the plant community. The importance value index (IVI) for the tree layer was calculated as the sum of relative density, relative frequency, and relative dominance. In contrast, the importance value (IV) for the ground cover layer was determined by summing relative frequency and relative dominance. Data analysis was performed using Microsoft Excel 2016.

Sigmaplot 12.5 software was used to draw scatter plots of the type distribution of the soil seed bank and horizontal spatial positions of trees. The Poisson distribution (i.e., expected value = variance = mean, $E[X] = V[X] = \lambda$) was used to calculate the coefficient of variance and analyze the spatial distribution pattern of dominant species within the soil seed bank (Sakai et al. 2005, Tzeng et al. 2018). When the ratio of variance to mean (V/M) equaled 1, the spatial pattern was random. A V/M ratio greater than 1 indicated a clumped pattern, while a V/M ratio less than 1 suggested a homogeneous pattern. Lloyd's mean crowding index (Lloyd 1967) and Iwao's regression method (Iwao 1968) were used to further analyze spatial distribution.

$$m^* = \sum_{i=1}^{Q} xi(xi - 1)$$

$$\mathrm{Ip} = m^*/m$$

$m^*$: Lloyd's mean crowding;
$Q$ : number of samples;
$xi$ : number of seeds in i-th sample;
$m$ : mean density

A paired-sample t-test was employed to compare the vertical distribution of species and seed storage between upper and lower soil layers. Simpson's diversity index (Simpson 1949) and the Shannon–Weiner

diversity index (Shannon and Weaver 1963) were used to assess species diversity in the soil seed bank across different sample sites. Furthermore, the Sørensen similarity index (Sørensen 1948) was utilized to calculate the similarity of species composition between the soil seed bank and aboveground vegetation.

Fruit and seed dispersal types were classified into five modes: autochory, gravity dispersal, anemochory, hydrochory, and zoochory (Kuo 2015). In this study, seed dispersal modes were inferred based on fruit types, following the definitions provided by Seider and Plotkin (2006). Seeds of berries, drupes, achenes with glochidium, and caryopses are dispersed through zoochory; those of caryopsis and achenes with pappus are dispersed through anemochory; and for groundcovers with tiny seeds, dispersal is presumed to occur through hydrochory or zoochory. Fruits with self-dispersal mechanisms are classified as autochorous. Plants with large seeds, for which autochory and other modes are not relevant, rely on gravity for dispersal. According to Whittaker's (1970) classification, plant growth forms are categorized into four types: trees, shrubs, vines, and herbs.

## RESULTS

### Composition of aboveground vegetation

A total of 85 vascular plant species were identified in the aboveground vegetation, comprising 74 species of Angiospermae and 11 species of Pteridophyta. Four rare plants were found in the study area: *Ormosia formosana* Kanehira (VU), *Eurya rengechiensis* Yamam. (EN), *Castanopsis kawakamii* Hayata (NT), and *Cinnamomum osmophloeum* Kaneh. (NT). No naturalized plants appeared in the study area.

The dominant tree species in the sample plot were *S. superba* (IVI = 65.9), *Diospyros morrisiana* Hance ex Walp. (IVI = 28.7), and *C. kawakamii* (IVI = 22.9). In the understory, the most prevalent species was the shadetolerant *Blastus cochinchinensis* Lour. (IV = 88.19), followed by saplings such as *Helicia rengetiensis* Masam. (IV = 5.22) and *Neolitsea aciculata* (Blume) Koidz. (IV = 4.97). The main herbaceous species were *Adiantum flabellulatum* L. (IV = 4.88) and *Plagiogyria falcata* Copel. (IV = 4.75).

### Composition of the soil seed bank

A total of 3,079 seedlings emerged from the soil seed bank, corresponding to a seed density of approximately 3,801 seeds/m². These seedlings represented 32 families, 47 genera, and 56 species (Table 1). Among them, 18 seedlings could not be identified and were excluded from subsequent analysis. The three species with the highest seed storage were *Melastoma septemnervium* Lour., *Ilex ficoidea* Hemsl., and *Maesa perlaria* (Lour.) Merr., collectively accounting for 48.55% of the total soil seed bank. Families with the highest species richness were Poaceae (eight species), Euphorbiaceae (four species), and Rosaceae (four species) (Table 1). Two endemic species were identified: *E. septata* Chi C.Wu, Z.F.Hsu & C.H.Tsou and *Colocasia formosana* Hayata. Naturalized plants included *Passiflora edulis* Sims, *Ageratum houstonianum* Mill., *Cuphea cartagenensis* (Jacq.) J.F.Macbr., *Crassocephalum crepidioides* (Benth.) S.Moore, *Conyza canadensis* (L.) Cronquist, *Zebrina pendula* (Schinz) D. R. Hunt, *Digitaria sanguinalis* (L.) Scop., and *Paspalum paniculatum* L., comprising less than 1% of all seeds stored (Table 1). Only one rare plant was identified, namely *Actinidia latifolia* (Gardner & Champ.) Merr.

**Table 1. List of species composition, seed storage, biological characteristics and spatial distribution of soil seed bank in the secondary forest of Huisun Forest Station (惠蓀林場)**

| Species | Family | Native/alien | Growth form | Fruit type | Dispersal type[1] | 0-5 cm | 5-10 cm | Sum | Percent (%) | Frequency |
|---|---|---|---|---|---|---|---|---|---|---|
| *Melastoma septemnervium* | Melastomataceae | native | shrub | berry | Z | 370 | 339 | 709 | 23.03 | 36 |
| *Ilex ficoidea* | Aquifoliaceae | native | tree | drupe | Z | 73 | 324 | 397 | 12.89 | 24 |
| *Maesa perlaria* | Myrsinaceae | native | shrub | berry | Z | 224 | 165 | 389 | 12.63 | 36 |
| *Buddleja asiatica* | Loganiaceae | native | shrub | capsule | W | 104 | 223 | 327 | 10.62 | 36 |
| *Mussaenda pubescens* | Rubiaceae | native | liana | berry | Z | 185 | 116 | 301 | 9.78 | 36 |
| *Rubus trianthus* | Rosaceae | native | shrub | drupe | Z | 86 | 206 | 292 | 9.48 | 33 |
| *Trema orientalis* | Ulmaceae | native | tree | drupe | Z | 55 | 62 | 117 | 3.80 | 34 |
| *Eurya septata* | Theaceae | native | tree | berry | Z | 17 | 50 | 67 | 2.18 | 20 |
| *Rubus corchorifolius* | Rosaceae | native | shrub | drupe | Z | 17 | 32 | 49 | 1.59 | 15 |
| *Tetradium glabrifolium* | Rutaceae | native | tree | capsule | Z | 16 | 24 | 40 | 1.30 | 18 |
| *Ilex micrococca* | Aquifoliaceae | native | tree | drupe | Z | 17 | 18 | 35 | 1.14 | 19 |
| *Melanolepis multiglandulosa* | Euphorbiaceae | native | tree | capsule | Z | 21 | 13 | 34 | 1.10 | 24 |
| *Ampelopsis cantoniensis* | Vitaceae | native | liana | berry | Z | 10 | 24 | 34 | 1.10 | 16 |
| *Glochidiona acuminatum* | Euphorbiaceae | native | tree | capsule | Z | 12 | 13 | 25 | 0.81 | 14 |
| *Callicarpa formosana* | Verbenaceae | native | shrub | drupe | Z | 12 | 13 | 25 | 0.81 | 15 |
| *Rhus javanica* | Anacardiaceae | native | tree | drupe | Z | 9 | 13 | 22 | 0.71 | 15 |
| *Actinidia latifolia* | Actinidiaceae | native | liana | berry | Z | 16 | 6 | 22 | 0.71 | 13 |
| *Sapium discolor* | Euphorbiaceae | native | tree | capsule | Z | 6 | 7 | 13 | 0.42 | 10 |
| *Alniphyllum pterospermum* | Styracaceae | native | tree | capsule | W | 8 | 5 | 13 | 0.42 | 9 |
| *Torenia concolor* | Scrophulariaceae | native | herb | capsule | H, Z | 6 | 6 | 12 | 0.39 | 10 |
| *Rubus formosensis* | Rosaceae | native | shrub | drupe | Z | 7 | 5 | 12 | 0.39 | 10 |
| *Passiflora edulis* | Passifloraceae | alien | liana | berry | Z | 3 | 8 | 11 | 0.36 | 5 |
| *Polygonum chinense* | Polygonaceae | native | herb | achene | Z | 3 | 7 | 10 | 0.32 | 9 |
| *Hydrangea chinensis* | Saxifragaceae | native | shrub | capsule | W | 3 | 7 | 10 | 0.32 | 6 |
| *Araliabi bipinnata* | Araliaceae | native | tree | drupe | Z | 3 | 6 | 9 | 0.29 | 8 |
| *Pericampylus formosanus* | Menispermaceae | native | liana | drupe | Z | 2 | 7 | 9 | 0.29 | 7 |
| *Ficus nervosa* | Moraceae | native | tree | drupe | Z | 7 | 1 | 8 | 0.26 | 3 |
| *Cayratia japonica* | Vitaceae | native | liana | berry | Z | 5 | 1 | 6 | 0.19 | 6 |
| *Ageratum houstonianum* | Compositae | alien | herb | achene | W | 4 | 2 | 6 | 0.19 | 5 |

