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Soil seed bank and aboveground vegetation along a successional gradient on the shores of an oxbow☆

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ABSTRACT

The soil seed bank and aboveground vegetation were investigated on the shores of the Tian-e-zhou oxbow in China along a successional gradient (i.e. mud flat, sedge and graminoid marsh, sedge and reed meadow, and willow shrub). We expected to explore the following questions: (1) Does seed density and species richness of the soil seed banks decline during succession? (2) Does the similarity between the soil seed bank and aboveground vegetation decrease during succession? (3) Can soil seed banks be considered as a potential source of material for wetland restoration? Results revealed that 19 species (about 61% of the species in the mud flat stage) were found in all successional stages. Both seed density and species richness increased with succession. Species of the soil seed bank showed greater compositional similarity (Sørensen's index) across four stages than did the aboveground vegetation. The similarity between soil seed bank and aboveground vegetation increased as succession proceeds. In conclusion, the seed bank of Tian-e-zhou oxbow wetland contains a relatively abundant seed density and species richness. The soil seed bank could thus play an important role in the restoration management of oxbow wetlands. However, the high dominance of mudflat annuals and the absence of most dominant perennials in the soil seed bank suggest that target species may require active introduction for further restoration

1. Introduction

The soil seed bank is one of the most important structural components in naturally occurring wetlands (Angeler and García, 2005) and may play an important role in vegetation development during succession (van der Valk and Davis, 1978; Grime, 1989; Leck et al., 1989; Thompson, 2000). Seed banks are also considered to be an important potential seed source for the restoration of plant communities (van der Valk and Pederson, 1989; van der Valk et al., 1992; Fenner and Thompson, 2005; Nishihiro et al., 2006; Bossuyt and Honnay, 2008). Knowledge of seed bank composition and dynamics is a crucial factor in the definition of restoration policies and strategies (Ma et al., 2010).

A general finding is that seed density and species richness usually decrease during succession in grasslands (Donelan and Thompson, 1980), old fields (Symonides, 1986; Roberts and Vankat, 1991) and forest (Plue et al., 2010). Thompson (2000) formulated a paradigm of "declining seed numbers and diversity and decreasing similarity between seed bank and vegetation as succession proceeds" based mainly on results from studies of agricultural ecosystems. However, this pattern is not universal and species diversity increased during the course of succession in dune slacks (Bossuyt and Hermy, 2004) and wetlands of the Tibetan Plateau (Ma et al., 2011) because of increasing seed production, seed density, we wanted to test these hypotheses proposed for seed bank characteristics under succession since these hypotheses have never been tested in an oxbow wetland.

Knowing the relation between soil seed bank and aboveground vegetation may help conservationists to manage against exotic species, plan for community responses to disturbances, restore diversity and better understand the resilience of an ecosystem (Hopfensperger, 2007). The relation between vegetation and its seed bank in different successional stages in wetlands have been well described. Wetlands with annual dominated communities often have a high similarity (Jutila, 2003). Moderate similarity values found in most wetland studies may be due to the presence of both transient and persistent seed bank species (Leck and Graveline, 1979). Poor similarity is found in later stages of succession because pioneer species with persistent seeds remain dominant in the seed bank (Willems, 1988; Thompson et al., 1994). Some studies of wetlands found decreases in similarity with succession due to the presence of seeds of persistent pioneers

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that remain in the seed bank and because germination is suppressed by a thick litter layer and shading (Grandin, 2001; Amiaud and Touzard, 2004). Although the seed bank has been studied in many types of stages, its functioning remains rather poorly understood, particularly in wetlands (Touzard et al., 2002).

As the Yangtze River emerges from the Three Gorges, it rushes headlong for hundreds of kilometers, feeding the largest floodplain in China (Li et al., 2002). Many wetlands with typical features are widespread in this vast area, and are almost all directly or indirectly connected to the river (Li et al., 2008). However, they are sensitive and threatened by human impact (Deil, 2005). With their fertile land and abundant natural resources, the wetlands are shrinking as they are reclaimed to make way for towns, cities and agricultural land (Cai and Zhou, 1996; Wang et al., 2005). These once healthy river ecosystems have been severely disrupted, and the consequences are now impacting society and economic development (Hao et al., 2004). In the middle Yangtze River floodplain, soil seed banks were studied in marshes (Liu et al., 2005, 2006a, 2006b; Yuan et al., 2007; Li et al., 2008), shallow freshwater lakes (Chen et al., 2001; Xiao et al., 2010) and returning farmland into lake (Wang et al., 2003; Hou et al., 2009). However, soil seed banks of the oxbows on the Yangtze River are poorly understood.

