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Bud banks of two perennial grasses: Composition, size, dynamics and contribution to population maintenance during the flooded restoration succession on the Songnen Meadow, China

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To describe the composition, size, temporal dynamics of bud banks of both perennial rhizomatous herbaceous *Leymus chinensis* and *Carex duriuscula* and to explore the contributions of bud banks to aboveground population persistence during the flooded restoration succession. Soil blocks $25 \times 25 \times 30$ cm^3 were sampled during two growing seasons from June to September. The total rhizome buds comprised the largest proportion of *L. chinensis* bud banks except for September of 2004 (juvenile tillers were the most). The top rhizome buds were the most of *C. duriuscula* bud banks. The percentages of total buds derived from tiller nodes and rhizomes of both species were nearly equal in the two-year study period. The productivity of *L. chinensis* and contribution of bud banks to population persistence were higher than those of *C. duriuscula*. Size of bud banks of *L. chinensis* was not significant between the end of two sampling seasons (1039.2 and 1232.0 buds/m^2), and buds significantly decreased in *C. duriuscula* (1140.0 and 581.6 buds/m^2). Over the two studied seasons, decreasing number of buds and low productivity as well as small contribution indicate that *C. duriuscula* which spread after flood event will be successively replaced by *L. chinensis*.

Key words: Bud bank, *Carex duriuscula*, *Leymus chinensis*, natural meadow, population persistence, restoration succession.

INTRODUCTION

Grassland plants have two ways to recruit their populations, namely, seedlings and vegetative shoots. The former originate from seed banks and the latter from bud banks. Seed bank usually is vital to vegetation restoration following severe environmental change (Li and Yang, 2004; Ma et al., 2010). Seed bank can also provide a reserve of genetic variability when long-lived dormant seeds act as a memory of past selection or as a source of new genetic variation through accumulating mutations (Levin, 1990). The composition and abundance of soil seed species may significantly differ from those of aboveground community, thereby influencing the structure and dynamics of plant communities and their responses to disturbances (Leck et al., 1989; Blaise et al., 2002; Wang and Zhu, 2002; Benson and Hartnett, 2006). Belowground bud bank has the potential to influence patterns of aboveground net primary production and community dynamics in grassland ecosystems (Knapp and Smith, 2001; Li and Yang, 2004). The seasonal emergence and population dynamics of aboveground plants is generally driven by the pattern of vegetative reproduction (Yang et al., 1995; Benson et al., 2004; Benson and Hartnett, 2006). The ecological and evolutionary consequences of seed banks have been well studied (Baskin and Baskin, 1998). However, despite vegetative reproduction is crucial to herbaceous communities, especially perennial grassland ecosystems,

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and only few empirical or theoretical studies have been conducted in recent years (Benson et al., 2004; Harmony and David, 2006, 2009; Klimešová and Klimeš, 2007; Zhang et al., 2009).

Numerous perennial grasses have demonstrated remarkable long-term persistence (Silvertown and Charlesworth, 2001), but their aboveground stems live for only one growing season in temperate zones (Yang et al., 1998). Therefore, the persistence of perennial grasses requires annual tiller recruitment to offset mortality losses associated with short tiller longevity (White, 1980; Briske and Butler, 1989; Hendrickson and Briske, 1997). In these perennial grass communities, successful establishment from seed is a rare event (Benson and Hartnett, 2006). Vegetative reproduction associated with rhizomes or other belowground perennial parts plays a fundamental role in population structure and community dynamics.

After different disturbances, seed banks and bud banks (Harper, 1977) play different roles to vegetation succession. The composition and role of seed banks have been well conducted during restoration of different grassland types all along, for example, the species-rich flood-meadows (McDonald et al., 1996), the calcareous grassland (Willems and Bik, 1998; Fagan et al., 2010), the open sand grassland (Halassy, 2001), the dry acidic dune grassland etc (Bossuyt et al., 2007; Bossuyt and Honnay, 2008). But there are a few studies about bud banks during restoration on grassland. Under heterogeneous environment (such as water and nutrient), bud bank can affect aboveground population establishment (Wang et al., 2008). Previous studies on bud bank have almost aimed at incompletely destroyed vegetation on grasslands. Therefore, it is necessary to study the composition, size, dynamics and contribution of main dominate species bud banks to population maintenance and community dynamics during community restoration originating from soil seed banks that occurred in a secondary bare area.

A series of experiments were conducted with main dominant species *Carex duriuscula* and *Leymus chinensis* during a flooded restoration succession. The primary objective of our study was to quantify the composition and size of bud banks of *L. chinensis* and *C. duriuscula* during the restoration succession. Here we emphasized the role of juvenile tillers. In addition, the temporal dynamics of bud banks of *L. chinensis* and *C. duriuscula* was presented. Finally, we explore the contribution of bud banks in population persistence and succession dynamics during the flooded restoration succession. Furthermore, the succession dynamics would be predicted in our study.

