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Responses of alpine meadow seed bank and vegetation to nine consecutive years of soil fertilization

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ABSTRACT

Decline in aboveground species diversity in response to nutrient enrichment has been demonstrated by many studies. However, information on the soil seed bank also is important for restoration of species-rich vegetation, but this subject has received little attention. The aim of this study was to investigate the relationship between the aboveground vegetation and the soil seed bank of an alpine meadow along a fertilization gradient that can germinate in spring. We determined species richness, density, life form and functional groups in the soil seed bank and in the aboveground vegetation along an N–P fertilization gradient from 0 to Fer_{120} (120 g/m^2; i.e. 25.4 g N and 28.2 P m^2/yr). Non-metric multidimensional scaling was used to test the similarity between soil seed bank and aboveground vegetation. Species richness of both soil seed bank and vegetation declined in response to 9 years of fertilization, but rate of decline in the seed bank was slower than that in the vegetation. Seed density did not differ along the fertilization gradient except for Fer_{30}, which had the highest seed density. Plant density in the vegetation declined along the fertilization gradient. Proportion of annuals increased both in the vegetation and the soil seed bank along a fertilization gradient. Percentage of different functional groups in the soil seed bank changed but less than that in the vegetation. The similarity between soil seed bank and vegetation increased from Fer_0 to Fer_{90} and then decreased in Fer_{120}. Fertilization influenced species composition of the soil seed bank, but the effect was smaller than that on the aboveground vegetation. The seed bank present in spring provides high species richness and high seed densities for restoration, but restoration to the non-fertilized state would be difficult due to the shift to a higher proportion of annuals and to a low proportion of sedges along the fertilization gradient.

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1. Introduction

One of the ongoing ecological problems of this century related to human activities is increased additions of nutrients to natural ecosystems (Wedin and Tilman, 1996; Vitousek et al., 1997; Smil, 2000; Bennett et al., 2001). The amount of nitrogen and other nutrients deposited on earth each year has increased, often resulting in a reduction of plant diversity and an increase in plant productivity (Clark et al., 2007; Ceulemans et al., 2013). Also, the abundance of species increased (Besaw et al., 2011), decreased (Gough et al., 2012), or remained the same (Craine et al., 2001) with nutrient additions.

Changes in the species composition of a community can cause shifts in the relative importance of various life forms (Suding et al., 2005), invasives (Huenneke et al., 1990) and functional groups (Theodose and Bowman, 1997). Further, fertilization may (Milberg, 1992; Akinola et al., 1998) or may not (Smith et al., 2002; Schneider and Allen, 2012) have an effect on total seed density and species richness of the soil seed bank, but the relative abundance of species may change (Kitajima and Tilman, 1996). Thus, no consistent conclusion has been obtained about the effect of fertilization on change in composition of soil seed banks.

The soil seed bank is of particular concern to ecologists because it is the primary source of seeds if a disturbance destroys the

Abbreviations: NMDS, non-metric multidimensional scaling.

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aboveground vegetation. Thus, in ecosystems that are subjected to disturbance, e.g. heavily grazed grasslands, it is important to have information about the soil seed bank to be able to judge "restoration ability" of the area after a disturbance. In evaluating the restoration potential of the soil seed bank, the kinds and numbers of seeds present in the soil regardless if they are transient or persistent at the time of the natural germination season need to be determined.

Floristic similarity of seed bank and aboveground vegetation is one of the primary variables measured in studies on soil seed bank ecology (Hopfensperger, 2007). Some studies in grasslands found high similarity between soil seed bank and aboveground vegetation (e.g. Henderson et al., 1988; Levassor et al., 1990; Bossuyt and Honnay, 2008), while others found a low similarity (Arroyo et al., 1999; Welling et al., 2004; Ma et al., 2009; Li et al., 2012). This similarity has been based on morphological and ecological attributes of the plant, such as life-form (Ungar and Woodell, 1993), seed dispersal ability (Dessaint et al., 1997; Bossuyt and Hermy, 2004), successional position (Grandin and Rydin, 1998; Grandin, 2001), reaction to disturbance (Jutila, 1998; Ma et al., 2010a) and invasiveness (Mason et al., 2007; Vosse et al., 2008).