| Species | Family | Native/alien | Growth form | Fruit type | Dispersal type[1] | 0-5 cm | 5-10 cm | Sum | Percent (%) | Frequency |
|---|---|---|---|---|---|---|---|---|---|---|
| *Eurya gnaphalocarpa* | Theaceae | native | tree | berry | Z | 2 | 4 | 6 | 0.19 | 5 |
| *Oreocnide pedunculata* | Urticaceae | native | tree | achene | Z | 0 | 6 | 6 | 0.19 | 4 |
| *Oplismenus compositus* | Gramineae | native | herb | caryopsis | Z | 3 | 1 | 4 | 0.13 | 4 |
| *Cuphea cartagenensis* | Lythraceae | alien | herb | capsule | W | 1 | 3 | 4 | 0.13 | 3 |
| *Litsea cubeba* | Lauraceae | native | tree | drupe | Z | 0 | 3 | 3 | 0.10 | 3 |
| *Setaria palmifolia* | Gramineae | native | herb | caryopsis | Z | 0 | 3 | 3 | 0.10 | 2 |
| *Sida rhombifolia* | Malvaceae | native | shrub | schizocarp | Z | 1 | 2 | 3 | 0.10 | 2 |
| *Paspalum paniculatum* | Gramineae | alien | herb | caryopsis | Z | 0 | 2 | 2 | 0.06 | 2 |
| *Colocasia formosana* | Araceae | native | herb | berry | Z | 1 | 1 | 2 | 0.06 | 2 |
| *Isachne globosa* | Gramineae | native | herb | caryopsis | Z | 2 | 0 | 2 | 0.06 | 2 |
| *Randia cochinchinensis* | Rubiaceae | native | tree | berry | Z | 2 | 0 | 2 | 0.06 | 2 |
| *Conyza canadensis* | Compositae | alien | herb | achene | W | 2 | 0 | 2 | 0.06 | 2 |
| *Crassocephalum crepidioides* | Compositae | alien | herb | achene | W | 1 | 1 | 2 | 0.06 | 1 |
| *Lycianthes biflora* | Solanaceae | native | shrub | berry | Z | 0 | 2 | 2 | 0.06 | 1 |
| *Ficus erecta* var. *beechayana* | Moraceae | native | tree | drupe | Z | 1 | 1 | 2 | 0.06 | 1 |
| *Zebrina pendula* | Commelinaceae | alien | herb | capsule | H, Z | 1 | 0 | 1 | 0.03 | 1 |
| *Lophatherum gracile* | Gramineae | native | herb | caryopsis | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Digitaria setigera* | Gramineae | native | herb | caryopsis | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Trema tomentosa* | Ulmaceae | native | tree | drupe | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Digitaria sanguinalis* | Gramineae | alien | herb | caryopsis | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Mariscus sumatrensis* | Cyperaceae | native | herb | achene | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Sacciolepis indica* | Gramineae | native | herb | caryopsis | Z | 0 | 1 | 1 | 0.03 | 1 |
| *Carex baccans* | Cyperaceae | native | herb | achene | Z | 0 | 1 | 1 | 0.03 | 1 |
| *Rubus croceacanthus* | Rosaceae | native | shrub | drupe | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Mallotus japonicas* | Euphorbiaceae | native | tree | capsule | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Ficus superba* var. *japonica* | Moraceae | native | tree | drupe | Z | 1 | 0 | 1 | 0.03 | 1 |
| *Blastus cochinchinensis* | Melastomataceae | native | shrub | capsule | W | 1 | 0 | 1 | 0.03 | 1 |
| unknown | | | | | | 12 | 6 | 18 | 0.59 | - |

[1]H: hydrochory; W: anemochory; Z: zoochory

(NT). In addition, two species were common to both the aboveground vegetation and the soil seed bank: *Me. eptemnervium* and *Bl. cochinchinensis*. The Sørensen similarity index was 1.54%, indicating low similarity in species composition between groundcover and aboveground vegetation.

Most fruits and seeds in the soil seed bank were dispersed by zoochory (Table 1). Among the 10 most common species in the seed storage, all except *Buddleja asiatica* Lour. (dispersed by anemochory) relied on zoochory as their primary dispersal method (Table 1). Plant growth form composition of the soil seed bank was dominated by trees (20 species), followed by herbs (18 species), shrubs (12 species), and vines (6 species). Seed storage density was highest for shrubs at 2,247 seeds/m², followed by trees at 990 seeds/m², vines at 473 seeds/m², and herbs at 69 seeds/m². This indicates that shrubs dominated the seed storage composition of the soil seed bank in the secondary forest of the study plot.

**Spatial distribution of soil seed bank components**

The soil seed bank layer from 0-5 cm contained 49 species, with a seed storage density of approximately 1,653 seeds/m². In contrast, the 5-10 cm layer contained 43 species, with a seed storage density of approximately 2,148 seeds/m² (Table 1). Paired t-test comparisons revealed that the average number of species in the lower soil layer (10.4 ± 3.0) was slightly higher than that in the upper soil layer (10.8 ± 3.5), but the difference was non-significant ($t$ = -0.537, $p$ = 0.595). However, seed density in the upper soil layer was significantly lower than that in the lower soil layer ($t$ = -2.147, $p$ = 0.039). This trend was also observed at the species level, with most species represented by a higher seed count in the lower soil layer. Specifically, the seed storage of *Bu. asiatica* ($t$ = -3.392, $p$ = 0.002), *E. septata* ($t$ = -2.124, $p$ = 0.041), and *I. ficoidea* ($t$ = -3.392, $p$ = 0.002) were significantly greater in the lower layer than in the upper layer. Among the 10 most common species, only *Mussaenda pubescens* W.T. Aiton ($t$ = 2.671, $p$ = 0.011) had significantly more seeds in the upper layer than the lower layer.

The spatial distribution of trees within the sample plot showed a gradient from sparse to dense distribution from the upper left to the bottom right in Figure 2. The relationships between the spatial distribution of trees and the characteristics of the soil seed bank were also plotted in Figure 2. No clear correspondence was identified between the spatial distribution of trees and species richness in the soil seed bank (Figure 2a). Seed storage tended to be greater in the tree-less subplot in the upper left and dense areas of the central forest of the sample plot (Figure 2b). The Shannon–Weiner diversity index (Figure 2c) and Simpson's diversity index (Figure 2d) for various sample sites in the soil seed bank revealed that species diversity was higher in densely forested areas and open areas without trees compared to other areas.

