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Seed supply and the regeneration potential for plantations and shrubland in southern China

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ABSTRACT

Assessing the characteristics of seed supply will be vital to better understand the dynamics of forest regeneration. In this study, we surveyed the aboveground vegetation, the seed rain, the seed bank, and natural seedling emergence in four typical 24-year-old plantations (eucalyptus, mixed-native, mixedlegume, and mixed-conifer) and a naturally successioned shrubland in southern China. The dominant species in the understory were similar among the five plant communities. The seed rain and the seed bank were dominated by shrubs and herbs but indigenous tree species were rare. Species that were common to all five-plant communities represented a great proportion of the seeds in the seed rain and seed bank. The seed rain consisted mostly of seeds derived from the local plant community. Seed abundance was greater in the seed bank than in the seed rain, and species richness was greater in the seed bank and in the corresponding plant community than in the seed rain. Species composition similarity between the seed rain, the seed bank, and the aboveground vegetation was low, because the seed rain contained much fewer species, and the seed bank and aboveground vegetation contained many different species, respectively. These findings indicate that both the seed rain and the seed bank play important roles in providing seeds for plant recruitment in the understory, but the seed bank contributes more than the current seed rain to the diversity of recruited plants. The current plant community has little impact on the qualitative composition of the seed rain and seed bank. Based on these data, it appears that succession to the desired zonal, mature forest community is unlikely to result from seeds in the seed rain or seed bank. Lack of seed availability of desired zonal mature forest species is the main bottleneck currently limiting succession in the plantations. Reintroduction of late-successional species could facilitate the desired succession.

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1. Introduction

During the last half-century in southern China and Southeast Asia, deforestation and land use change have severely reduced forest cover. Because of economic transformation and conservation initiatives, however, forest cover has steadily increased since the 1990s as a result of plantation establishment and natural restoration (Howlett and Davidson, 2003; Peng, 2003). For example, the forest cover in Guangdong Province in South China increased from 26% in 1979 to 50% in 1998. Still, the understories of established plantations, which are mainly planted with exotic trees species, are dominated by shrubs and herbs and are rarely colonized by indigenous tree species (Ren et al., 2002; Duan et al., 2008). Such plantations remain in the pioneer stages, and succession to more natural communities is inhibited (Ren et al., 2007).

Recruitment of indigenous woody plants may be constrained at different life stages. Seedling emergence and establishment are critical in determining the fate of individual plants, and these processes greatly influence forest regeneration (Grubb, 1977; Harper, 1977). For emergence and establishment to occur, however, seeds must be available (Denslow et al., 2006; Shono et al., 2006; Lentink et al., 2009). Therefore, understanding the characteristics of seed supply in the current plantations, which cover a large portion of southern China, is crucial for understanding long-term community dynamics in general and succession to more natural communities in particular.

In many ecosystems, forest regeneration relies on the seed rain and soil seed bank (McClanahan, 1983; Urbanska et al., 1998; Bossuyt and Hermy, 2004; Pakeman and Small, 2005). The seed rain of a community is the result of seed production from plants within the community and seed input from adjacent communities (Booth and Larson, 1998). Seed rain plays a key role in the subsequent recruitment of new plants and thus underlies forest community structure, dynamics, and regeneration (Fuller and

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Moral, 2003; Pakeman and Small, 2005; Tackenberg and Stocklin, 2008). Previous research has also demonstrated that seed dispersal can facilitate recolonization by indigenous species and thereby accelerate forest succession to more natural stages (Hubbard and McPherson, 1999; Shono et al., 2006).

Besides influencing the future plant community, seed rain also greatly affects the seed-bank composition because seed-bank renewal depends on seed rain (Alvarez-Buylla and Martinez-Ramos, 1990). The soil seed bank, which reflects the current and past plant community, can help prevent local species extinction and can also act as a seed source in forest regeneration (Maranon, 1998; Olano et al., 2002; Auld et al., 2007). Most importantly, the soil seed bank can be a source of colonizing species (e.g., zonal mature forest species) that can accelerate forest succession (Augusto et al., 2001; Luzuriaga et al., 2005).

The contributions of the seed rain and seed bank to vegetation regeneration depend on seed quantity and composition (Thompson and Grime, 1979; Fuller and Moral, 2003). To date, however, the effects of the seed rain and seed bank on early stages of regeneration in the established plantations in southern China have not been well studied.

In this study, we investigated the quantitative and qualitative composition of the seed rain and soil seed bank and natural seedling emergence in four typical plantations and in a natural shrubland, located in southern China. All five sites had experienced 24 years of succession. The general question asked was whether the seed rain and seed bank can speed up the succession of current plantations to more natural stages. The specific questions were: (1) How does species composition of the seed rain and the seed bank relate to species composition of the aboveground vegetation? (2) What is the pattern of seedling recruitment in the field? (3) How does species composition differ in the seed rain and the soil seed bank? In addition, we discuss the relative importance of the seed rain and seed bank in contributing to plant recruitment.