The alpine meadows on the Tibetan Plateau in China are high diversity grasslands (Chu et al., 2007; Harris, 2010; Zhang et al., 2013), but they are sensitive to climate change (Liu et al., 2013a,b), e.g. increased N deposition. Due to an increase in regional economic development, N deposition is very obvious in the eastern Tibetan Plateau, ranging from 4 to 13.8 kg N/ha/yr (Liu et al., 2013a,b; Lü and Tian, 2007), and is predicted to increase in another two or threefold in the coming decades (Jiang et al., 2013). N addition reduced species richness of plants, arbuscular mycorrhizal fungi and Glomeromycota in Tibetan Plateau (Yang et al., 2011; Liu et al., 2012). Thus, it is becoming increasingly important to understand the role of the seed bank in change of these grasslands community composition after N addition. That is, the seed bank is an important resource for plant community conservation and restoration in terms of regeneration and serves as a supplement of the vegetation (Van der Valk and Pederson, 1989; Bakker et al., 1996; Ma et al., 2011, 2013; Hong et al., 2012; Rivera et al., 2012). However, understanding the role of the seed bank in vegetation to the original state may be complicated by the fact that changes may occur in the standing vegetation due to addition of nutrients to the system, which could in turn have consequences on the composition of the soil seed bank. Phosphorus (P), together with Nitrogen (N), is a common nutrient element shaping plant and microbial community construction (Vitousek and Howarth, 1991; Elser et al., 2007), and furthermore, can greatly affect nitrogen cycles through its effects on vegetation growth and microbial activity (Vitousek et al., 2010). Thus, we set an N–P addition experiment in an alpine meadow of the Tibetan Plateau to detect the responses of soil seed bank and vegetation to nine consecutive years of soil fertilization. With regard to the alpine grasslands on the Tibetan Plateau, what effect does increased fertilization have on the soil seed bank and consequently on the long-term restoration potential of the vegetation? That is, does fertilization change the aboveground vegetation, and does it, therefore, change the diversity of species and numbers of seeds of each species present and germinable in spring when seed germination occurs in the grassland?

The alpine meadow of the Tibetan Plateau are dominated by perennial forbs and graminoids, and the dominant families are Poaceae, Cyperaceae, Asteraceae, Ranunculaceae, Leguminnosae, Scrophulariaceae, Polygonaceae and Gentianaceae (Bu et al., 2008). The soil seed bank was always dominant by earlier successional species (Ma et al., 2009, 2010a), such as *Artemisia*, *Chenopodium*. In this study, we tested the hypothesis that there is high similarity in species richness, density, life form and functional group of the aboveground vegetation and the soil seed bank in an alpine meadow on the Tibetan Plateau after nine consecutive years of fertilization. To test this hypothesis, we sought answers to the following questions. (1) Does the species composition of soil seed bank and aboveground vegetation change along a fertilization gradient, and if so how? (2) What is the change in similarity between soil seed bank and aboveground vegetation along a fertilization gradient? Thus, we compared the effect of fertilization on species composition, life form and functional group in the soil seed bank and the aboveground vegetation. No studies have been done on the effects of fertilization on soil seed bank of Tibetan alpine meadows.

2. Material and methods

2.1. Site description and experimental design

The study was carried out at the Walaka experimental site of the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University (Maqu Branch Station) (33°58′N, 101°53′E) located at Maqu, Gansu Province, China. The elevation is 3500 m above sea level (a.s.l.), mean annual temperature 1.2 °C (−11 °C in January to 11.7 °C in July) and mean annual rainfall 620 mm. Soil type of our study area is alpine meadow soil, with a soil depth of 80 cm (Chen and Wang, 1999). Total N and P in the alpine meadow are 3.6 g/kg soil (total N was determined by the Kjeldahl method) and 0.56 g/kg soil (total P was digested by $HClO_4$–H_2SO_4 and determined by molybdenum-blue colorimetry), respectively. Aboveground vegetation is dominated by the perennial graminoids, such as *Kobresia capillifolia*, *Elymus nutans* and *Poa araratica*. The experimental site has been fenced and grazed only in non-productive winter months since 2001 (seed dispersal have completed).

The fertilization experiment, which began in March 2002, was a random block design with five replicates and five fertilization levels (5 × 5 = 25 plots). Each plot had an area of 60 m^2 (6 m × 10 m), and the plots were distributed in five columns and five rows. Each plot was surrounded by a 1 m-wide buffer strip, which was not fertilized.

A fertilization gradient was established by applying different amounts of $(NH_4)_2HPO_4$ (The Tianjin International Trading Company, Tianjin, China) in mid-May of each year beginning in 2002. The growing season begins in mid-May, and at this time the soil is moist. The quantity of fertilizer applied was 0 (control), 30 g/m^2, 60 g/m^2, 90 g/m^2 and 120 g/m^2, hereafter referred to as Fer_0, Fer_{30}, Fer_{60}, Fer_{90} and Fer_{120}, respectively. The corresponding N and P content of the five fertilization levels is: Fer_0, control; Fer_{30}, 6.4 g N and 7.0 g P/m^2/yr; Fer_{60}, 12.7 g N and 14.1 g P/m^2/yr; Fer_{90}, 19.1 g N and 21.1 g P/m^2/yr; Fer_{120}, 25.4 g N and 28.2 g P/m^2/yr.

2.2. Soil collection and processing

Soil samples were collected at the end of April 2011, before seed germination had begun (Ma et al., 2010a). Fifty 3.2 cm-diameter samples from each of the five plots for each fertilization treatment were divided into three layers of 0–5 cm, 5–10 cm and 10–15 cm, and soil from the same depth from a plot was pooled. The samples (3 depths × 5 plots × 5 treatments) were allowed to air-dry in front of a north-facing window for 15 days, after which they were sieved through a 4 mm wire mesh to remove plant fragments and stones. Visual inspection of the coarse particles retained by the wide-mesh sieve revealed no seeds.

2.3. Maintenance of seed trays

The direct germination method was used to access the readily germinable seeds (Ma et al., 2012). Soil samples were put into round

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