Frequencies of the 10 most dominant species appearing across the sample sites in the seed storage are shown in Table 2 and Figure 3. *Melastoma septemnervium*, *Ma. perlaria*, *Bu. asiatica*, and *Mu. pubescens* appeared in all the sample sites. Except for *Rubus corchorifolius* L.f., the frequency of occurrence of these species was greater than 0.5, indicating that the most common species in seed storage frequently appeared in the plot. The coefficient of variation showed that at the spatial scale of 5 m, *Me. septemnervium*, *Ma. perlaria*, *Mu. pubescens*, and *Trema orientalis* (L.) Blume were distributed uniformly. In

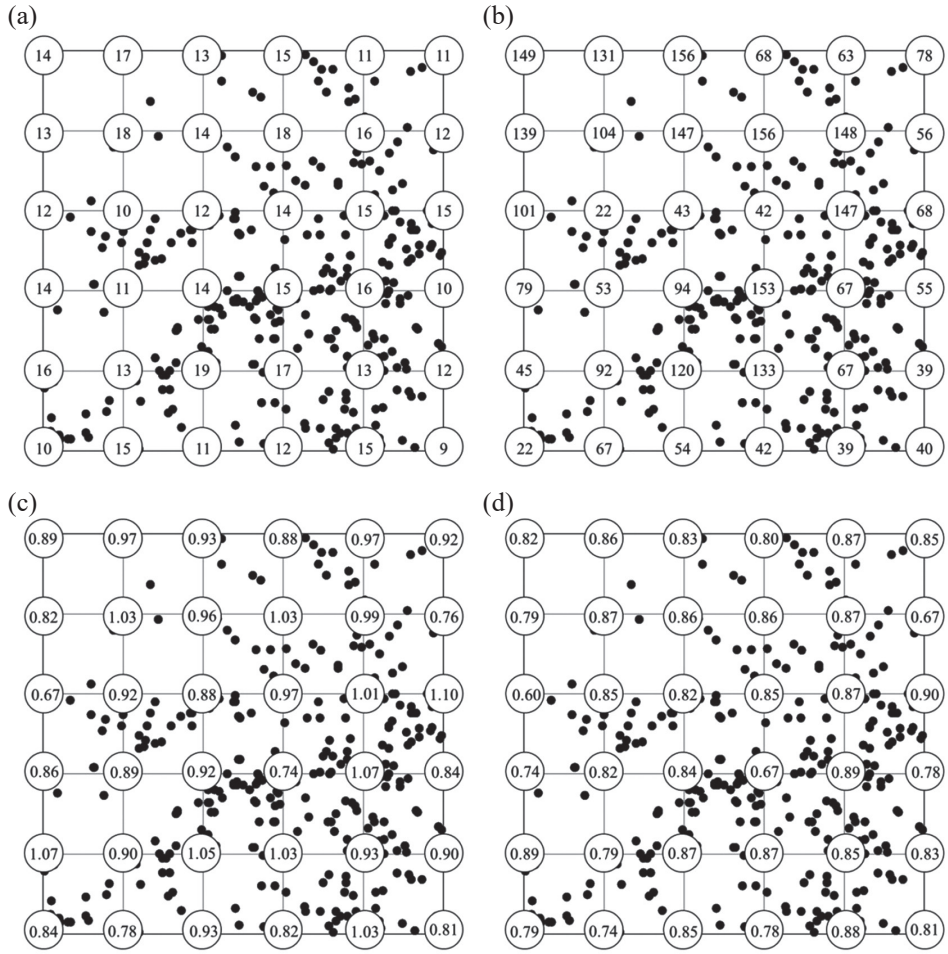


**Figure 2. Relationship of spatial distribution between trees and soil seed bank in secondary forest of Huisun Forest Station (惠蓀林場). (a) species richness, (b) seed storage, (c) Shannon-Weiner diversity index and (d) Simpson diversity index.**

**Table 2. Spatial statistics of species in the soil seed bank of a secondary forest**

| | mean/m$^2$ | Variance | Frequency | CV | Mean crowding | m$^*$/m |
|---|---|---|---|---|---|---|
| *Melastoma septemnervium* | 875.31 | 306321.8 | 1.00 | 0.63$^{***}$ | 1216.55 | 1.39 |
| *Ilex ficoidea* | 490.12 | 496139.5 | 0.67 | 1.44$^{***}$ | 1473.28 | 3.01 |
| *Maesa perlaria* | 480.25 | 97503.43 | 1.00 | 0.65$^{***}$ | 676.63 | 1.41 |
| *Buddleja asiatica* | 403.70 | 130638.4 | 1.00 | 0.90$^{***}$ | 717.31 | 1.78 |
| *Mussaenda pubescens* | 371.60 | 81964.33 | 1.00 | 0.77$^{***}$ | 585.05 | 1.57 |
| *Rubus trianthus* | 360.49 | 378218.3 | 0.92 | 1.71$^{*}$ | 1379.52 | 3.83 |
| *Trema orientalis* | 144.44 | 9862.434 | 0.94 | 0.69$^{***}$ | 209.83 | 1.45 |
| *Eurya septata* | 82.72 | 12884.97 | 0.56 | 1.37$^{*}$ | 233.16 | 2.82 |
| *Rubus corchorifolius* | 60.49 | 12546.35 | 0.42 | 1.85$^{***}$ | 261.13 | 4.32 |
| *Tetradium glabrifolium* | 49.38 | 5731.53 | 0.50 | 1.53$^{***}$ | 161.22 | 3.26 |