2. Materials and methods

2.1. Study site

The study site is located at the Heshan National Field Research Station of Forest Ecosystem, Chinese Academy of Science (112°54′E, 22°41′N), Heshan City, Guangdong, southern China. This site is characterized by a typical subtropical monsoon climate with a mean annual temperature of 21.7 °C. The mean annual rainfall is 1700 mm, which is concentrated between April and September. The mean annual evaporation is approximately 1600 mm, and the elevation ranges from 0 to 90 m. The soil is an acrisol. The zonal climax vegetation is lower subtropical monsoon evergreen broad-leaved forest (typically comprising Cryptocarya concinna, Cryptocarya chinensis, and Aporosa yunnanensis), but this zonal climax vegetation is not represented at the research station; the closest remnant of the zonal climax vegetation is located at Dinghushan Mountain, about 70 km north of the research station. The closest Fengshui forests (i.e., secondary forests that consist of native tree species and that are usually located adjacent to villages) are approximately 3 km from the research station.

In 1984 (24 years before this study was conducted), experimental plantations of native and introduced species were established on degraded hilly-land at the research station to restore the degraded ecosystem. Topography, initial soil properties, and initial vegetation composition were similar across this hilly-land. At the same time, part of the degraded land was left unplanted and without further disturbance and had naturally succeeded to the shrubland stage when the current study was started. The dominant species in the degraded land before plantation establishment were

Ischaemum indicum, Eriachne pallescens, and Baeckea frutescens. The experimental plantations and the shrubland consisted of five sites. The main established species at the EP site (1.79 ha) were Eucalyptus exserta and Eucalyptus citriodora, with a mean basal area of 154 cm². The main established species at the NP site (2.68 ha) were native species Schima superba and Cinnamomum burmanii, with a mean basal area of 201 cm². The main established species at the LP site (3.99 ha) were legume species Acacia mangium, Acacia auriculaeformis. Acacia confuse, and Acacia holosericea, with a mean basal area of 255 cm². The main established species at the CP site (3.17 ha) were coniferous species Pinus massoniana and Cunninghamia lanceolata, with a mean basal area of 227 cm². The SL site (3.5 ha) was a shrubland that had undergone 24 years of natural succession from the former degraded land and that was currently dominated by *Ilex* asprella, Evodia lepta, and Trema tomentosa, with a mean basal area of 28 cm². All trees in the plantations were planted at a 2.5 m \times 2.5m spacing. All four plantations and the shrubland had been left to develop naturally without anthropogenic disturbance.

2.2. Experiment and sampling design

To assess seed rain in each site, we established three transects $(10 \,\mathrm{m} \times 40 \,\mathrm{m})$ at each site; these transects were located on upper slope, middle slope, and basal slope of each site, respectively. The slopes within each site were homogeneous, i.e., with the topsoil and inclination similar. Each transect was divided into four quadrants $(10 \text{ m} \times 10 \text{ m})$. One seed trap $(0.5 \text{ m} \times 0.5 \text{ m} = 0.25 \text{ m}^2 \text{ trapping area})$ was established in the middle of each quadrant; thus, adjacent seed traps in a transect were 10 m apart, and there were 12 seed traps per site. Seed traps were positioned in the field in December 2007. A seed trap consisted of plastic mesh (0.5-mm mesh) whose shape was maintained by the attachment of PVC tubes to the four corners. The seed trap was 10 cm deep, and its bottom was positioned 10 cm above the ground (Zou and Yang, 2005; Barbosa and Pizo, 2006). Once each month, from January 2008 through December 2008, all seeds, fruit and seed-bearing fruit fragments were collected from each trap, taken back to the laboratory, sorted by species, and then counted.

To assess the seed bank, we collected soil samples from one plot $(1 \text{ m} \times 1 \text{ m})$ adjacent to each seed trap. In March 2008, five soil samples ($10 \times 10 \times 10$ cm) with litter intact were randomly and carefully excavated from each plot. The soil samples were divided into three depths (0-2, 2-5, and 5-10 cm), and the five soil samples were pooled for each plot and depth class, as suggested by Bossuyt et al. (2002). The total sampling area at each site was 0.6 m^2 . Seed abundance and species composition in the seed banks were determined with germination assays, which were performed as described by Ter Herdt et al. (1996). Each soil sample was passed through a 2-mm sieve to remove coarse debris. Seeds with diameter >2 mm were retrieved and returned to the soil samples. Each soil sample was spread on a seed germination tray with perforations on the bottom for drainage. Before the soil samples were spread, the bottom of each germination tray was covered with a 2-cmthick layer of heat-sterilized (120 °C for 10 h) sand to prevent the soil samples from becoming water-saturated. All germination trays were placed in an experimental greenhouse and watered daily to keep the soil moist. The mean temperature in the greenhouse was 28 °C, and the mean relative humidity was 66%. Newly germinated seedlings that were identified at the species level were counted and then removed from the seed trays every 2-5 days. Unidentified seedlings were transplanted into additional germination trays for further growth until the species could be identified. After the newly germinated seedlings were identified and removed, the soil in each tray was thoroughly stirred to stimulate germination of remaining viable seeds (Smith et al., 2002). Twelve seed trays filled with sterilized sand only were kept under the same conditions as a control for

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