MATERIALS AND METHODS

Species characteristics

L. chinensis (Poaceae), a perennial rhizomatous herb with long rhizomes, is widely distributed in the eastern region of the Eurasian steppe zone including the outer Baikal area of Russia, the northern and eastern parts of the People's Republic of Mongolia, the Northeast and Northern Plain and the Inner Mongolian Plateau of China (Li et al., 2001). With its combined considerable biomass and high nutrition, *L. chinensis* is one of the most important natural grass species (Zhu, 2004). *C. duriuscula* belongs to the Cyperaceae family. It, too, produces long rhizomes, and is distributed widely in meadows, meadow steppes, immobile sand dunes, and the edges of cropland. Disturbances such as grazing, mowing, etc. usually reduce *L. chinensis*, but increase *C. duriuscula* and *C. duriuscula* even become a dominant species (Yang and Li, 2001). In this experimental area, *L. chinensis* returns to green during the first ten days of April, flowering in the last ten days of June, and seeding in late July. Tillering nodes located at the joint of tillers and rhizomes are important clonal reproduction sites for both *L. chinensis* and *C. duriuscula*. The rhizome is also an important clonal reproduction organ for them. *L. chinensis* and *C. duriuscula* rhizomes usually distributed at 10 to15 cm and 5 to10 cm soil layer, respectively. A *L. chinensis* rhizome lives for about four years and a *C. duriuscula* rhizome lives for about five years (Yang et al., 1995).

Study site

The study was conducted at the Pasture Ecology Research Station of Northeast Normal University, a *L. chinensis* meadow located in the southern region of Songnen Plain, Changling county, Jilin province of China (44°45′N, 123°31′E). The average annual temperature is 4.9°C. The average annual precipitation is 470.6 mm. The frost free period is about 150 days. The annual evapotranspiration is 1668 mm, 3.5 times that of the average precipitation. The soil is an alkaline soil, characteristic of meadow habitats. The study area was considered as a sluiceway during the flooding from August 1994 to September 1995. This region belongs to a low floodplain in the southern Songnen Plain, which was formed by an alluvial flood area and low meadow land that is flat. The floodwater was at the surface of the soil for the flood's duration. The experimental site is an approximately 2000-ha *L. chinensis* meadow (with a density of 1000 to 1200 tillers/m^2, a height of 20 to 35 cm, and coverage of 70 to 80%) before the flood. *C. duriuscula* was a companion species in the community (with a density of 1000 to 1500 tillers/m^2, a height 5 to 10 cm, and coverage of 5 to 10%). *L. chinensis* was mowed for hay in autumn. All mesophytes and xerophils were dead due to long-term flooding beyond plant tolerance thresholds. In the next year, the meadow was fenced and being in natural restoration processes.

Experimental plots

The study site was located on the flat meadow. *C. duriuscula* became the first species to occupy the site after the flood waters retreated. *C. duriuscula* seedlings gradually expanded via vegetative reproduction until it became the monodominant species. *L. chinensis* seedlings emerged in the *C. duriuscula* community in 1997 and then they gradually expanded via vegetative reproduction. To 2003, *C. duriuscula* became background plant, and *L. chinensis* patches with different sizes distributed into the *C. duriuscula* community. *Artemisia anethifolia* and *Polygonum sibiricum* were sporadicly distributed.

To explore the composition, size, dynamics and contribution of bud banks during the restoration succession, three rectangular plots of 50 ×100 m^2 were selected for monthly investigation in June 2003. The spots were similar in density of *L. chinensis* and *C. duriuscula*. These spots were enclosed to avoid disturbance from livestock and people and they would not be destroyed until at the end of the 2004 growing season. Each of these plots was nearly

Table 1. Composition and size of *Leymus chinensis* bud bank (M ± SE) in 2003 and 2004.

Sampling date		TN	TJ	RT	RN	RJ	Total buds
2003	29 Jun.	80.0±15.9 a	-	44.0±8.8 a	72.0±14.8 a	-	196.0±35.1 a
	21 Jul.	233.6±44.4 b	-	439.2±140.5 b	153.6±35.5 a	-	826.4±168.7 b
	1 Sep.	281.6±44.0 b	46.7±9.4	340.8±44.8 b	308.8±76.9 b	61.3±14.0	1039.2±132.8 b
2004	5 Jun.	3.2±1.9 a	-	24.0±5.7 a	368.0±58.7 a	-	395.2 ±62.5 a
	8 Jul.	147.2±22.4 b	-	41.6±9.5 a	228.0±57.3 b	-	416.8±65.4 a
	16 Sep.	163.2±18.0 b	588.8±59.3	150.4±18.5 b	215.2±31.2 b	114.4±17.2	1232.0±91.5 b

Different letters in same column indicate significant differences (P < 0.05) among months in same year.

parallel to all others. Each of the neighboring plots was 0.5 to 1.0 km apart.