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

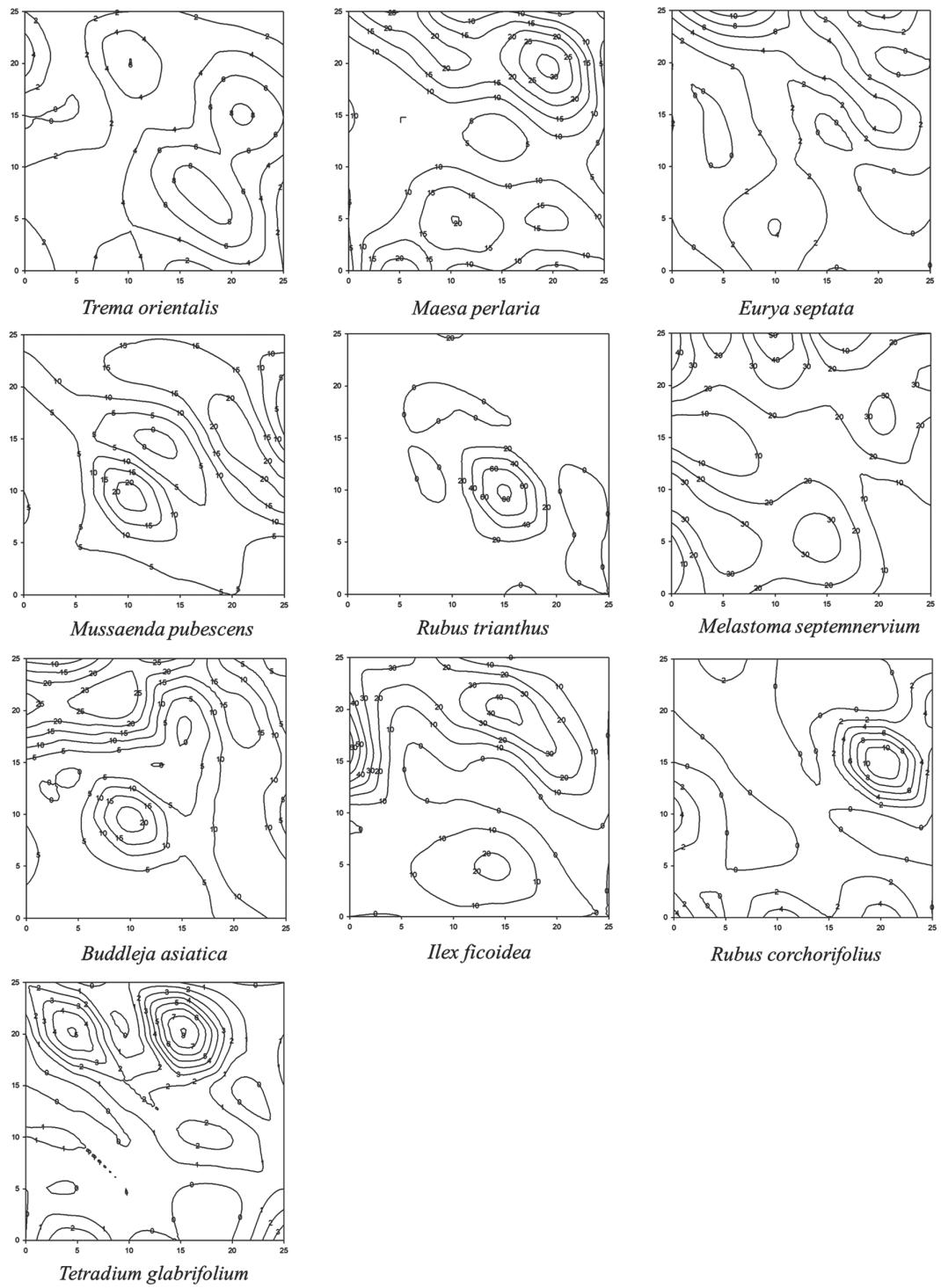


**Figure 3. Spatial distribution of seed storage for dominant species and all species in the soil seed bank of the secondary forest of Huisun Forest Station (惠蓀林場).**

contrast, *I. ficoidea*, *R. trianthus* Focke, *R. corchorifolius*, *E. septata*, and *Tetradium glabrifolium* (Champ. *ex* Benth.) T.G. Hartley exhibited clumped distributions, while *Bu. asiatica* was distributed randomly. The $m^*/m$ analysis revealed that at the spatial scale of 5 m (Figure 4), *I. ficoidea*, *R. trianthus*, *R. corchorifolius*, *E. septata*, and *Te. glabrifolium* were more clumped compared to other species.

## DISCUSSION

### Soil seed bank composition in the secondary forest

The soil seed bank in the secondary forest of the *S. superba* Protected Area in Huisun Forest Station was predominantly characterized by zoochory, suggesting that the study plot is in the late stage of forest succession (Hirayama et al. 2019). The composition of the soil seed bank was primarily woody plants (shrubs and trees), with herbs being the least common, aligning with the findings of Wu et al. (2014), who also studied the soil seed bank in the secondary forest at Huisun Forest Station. Li et al. (2010) observed that the tree seed density in the soil seed bank increased from secondary to primary forests, suggesting that as forest succession progresses, the composition of the soil seed bank transitions from herb to woody species dominance.

The seed density of 3,801 seeds/$m^2$ in the study plot was higher than the densities reported by Chang et al. (2019) and Wu et al. (2014) for Huisun Forest Station, which reported 1,760 and 2,904 seeds/$m^2$, respectively. This discrepancy was mainly due to differences in the seed storage of dominant species such as *Me. septemnervium* and *I. ficoidea*. The soil seed bank and aboveground vegetation shared only two species: *Melastoma septemnervium*

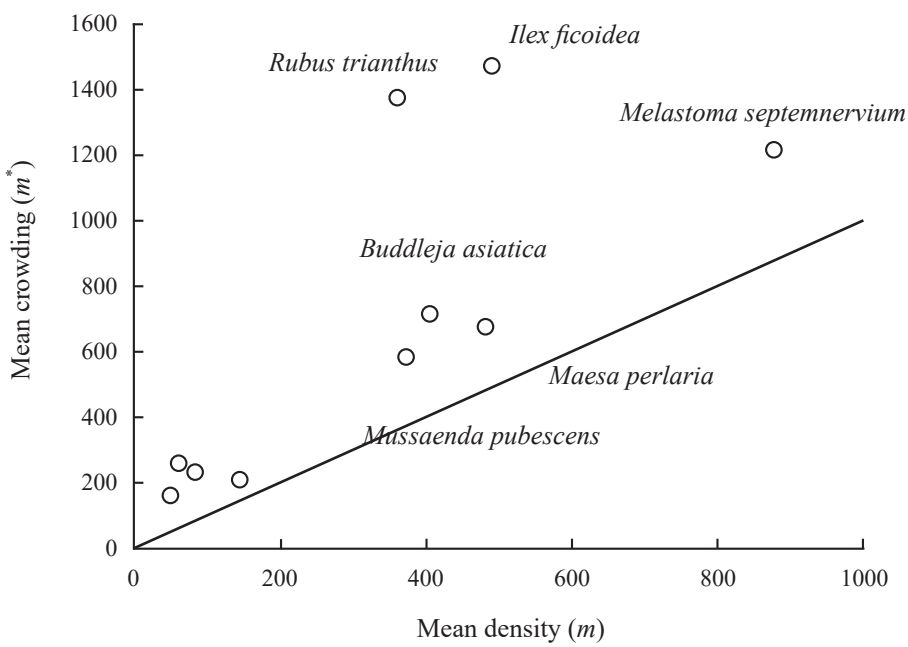


**Figure 4. Mean crowding ($m^*$) plotted against mean density (m). Data is for the top ten species.**

**Table 3. Spatial distribution of species diversity in the soil seed bank of the secondary forest of Huisun Forest Station (惠蓀林場)**