This paper was designed to determine the composition and dynamics of soil seed banks associated with aboveground vegetation in different successional stages of the Tian-e-zhou oxbow wetland. We wanted to explore the following questions for soil seed bank characteristics under succession: (1) Does seed density and species richness of the soil seed banks decline during succession? (2) Does the similarity between the soil seed bank and aboveground vegetation decrease during succession? (3) Can soil seed banks be considered as a potential source of material for wetland restoration? By answering these questions, it was hoped that this study would guide later restoration and management measures in such environments.

2. Materials and methods

2.1. Study sites

The study was carried out in the Tian-e-zhou oxbow wetland (29°49′ N, 112°33′ E, Fig. 1), Shishou, China. It is the most well-preserved floodplain wetland in the middle Yangtze River (Hao et al., 2004). The course was cut off from the main stream of the Yangtze River and formed naturally by water forces in 1972, remaining connected with the Yangtze River in the flood season (late-May or early-June to September) and was held intact as a river bank wetland in the lower-middle reaches of the Yangtze River. This connection between the oxbow and the Yangtze River was obstructed by the Sha-tan-zi Dike which was completed by the end of 1998, limiting the exchange of water and sediment (Wu et al., 2009). The total area of the Tian-e-zhou oxbow wetland is about 6865 ha, the altitude is 31–36 m, annual rainfall is 1099–1230 mm and mean annual temperature is 16.4 °C (Wu et al., 2006). The soil type is sandy clay loam. The Tian-e-zhou oxbow wetland attracts more and more attention because of the successful reintroduction of Pere David's deer (*Elaphurus davidianus*; Jiang et al., 2000) and ex situ conservation of the Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*; Ding et al., 2000). Human activities in the study areas were quite low because of the seasonal flooding. We selected four stages: mud flat, graminoid and sedge marsh, sedge and reed meadow and willow shrub (Table 1), to represent early to late successional series in the floodplain (Zhang and Zhu, 2009).

2.2. Seed bank sampling and germination

Soil seed banks were sampled in the beginning of April 2009, before the spring germination season in the field. At each stage, ten randomly located 1 m × 1 m plots were used for sampling. After thoroughly removing the plant materials from the soil surface, five soil cores of 10 cm depth were taken at regular intervals with an iron cylinder (diameter 8 cm) in each plot. The cores were then divided into two 5-cm deep soil strata and respective strata were combined across plot (TerHeerdt et al., 1996).

Methods for seedling emergence followed van der Valk and Davis (1978). Visible tubers, turions, roots, rhizomes and litter were removed carefully after washing the sediment. Each sample was wet-sieved (0.2 mm) and the retained material was spread in a layer (<1 cm deep) over 10 cm of sand in plastic trays (diameter 30 cm). The sand had previously been dried for 24 h at 75 °C to kill any weed propagules (Dahlquist et al., 2007). All trays were randomly arranged in an unheated greenhouse at the Wuhan Botanical Garden (30°32′82″ N, 114°25′18″ E) and were watered regularly with tap water to maintain a saturated condition. These conditions are appropriate in studies involving the germination of both submerged macrophytes and helophytes (Boedeltje et al., 2002). Seedlings were counted weekly and were removed as soon as they could be identified. Seedlings that could not be identified.were transplanted to empty trays and allowed to grow until they could be identified. Germination was recorded until there had been no further germination for more than 1 month. Nomenclature followed the Flora of China (Wu et al., 2008).

2.3. Aboveground vegetation survey

In each stage the composition of the herbaceous vegetation was surveyed with quadrats (50 cm × 50 cm) from which seed bank samples were obtained at the end of April 2009. A total of forty quadrats were surveyed. Within each quadrat, the species composition and number of individuals or shoots (for clonal species) were recorded.

2.4. Data analysis

We combined the data from the two germination layers in order to estimate the seed density of each species in each stage (Liu et al., 2005). Species densities were calculated as the density of seeds per m^2. The distribution percentage in life form categorization (annual and perennial) of each stage was determined. The differences in seed density and species richness among different stages and different layers in the soil seed bank and species richness in the vegetation were compared by one way analysis of variance (ANOVA) and subsequent Tukey range test. Data for each depth (0–5 cm, 5–10 cm) and the whole profile (0–10 cm) were analyzed separately. Where the assumption of homogeneity of variance was not met, a Kruskal–Wallis H test was performed. If significant differences were detected, then Mann–Whitney U tests were used to conduct multiple comparisons. Sørensen's index of similarity (Kent and Coker, 1994) was used to describe and compare the composition between soil seed bank and aboveground vegetation. All the above analyses were performed using SPSS 19.0.

The relation between the soil seed bank and aboveground vegetation was examined using Non-metric Multidimensional Scaling (NMDS) which is considered to be the best method for graphical representation of floristic relations (Clarke, 1993). The resulting NMDS axis values are produced such that sites with similar species composition lie close to one another in ordination space. We calculated similarity matrices using the Bray–Curtis similarity index, which has been found to be robust with respect to ecological distance (Faith et al., 1987). All ordinations were based on