Sampling and measurement methods

In June, July and September 2003 and 2004, respectively, 20 replicate quadrats (each 0.25×0.25 m^2 in area and 30 cm deep) in each spot were sampled by taking soil cores, including all aboveground stems and belowground perennial rhizomes. To maintain the inherent links among tillers and rhizomes, belowground samples were washed free of soil.

The number of aboveground tillers of *L. chinensis* and *C. duriuscula* was recorded. TN (tiller node buds, developing from tiller nodes), RT (rhizome buds, originated from the top of rhizome), RN (rhizome buds, on the nodes of rhizomes), TJ (juvenile tiller, deriving from tiller nodes) and RJ (juvenile tiller, deriving from rhizomes) were counted. Those juvenile tillers form at the late growing season with a rosette of leaves and have no nodes in the autumn, and which either flower or grow vegetatively in the second season. *C. duriuscula* bud bank only is composed of TB and RT. All buds and juvenile tillers are defined as the total bud bank. Dry biomass of two species tillers and rhizomes was determined after oven-drying to a constant weight at 80°C.

Data analysis

All statistical analyses were performed using SPSS (13.0) (SPSS Inc, Chicago, Illinois). The density tillers and bud densities were converted into the number in each square meter. Statistical analysis was by one-way ANOVA followed by Duncan's test. The criterion for all variables was a 0.05 or 0.01 significant level. The bud bank densities were compared to the stem densities in 2003 and 2004, respectively, to provide insight into the extent to which bud banks may contribute to population persistence. The figure was performed using Sigmplot10.0 (SPSS Inc, Chicago, Illinois).

RESULTS

Composition and size of bud banks

Table 1 shows that *L. chinensis* bud banks are composed of TN, TJ, RT, RN and RJ. TJ and RJ, which could only be found in September of both years. The total rhizome buds including RT, RN and RJ comprised the largest proportion of the bud banks: respectively, 59.2, 71.7, 68.4, 99.2 and 64.7% of total buds in 2003 and in June

and July 2004. But in September 2004, TJ was the most numerous with 47.8% of total buds.

Remarkably, the sum of TJ and RJ of *L. chinensis* was 3.5 and 19.0% of total buds in 2003 and 2004, respectively (Table 1), and approximately 95% of them can overwinter (Yang et al., 1995). Therefore, approximately 3.3 and 18.0% of total buds grew up as tillers in the following year. These results suggested juvenile tillers were very important to population persistence. RT maintains a similar level of importance due to apical dominance, demonstrating 32.8 and 12.2% in September 2003 and 2004, respectively. Based on our interpretations of the above results, approximately 35.0 and 30.0% of total buds would develop into the established shoots in the subsequent year.

C. duriuscula bud banks are only comprised of TN and RT (Table 2). RT comprised the largest proportion of the bud banks: respectively, 72.9, 62.2, 59.2, 74.0, 73.7 and 71.7% of total buds in June, July and September of 2003 and 2004. In *L. chinensis*, the percentages of total buds derived from tiller nodes (the sum of TN and TJ) and rhizomes (the sum of RT, RJ and RT) were nearly equal, 33.6 and 66.4% in 2003, and 32.4 and 67.6% in 2004. In *C. duriuscula*, the percentages were 35.2 and 64.8% in 2003 and 26.9 and 73.1% in 2004. These results indicated the stability of bud production of rhizomes and tiller nodes in the two-year study period.

Temporal dynamics of bud banks

In both 2003 and 2004, the total buds of *L. chinensis* gradually increased from June to September (Table 1). The minimum number of TN and RT were observed in June, and the maximum of them appeared in September in both years. TN and RT of September were 3.5 and 7.7 times those of June in 2003, but in 2004, those values were 51.0 and 6.3 times, respectively. In 2003, TN and RT of both June and July were significantly different with those of September, and RN showed the same results too. In 2004, TN and RN of both June and July were significantly different with those of September, and RT and total buds were so.

Table 2. Composition and size of *Carex duriuscula* bud bank (M ± SE) in 2003 and 2004.