| Soil depth site | 0-5 cm | | | | 5-10 cm | | | | 0-10 cm | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | spp. no.[1] | Seed no. | D[2] | H'[3] | spp. no. | Seed no. | D | H' | spp. no. | Seed no. | D | H' |
| 1 | 10 | 37 | 0.75 | 0.76 | 13 | 112 | 0.81 | 0.85 | 17 | 149 | 0.82 | 0.89 |
| 2 | 11 | 43 | 0.76 | 0.79 | 12 | 88 | 0.79 | 0.84 | 18 | 131 | 0.86 | 0.97 |
| 3 | 11 | 83 | 0.76 | 0.79 | 14 | 73 | 0.85 | 0.94 | 18 | 156 | 0.83 | 0.93 |
| 4 | 15 | 50 | 0.83 | 0.93 | 4 | 18 | 0.45 | 0.38 | 16 | 68 | 0.80 | 0.88 |
| 5 | 10 | 22 | 0.86 | 0.92 | 11 | 41 | 0.85 | 0.90 | 13 | 63 | 0.87 | 0.97 |
| 6 | 10 | 29 | 0.78 | 0.82 | 10 | 49 | 0.84 | 0.86 | 13 | 78 | 0.85 | 0.92 |
| 7 | 8 | 19 | 0.81 | 0.80 | 10 | 37 | 0.53 | 0.57 | 14 | 56 | 0.67 | 0.76 |
| 8 | 12 | 49 | 0.83 | 0.88 | 15 | 99 | 0.86 | 0.96 | 19 | 148 | 0.87 | 0.99 |
| 9 | 18 | 77 | 0.89 | 1.07 | 14 | 79 | 0.78 | 0.83 | 21 | 156 | 0.86 | 1.03 |
| 10 | 16 | 90 | 0.85 | 0.95 | 10 | 57 | 0.83 | 0.87 | 18 | 147 | 0.86 | 0.96 |
| 11 | 15 | 46 | 0.85 | 0.97 | 13 | 58 | 0.82 | 0.91 | 21 | 104 | 0.87 | 1.03 |
| 12 | 11 | 78 | 0.78 | 0.80 | 11 | 61 | 0.71 | 0.69 | 15 | 139 | 0.79 | 0.82 |
| 13 | 10 | 16 | 0.86 | 0.93 | 9 | 85 | 0.50 | 0.52 | 15 | 101 | 0.60 | 0.67 |
| 14 | 4 | 11 | 0.68 | 0.54 | 9 | 11 | 0.86 | 0.91 | 11 | 22 | 0.85 | 0.92 |
| 15 | 5 | 8 | 0.69 | 0.60 | 11 | 35 | 0.83 | 0.88 | 12 | 43 | 0.82 | 0.88 |
| 16 | 9 | 24 | 0.77 | 0.78 | 10 | 18 | 0.86 | 0.93 | 14 | 42 | 0.85 | 0.97 |
| 17 | 12 | 48 | 0.86 | 0.92 | 15 | 99 | 0.85 | 0.96 | 18 | 147 | 0.87 | 1.01 |
| 18 | 12 | 22 | 0.88 | 1.00 | 14 | 46 | 0.88 | 1.01 | 18 | 68 | 0.90 | 1.10 |
| 19 | 8 | 32 | 0.71 | 0.69 | 8 | 23 | 0.82 | 0.81 | 12 | 55 | 0.78 | 0.84 |
| 20 | 14 | 46 | 0.88 | 1.01 | 11 | 21 | 0.85 | 0.93 | 18 | 67 | 0.89 | 1.07 |
| 21 | 13 | 39 | 0.83 | 0.92 | 10 | 114 | 0.56 | 0.57 | 16 | 153 | 0.67 | 0.74 |
| 22 | 8 | 35 | 0.79 | 0.76 | 13 | 59 | 0.79 | 0.85 | 15 | 94 | 0.84 | 0.92 |
| 23 | 9 | 23 | 0.72 | 0.73 | 10 | 30 | 0.84 | 0.89 | 12 | 53 | 0.82 | 0.89 |
| 24 | 13 | 39 | 0.79 | 0.89 | 11 | 40 | 0.67 | 0.73 | 17 | 79 | 0.74 | 0.86 |
| 25 | 11 | 18 | 0.88 | 0.98 | 11 | 27 | 0.85 | 0.92 | 16 | 45 | 0.89 | 1.07 |
| 26 | 9 | 56 | 0.66 | 0.67 | 12 | 36 | 0.89 | 1.01 | 14 | 92 | 0.79 | 0.90 |
| 27 | 13 | 50 | 0.85 | 0.93 | 17 | 70 | 0.86 | 0.99 | 22 | 120 | 0.87 | 1.05 |
| 28 | 10 | 27 | 0.85 | 0.90 | 19 | 106 | 0.84 | 0.97 | 21 | 133 | 0.87 | 1.03 |
| 29 | 9 | 41 | 0.79 | 0.78 | 11 | 26 | 0.83 | 0.90 | 13 | 67 | 0.85 | 0.93 |
| 30 | 6 | 14 | 0.73 | 0.67 | 10 | 25 | 0.79 | 0.84 | 12 | 39 | 0.83 | 0.90 |
| 31 | 9 | 25 | 0.84 | 0.86 | 4 | 15 | 0.68 | 0.54 | 9 | 40 | 0.81 | 0.81 |
| 32 | 8 | 26 | 0.80 | 0.77 | 11 | 13 | 0.90 | 1.02 | 15 | 39 | 0.88 | 1.03 |
| 33 | 9 | 34 | 0.70 | 0.68 | 6 | 8 | 0.78 | 0.72 | 12 | 42 | 0.78 | 0.82 |
| 34 | 8 | 29 | 0.73 | 0.70 | 10 | 25 | 0.85 | 0.91 | 12 | 54 | 0.85 | 0.93 |
| 35 | 10 | 32 | 0.76 | 0.77 | 8 | 35 | 0.70 | 0.65 | 15 | 67 | 0.74 | 0.78 |
| 36 | 9 | 21 | 0.77 | 0.80 | 1 | 1 | 0.00 | 0.00 | 10 | 22 | 0.79 | 0.84 |

spp. no[1]: species number.

D[2]: Simpson's diversity index

H'[3]: Shannon–Weiner diversity index

and *Bl. cochinchinensis*, both of which are Melastomataceae shrubs. *Melastoma septemnervium*, a pioneer shrub species that establishes after forest edge disturbances, had the largest seed storage, indicating its ability to utilize the soil seed bank for population establishment post-disturbance (Liu et al. 2008). However, the presence of *Me. septemnervium* in the study plot was minimal, and the plants struggled to survive in forest gaps. *Blastus cochinchinensis*, a shade-tolerant shrub widely distributed in the forest plantation and lower secondary forest of Huisun Forest Station (Wang et al. 2003, Chang et al. 2019), had only one seedling germinate late in the experiment. This suggests that *Bl. cochinchinensis* is either not common in the soil seed bank or its seeds have a prolonged germination period.

Our findings suggest that the secondary forest's succession had advanced to a later stage, with limited contribution from existing plants to the soil seed bank. This suggests that the composition of the soil seed bank in the study plot was influenced by historical vegetation or was sustained through the dispersal of seeds from introduced species. The composition of the soil seed bank is related to the stage of succession, and the number of seeds and species diversity decreases as succession proceeds (Li et al. 2010, He et al. 2020). Although this phenomenon aligns with related studies (Wu et al. 2014, Chang et al. 2019, Kuo et al. 2020), the extremely low similarity between aboveground vegetation and soil seed bank composition in the study plot indicates that species diversity may have been underestimated when relying on aboveground vegetation surveys. Furthermore, plants that disappeared from the ground cover during succession may not be extinct but may persist in a different life pattern (Milberg 1995). Additionally, the soil seed bank of this secondary forest, in a later stage of succession exhibited characteristics that contribute to maintaining regional species diversity, underscoring the importance of species diversity conservation.

**Spatial pattern of soil seed bank components**

This study found that species composition in the upper soil layer was greater than in the lower soil layer, yet seed storage was significantly higher in the lower soil layer. This finding contrasts with most related studies, which report greater seed storage in the upper layer than the lower layer (Lin et al. 2004, Wang and Ren 2004, Erfanzadeh et al. 2010, Tang et al. 2011, Wu et al. 2014, Schmidt et al. 2020). The soil seed bank comprises continually accumulating and overlapping seed footprints, with seeds buried deeper in the soil often surviving longer than those near the surface (Dalling et al. 1998). Thus, the composition of the soil seed bank reflects the area's vegetation history to some extent. Furthermore, the vertical stratification of a soil seed bank may also relate to seed characteristics. For example, round seeds tend to be more prevalent in surface soil, while flat and slender seeds are more common in deeper soil layers (Li et al. 2008). Additionally, small seeds undergo spatial changes over time, ensuring a high survival rate (Tsuyuzaki and Goto 2001).

Generally, changes in the vertical structure of soil occur only when the soil is subjected to disturbance. Since the plot was located in a long-established secondary forest with minimal disturbance, it is speculated that species with significant seed storage in the lower soil layer entered the soil seed bank in large quantities during a specific period of forest development. After a plant's death, no seeds were available to replenish the soil

seed bank. Moreover, a higher germination rate in the upper soil layer (Gruber et al. 2010) leads to the loss of upper-layer seeds, resulting in significantly lower seed storage in the upper soil layer compared to the lower layer. Additionally, since the uphill slope of the sample plot was a forest road, it is possible that the soil may have been covered by earthwork due to the construction and maintenance of the forest road long ago, leading to lower input of new seeds in the upper soil layer compared to the lower layer.

Seed dispersal types influence the distribution distance and spatial location of seeds (Heinken et al. 2006). Among species with dominant seed storage in the soil seed bank, only *Bu. asiatica* seeds are dispersed through anemochory. Species richness dispersed through anemochory in the soil seed bank of the secondary forest was low because plants are easily replaced during succession (Hirayama et al. 2019). This study found that *Bu. asiatica* seeds were randomly distributed in the sample plot, mainly concentrated in an open area near the forest road. Thus, forest location and canopy structure affected the spatial distribution of *Bu. asiatica* in the soil seed bank. Tzeng et al. (2018) also noted that in a *Taiwania cryptomerioides* Hayata plantation, *Bu. asiatica* seeds were uniformly distributed over a small area, indicating that vegetation development processes affect the spatial distribution of these anemophilous plants in the soil seed bank.

This study revealed that some zoophilous species like *R. trianthus*, *R. corchorifolius*, *I. ficoidea*, and *E. septata* exhibited a clumped distribution (Figure 3). Plue et al. (2010) studied the spatial structure of a soil seed bank within a 2 m pattern and noted that the spatial dependence of the soil seed bank occurred within a small distance, indicating that a large proportion of seeds were deposited near the mother plant. Li (2009) also noted that *Ilex* and *Rubus* mainly rely on birds for seed dispersal, resulting in many seeds clumping due to bird excretion. Furthermore, the feeding habits of certain birds cause some seeds to fall under the mother plant (Chen and Chou 1999), resulting in a clumped distribution.

Seeds of *Me. septemnervium*, *Ma. perlaria*, and *Mu. pubescens* were uniformly distributed. These species are common shrubs and vines that grow at low-altitude forest edges, in open areas, and near logging activity. Although they were few or absent in the investigated plot, they have been observed in Huisun Forest Station. It is speculated that these species were widely distributed in the woodland during the early stages of forest disturbance. Because they left a large number of seeds, their seed numbers were high, and their distribution was uniform. Tzeng et al. (2018) also claimed that the small-scale spatial distribution of *Me. septemnervium* in the soil seed bank of the planted forest of *Ta. cryptomerioides* indicated a uniform distribution.

*Trema orientalis* is a common pioneer tree at low altitude in tropical and subtropical regions (Tang et al. 1997, Feng et al. 1999, Wang et al. 2016). *Trema orientalis* seeds are typically dispersed by birds, and seeds eaten by birds have a higher germination rate (Lu and Chang 1998, Wang et al. 2002). This species is a crucial component of tropical forest soil seed bank (Cao et al. 1997, Tang et al. 1998, Tang et al. 2011, Wu et al. 2014, Tzeng et al. 2018, Chang et al. 2019, Kuo et al. 2020, Lin et al. 2022). The fruit of *Tr. orientalis* is suitable for feeding various small and medium-sized birds, and the species has a long fruiting period, providing abundant food over a long period, with birds then dispersing the seeds (Wang et al. 2002). Wu et al. (2014) investigated the soil seed bank of

five plant communities including secondary forests, burned areas, mono-plantations of *Ta. cryptomerioides*, *Cunninghamia lanceolata* (Lamb.) Hook., and *Calocedrus formosana* (Florin) Florin in the Huisun Forest Station. They discovered that *Tr. orientalis* was the only tree among the 10 most abundant species in the soil seed bank. *Trema orientalis* appeared in each sample plot across the five plant communities, and the seed storage was similar in each plot. The uniform distribution of *Tr. orientalis* seeds in the study plot likely reflects the seed dispersal characteristics of canopy tree birds after feeding.

## CONCLUSIONS

The composition of the soil seed bank and the aboveground vegetation in the secondary forest of the *S. superba* Protected Area in Huisun Forest Station were markedly dissimilar, indicating that the soil seed bank is not the primary regeneration mechanism for the existing vegetation. Additionally, the current vegetation is dominated by shade-tolerant plants, which reflects the progession of the secondary forest towards a later stage of succession. This observation suggests that the species diversity of late-successional secondary forests may be underestimated. These secondary forests possess significant ecological value, and should be conserved. Spatial analysis of the dominant species in the soil seed bank revealed that physiological characteristics of plants, seed dispersal types, vegetation history, and human disturbance all influence the spatial distribution of seeds.

## ACKNOWLEDGMENTS

We are grateful to NSTC subsidies for undergraduate research projects, and the Huisun Forest Station for administrative assistance. We also thank the anonymous reviewers for their valuable comments.

## LITERATURE CITED

**Boufford DE, Ohashi H, Huang TC, et al. 2003.** A checklist of the vascular plants of Taiwan. In Editorial Committee of the Flora of Taiwan Second Edition, Flora of Taiwan. Department of Botany, National Taiwan University. p 15-343.

**Cao M, Tang Y, Zhang JH, Sheng CY. 1997.** Storage and dominants in soil seed banks under the tropical forests of Xishuangbanna. Acta Bot Yunnan 19(2):177-83. [in Chinese with English abstract].

**Chang NH, Ma FC, Yu HM, Hsui YR. 1998.** Dynamics of soil seed bank and seedlings in the Fushan broadleaf forest. Taiwan J For Sci 13(4):279-89. [in Chinese with English abstract].

**Chang CY, Tzeng HY, Lu KC, Tseng YH. 2008.** Invasiveness assessment system of naturalized plants in Taiwan. Q J For Res 30(4):29-39. [in Chinese with English abstract].

**Chang JL, Wang W, Lin CY, et al. 2019.** Comparison of soil seed bank compositions between patch cutting of a Chinese fir plantation and nearby forests in Hui-Sun Forest Station. Q J For Res 41(3):177-90. [in Chinese with English abstract].

**Chang-Yang CH, Su MH, Chiang PH, Hsieh CF. 2022.** Updating the checklist of the naturalized flora in Taiwan. Taiwania 67(1):1-8.

**Chen CC, Chou LS. 1999.** The diet of forest birds at Fushan Experimental Forest. Taiwan J For Sci 14(3):275-87. [in Chinese with English abstract].

**Chiu CA, Lin PH, Lu KC. 2012.** GIS-based tests for quality control of meteorological data and spatial interpolation of climate data.

Mt Res Dev 29(4):339-49.

**Chun M, Wang CM, Chiu CA, Tzeng YH, Tzeng HY, Lu KC. 2010.** Vegetation ecology at Dakeng Area, Taichung. Q J For Res 32(4):7-22. [in Chinese with English abstract].

**Dalling JW, Swaine MD, Garwood NC. 1998.** Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecol 79(2):564-78.

**Editorial Committee of the Red List of Taiwan Plants. 2017.** The Red List of Vascular Plants of Taiwan, 2017. Taiwan: Endemic Species Research Institute, Forestry Bureau, Council of Agriculture, Executive Yuan, and Taiwan Society of Plant Systematics. 187 p.

**Erfanzadeh R, Hendrickx F, Maelfait JP, Hoffmann M. 2010.** The effect of successional stage and salinity on the vertical distribution of seeds in salt marsh soils. Flora 205:442-8.

**Feng ZL, Tang JW, Zheng Z, et al. 1999.** Biomass dynamics of the pioneer *Trema orientalis* community in the early stages of secondary succession of tropical forest in Xishuangbanna. Chinese J Ecol 18(5):1-6. [in Chinese with English abstract].

**Fenner M, Thompson K. 2006.** The Ecology of Seed. Reprinted. UK: Cambridge University Press, 264 p.

**Gruber S, Bühler A, Möhring J, Claupein W. 2010.** Sleepers in the soil-vertical distribution by tillage and long-term survival of oilseed rape seeds compared with plastic pellets. Europ J Agro 33:81-8.

**Haase P. 1995.** Spatial pattern analysis in ecology based on Ripley's K-function: Introduction and methods of edge correction. J Veg Sci 6:575-82.

**He X, Yuan L, Wang ZH, Zhou Z, Wan L. 2020.** A study of soil seed banks across one complete chronosequence of secondary succession in a karst landscape. PeerJ 8:e10226. https://doi.org/10.7717/peerj.10226

**Heinken T, Schmidt M, von Oheimb G, Kriebitzsch WU, Ellenberg H. 2006.** Soil seed banks near rubbing trees indicate dispersal of plant species into forests by wild boar. Basic Appl Ecol 7(1):31-44. https://doi.org/10.1016/j.baae.2005.04.006

**Hirayama K, Yamada S, Inui A, Takahashi M. 2019.** Soil seed bank composition of three forest stands at different developmental stages in a warm temperate forest in western Japan. J For Res 4:255-60. https://doi.org/10.1080/13416979.2019.1641883

**Howe HF, Smallwood J. 1982.** Ecology of seed dispersal. Ann Rev Ecol Syst 13:201-28. https://doi.org/10.1146/annurev.es.13.110182.001221

**Ho CS. 2006.** An Introduction to the Geology of Taiwan Explanatory Text of the Geologic Map of Taiwan. Taiwan: Central Geological Survey. 192 p.

**Iwao S. 1968.** A new regression method for analyzing the aggregation pattern of animal population. Res Pop Ecol 10:1-20.

**Kuo WHJ. 2015.** Seed Biology. Taipei: National Taiwan University Press. 399 p. [in Chinese with English abstract].

**Li JM, Xu HL, Zhang ZJ, Li Y, Wang ZR. 2008.** Influence of seed morphology on the vertical distribution of a soil seed bank in the lower reaches of the Tarim River. Acta Pratacul Sin 17(6):9-17. [in Chinese with English abstract].

**Li KF, Wang W, Tzeng HY, Tseng SH, Kuo CC, Lin CY. 2018.** Composition of the soil seed bank and its effects on forest restoration in Beikeng, Zhukeng Area of Dadu Terrace, Taichung. J Taiwan Agric Engin 64(2):30-48. https://doi.org/10.29974/JTAE.201806_64(2).0003 [in Chinese with English abstract].

**Li XH. 2009.** Ecological significance of bird perches on the restoration of forest vegetation. Acta Ecol Sinica 29(8):4448-54. [in Chinese

with English abstract].

**Li XS, Liu WY, Tang CQ. 2010.** The role of the soil seed and seedling bank in the regeneration of diverse plant communities in the subtropical Ailao Mountains, Southwest China. Ecol Res 25(6):1171-82. https://doi.org/10.1007/s11284-010-0742-y

**Lin CY, Lin YC, Lin PJ, Wang HH, Sun IF. 2010.** Development and evaluation of seed dispersal functions in the Kenting forest dynamics plot. Taiwan J For Sci 25(1):53-62. https://doi.org/10.7075/TJFS.201003.0053 [in Chinese with English abstract].

**Lin CY, Liao MC, Wang W, Tzeng HY. 2022.** Composition characteristics of urban forest soil seed bank and its influence on vegetation restoration-Case study in Dadu Terrace, central of Taiwan. Sustainability 14(7):4178. https://doi.org/10.3390/su14074178

**Lin WC, Kuo YL, Chen YH, et al. 2004.** Soil seed bank and forest regeneration in a broadleaf-coniferous forest of Dona, Southern Taiwan. Taiwan J For Sci 19(1):33-42. https://doi.org/10.7075/TJFS.200403.0033 [in Chinese with English abstract].

**Liu SC, Wen HH, Chen MY, Yang YT. 2008.** Study on pollination ecology of four species of Melastotomataceae in Taiwan. Formoson Entomol 28:67-85. https://doi.org/10.6661/TESFE.2008007 [in Chinese with English abstract].

**Lloyd M. 1967.** Mean crowding. J Anim Ecol 36(1):1-30.

**Lu CH, Chang JC. 1998.** Effect of the fleshy fruits eating birds on seed dispersal. Chinese J Ecol 17(1):61-4. [in Chinese with English abstract].

**Lu KC, Ou CH. 1996.** A preliminary study on forest vegetation of Guandaushi Forest Ecosystem. J Expr For NCHU 18(1):77-108. [in Chinese with English abstract].

**Molles MCJ. 2016.** Ecology Concepts and Applications, Seven Edition. New York (USA): McGraw-Hill Education. p 210-29.

**Milberg P. 1995.** Soil seed bank after eighteen years of succession from grassland to forest. Oikos 72:3-13.

**Olano JM, Caballero I, Laskurain NA, Loidi J, Escudero A. 2002.** Seed bank spatial pattern in a temperate secondary forest. J Veg Sci 13(6):775-84.

**Plue J, Goyens G, Van Meirvenne M, Verheyen K, Hermy M. 2010.** Small-scale seed-bank patterns in a forest soil. Seed Sci Res 20(1):13-22. https://doi.org/10.1017/S0960258509990201

**Sakai A, Sato S, Sakai T, Kuramoto S, Tabuchi R. 2005.** A soil seed bank in a mature conifer plantation and establishment of seedlings after clear-cutting in southwest Japan. J For Res 10:295-304.

**Schmidt KT, Maltz M, Ta P, et al. 2020.** Identifying mechanisms for successful ecological restoration with salvaged topsoil in coastal sage scrub communities. Diversity 12(4):150. https://doi.org/10.3390/d12040150

**Seider TG, Plotkin JB. 2006.** Seed dispersal and spatial pattern in tropical trees. PLoS Biol 4(11):2132-7.

**Shannon CE, Weaver W. 1963.** The Mathematical Theory of Communication. University of Illinois Press, Urbana, 117p.

**Simpson EH. 1949.** Measurement of diversity. Nature 163:688. https://doi.org/10.1038/163688a0

**Sørensen T. 1948.** A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. Biol Skr, K Danske Vidensk Selsk 5(4):1-34

**Tang KC, Tseng YH, Tseng HY, Lu KC. 2011.** Soil seed bank composition of secondary forest in Dakeng Area, Taichung. Q J Chinese For 33(1):35-48. [in Chinese with English abstract].

**Tang Y, Cao M, Zang JH, Ren YH. 1997.** The impact of slash-and-burn agriculture on the soil seed bank of *Trema Orientalis* forest. Acta Bot Yunnan 19 (4):423-8. [in Chinese with English abstract].

**Tang Y, Cao M, Zang JH, Sheng CY. 1998.** Study on the soil seed bank and seed rain of *Mellotus paniculatus* forest in Xishuangbanna. Acta Bot Yunnan 22(6):505-12. [in Chinese with English abstract].

**Tsuyuzaki S, Goto M. 2001.** Persistence of seed bank under thick volcanic deposits twenty years after eruptions of Mount Usu, Hokkaido Island, Japan. Am J Bot 88(10):1813-7.

**Tzeng HY, Lan H, Wang W, Hsu CK, Tseng YH, Kuo CC. 2018.** Composition and spatial distribution of the soil seed bank at *Taiwania* Plantation in Lienhuachi Research Center, Central Taiwan. Q J Chinese For 51(4):309-29. [in Chinese with English abstract].

**Vandvik V, Klanderud K, Meineri E, Måren IE, Töpper J. 2016.** Seed banks are biodiversity reservoirs: Species-area relationships above versus below ground. Oikos 125:218-28.

**Wang CC, Ou CH, Lu KC. 2003.** Species composition and diversity of understory woody plants in *Chamaecyparis obtusa* var. *obtusa* plantation of Hui-Sun Forest Station. Q J Chinese For 23(2):25-42. [in Chinese with English abstract].

**Wang H, Ren JZ. 2004.** Research on seed bank of *Pinus tabulaeformis* in the Ziwu Mountains. J Gansu Agric Univ 39(1):1-5. [in Chinese with English abstract].

**Wang W, Chiu CA, Tsai ST, Kuo CC, Tseng YH, Tzeng HY. 2016.** Vegetation classification of Huoyanshan Area, Miaoli, Taiwan. Q J Chinese For 49(2):131-50. [in Chinese with English abstract].

**Wang ZJ, Cao M, Li GF, et al. 2002.** *Trema orientalis* seeds dispersed by birds and its ecological role. Zool Res 23(3):214-9. [in Chinese with English abstract].

**Warren HJ Kuo. 2004.** Seed ecology and weed management. Weed Sci Bull 25(2):53-68. [in Chinese with English abstract].

**Whittaker RH. 1970.** The population structure of vegetation. In: Tüxen R, editor. Gesellschaftsmorphologie. Dordrecht: Springer. p 39-59. https://doi.org/10.1007/978-94-010-3353-4_5

**Wódkiewicz M, Kwiatkowska-Falińska A. 2010.** Small scale spatial pattern of a soil seed bank in an old-growth deciduous forest. Polish J Ecol 58(3):487-500.

**Wu TH, Tsai ST, Chiu CA, Wang W, Tzeng HY, Lu KC. 2014.** Soil seed bank composition of Hui-Sun Experimental Forest Station. Q J Chinese For 36(2):85-100. [in Chinese with English abstract].

**Yu FC. 2001.** Meteorology. In: Chen MY, Sheu BH, Wu SH, editors. Ecology of Guandaushi Forest Station. Taichung, Taiwan: Experimental Forest of National Chung Hsing University. p 22-35. [in Chinese].

研究報告

# 亞熱帶次生林土壤種子庫小尺度空間格局及其對物種多樣性維持管理的意義

張芷寧[1]、王偉[1,2]、曾彥學[1,2]、曾喜育[1]

## 摘 要


### 背景

土壤種子庫是存在於土壤表層及土壤內仍具有生命力種子組成的總和，為種子植物生命史動態過程的重要階段，一定程度反映物種族群的繁殖更新能力和種子散佈特性。土壤種子庫研究能夠提供了解地上植被群落的過去與未來發展預測，對於生物多樣性維持、植被更新恢復與演替，以及生態重建與修復等具有重要意義。

### 材料與方法

本研究於惠蓀林場木荷保護區的老熟次生林進行地上部植群與土壤種子庫組成空間散布調查，分析土壤種子庫組成的果實/種子傳播方式對其空間分布的影響，並探討與地上植群組成的相似性。樣區大小為25 m × 25 m，區分成25個5 m × 5 m小區，在各小區交界共採取36個土壤種子庫樣點。地上部植群調查每個小區的喬木層胸徑>1cm的樹種、株數、胸徑，同時標定林木之相對位置；地被層的灌木與草本植物則記錄每小區的種類及其覆蓋度。土壤種子庫以15 cm × 15 cm取土鐵框進行取樣，共取0-5 cm(含枯落物)、5-10 cm兩層。使用卜瓦松分布序列、Lloyd擁擠指數和Iwao線($m^*/m$)分析土壤種子庫種子儲量優勢組成物種之空間分布。利用獨立樣本t檢定分析，比較土壤種子庫物種組成與種子儲量在上下土層的垂直分布狀況。使用Simpson歧異度指數和Shannon-Weiner歧異度指數分析各樣點間土壤種子庫的種類歧異度。利用Sørensen相似性指數計算土壤種子庫與地上部植群的物種組成相似性。


[1] 國立中興大學森林學系，402202臺中市南區興大路145號 Department of Forestry, National Chung Hsing University. No. 145 Xingda Rd., Taichung City 40227, Taiwan.

[2] 林業試驗所，100051 臺北市中正區南海路53號 Taiwan Forestry Research Institute, No. 53 Nanhai Rd., Taipei 100051, Taiwan.

通訊作者：曾喜育 Corresponding author, Hsy-Yu Tzeng, Email: erecta@nchu.edu.tw

2024年9月送審，2025年3月通過。Received September 2024, Accepted March 2025.

## 結果與討論

地上部植物調查85種維管束植物，含11種蕨類植物；喬木優勢組成為木荷(*Schima superba* Gardner & Champ.)、山紅柿(*Diospyros morrisiana* Hance)和大葉苦櫧(*Castanopsis kawakamii* Hayata)，地被以灌木柏拉木(*Blastus cochinchinensis* Lour.)最優勢。試驗採取種子發芽法，共發出3,079顆幼苗，包含56種的種子植物，種子密度約3,801 粒/$m^2$。種子儲量最高前三名物種分別為野牡丹(*Melastoma septemnervium* Lour.)、臺灣糊樗(*Ilex ficoidea* Hemsl.)及臺灣山桂花(*Maesa perlaria* (Lour.) Merr.)，佔總種子儲量的48.55%，顯示土壤種子庫由少數種類佔優勢組成。歸化種有9種，僅佔總種子儲量約1%。土壤種子庫植物生長型物種組成比例依序為喬木、草本、灌木和藤本，而種子儲量的比例依序為灌木、喬木、藤本和草本。土壤種子庫的種子儲量優勢物種空間分布顯示與種子傳播方式、植群歷史及人為干擾有關。土壤種子庫種子儲量優勢前10的物種樣點出現頻度顯示，野牡丹、臺灣山桂花、揚波(*Buddleja asiatica* Lour.)和玉葉金花(*Mussaenda pubescens* W.T. Aiton)於所有樣點皆有出現；除了變葉懸鉤子(*Rubus corchorifolius* L.f.)，其他物種出現頻度皆大於0.5，顯示種子儲量優勢種類常於樣區中普遍出現。變異係數顯示在5 m的空間尺度下，臺灣山桂花、玉葉金花、山黃麻(*Trema orientalis* (L.) Blume)、野牡丹為均勻分布，苦懸鉤子(*Rubus trianthus* Focke.)、臺灣糊樗、變葉懸鉤子、臺灣格柃(*Eurya septata* Chi C.Wu, Z.F.Hsu & C.H.Tsou)為聚集分布，揚波則為隨機分布。$m^*$/m結果顯示在5 m的空間尺度下，苦懸鉤子、變葉懸鉤子、臺灣糊樗以及臺灣格柃聚集程度較大。動物傳播的土壤種子庫種子儲量優勢物種的水平空間呈現均勻與聚集分布；風媒傳播的揚波種子儲量在樣區呈明顯隨機分布。土壤種子庫與地上部的物種組成相關低，共有種僅野牡丹和柏拉木2種，顯示絕大多數地上部植物組成並非依賴土壤種子庫為更新方式。

## 結論

惠蓀林場木荷保護區次生林與土壤種子庫之組成相似性極低，顯示土壤種子庫並非現生植群主要更新模式，加上現生植群物種組成以耐陰性植物為主，反映次生林朝向演替後期發展。此現象說明土壤種子庫具有物種保存的功能，亞熱帶老熟次生林植物組成物種多樣性被嚴重低估，顯示著土壤種子庫對於維持森林群落的物種多樣性具有其重要性。土壤種子庫種子儲量優勢物種空間分析顯示，種子植物的種子生理特性、種子傳播方式、植被歷史和人為干擾等作用影響種子的空間分布。

**關鍵詞：**種子庫、次生林、空間分布、種子傳播、惠蓀林場

**張芷寧、王偉、曾彥學、曾喜育。2025**。亞熱帶次生林土壤種子庫小尺度空間格局及其對物種多樣性維持管理的意義。台灣林業科學 40(1):1-20。