Sampling date		TN	RT	Total buds
2003	29 Jun	168.8±31.8 a	453.6±44.8 a	622.4±61.4 a
	21 Jul	435.2±222.5 a	717.6±92.2 b	1152.8±248.1 b
	1 Sep	464.8±62.0 a	675.2±76.5 b	1140.0±130.0 b
2004	5 Jun	60.8±11.2 a	173.4±16.5 a	234.2±11.8 a
	8 Jul	81.6±10.9 a	228.7±28.4 a	310.3±38.8 a
	16 Sep	164.8±47.9 b	416.8±84.3 b	581.6±125.6 b

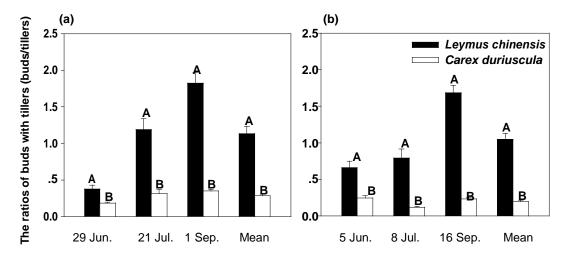Different letters in same column indicate significant differences (P < 0.05) in same year.

Figure 1. The ratios of buds of both *Leymus chinensis* and *Carex duriuscula* with their successful tillers in 2003 (a) and 2004 (b). Different uppercase letters represent significant difference between *Leymus chinensis* and *Carex duriuscula* at the 0.01 level within each month.

In 2003, the minimum TN and RT of *C. duriuscula* were observed in June, and the maximum were found in September and July respectively (Table 2). In 2003, TN values of September were 2.8 times that of June. Similarly, the July RT values were 1.6 times that of June. In 2004, the lowest TN and RT values were observed in June, and the highest values appeared in September. In 2003, the RT values in June were significantly different at the 0.05 level from July and September. In 2004, both TN and RT in June and July were significantly different from September. Furthermore, the number of total *L. chinensis* buds between September 2003 and 2004 were nearly equal (P>0.05) (Table 1), and the number of total *C. duriuscula* buds in 2004 was significantly lower than those in 2003 (Table 2).

Contributions of bud banks to population persistence

Figure 1 shows the ratios of *L. chinensis* and *C. duriuscula* buds with their successful tillers in both years.

The comparison represented the productivity of every species and determined the degree to which bud banks may contribute to aboveground population in the next season and year. In both years, the ratios of *L. chinensis* gradually increased from June to September. The highest ratios occurred in September. For *C. duriuscula,* the same trend was evident. In the two years, the ratios of *L. chinensis* were 2.0, 3.8 and 5.2 times that of *C. duriuscula* in 2003, and in 2004, the times were 2.7, 6.6 and 7.1, respectively. The average values of two years were 4.0 and 5.2. And the ratios between *L. chinensis* and *C. duriuscula* were extremely significant (P<0.01) in study period. These data demonstrated that the productivity of *L. chinensis* and the contribution of *L. chinensis* bud banks were higher than those of *C. duriuscula* to population persistence.

DISCUSSION

Juvenile tillers, because of a well developed root system,

larger food reserves derived from buds at the end of the growing season and successful over-wintering, are very important to population regeneration (Yang et al., 1995). This differentiation is extremely important because it not only prevents errors in the tiller census but also in the estimate of bud banks. The contribution ratio of juvenile tillers to population persistence is a novel discovery not yet reported in the literature. Only, the winter dormancy characters and age structure of *L. chinensis* at natural meadow and during restoration succession after the flooded meadow in the Songnen Plains were studied (Yang and Zhu, 1994; Yang et al., 1995; Li and Yang, 2004).

The *L. chinensis* meadow is strongly dominated by perennial grasses. A prior census conducted for all emerging and establishing shoots of *L. chinensis* revealed that >99% of the established shoots arose from rhizomes or tiller nodes, whereas new seedlings derived from seed accounted for <1% of the total aboveground population (Yang et al., 1995). Thus, the contribution of seedlings to the established aboveground population was negligible after the establishment of vegetation. Our previous study supports the above results (Li and Yang, 2004). Although variation in density was observed within years, the bud bank was the principal source of emerging shoots in each season (Yang and Zhu, 1994). However, the soil seed bank played a crucial role in vegetation reestablishments at initial stages of restoration. As soon as vegetation was established, vegetative reproduction was superior to sexual reproduction in population regeneration and expansion. Thus, sexual reproduction prevented plant species extinction on this site. However, vegetative reproduction maintained the regeneration process after establishment due to consistent expansion and high reproductive potential.

C. duriuscula firstly emerged due to high seed fecundity and germination (Xiao and Chen, 1996). However, in virtue of unfavorable habitat and low sexual reproductive ability, *L. chinensis* emerged after approximately 2 years. Our previous study revealed that *C. duriuscula* gradually decreased with the increase of *L. chinensis* from the edge to the center of all *L. chinensis* patches (Li and Yang, 2004), and the result was similar in the paper. According to plant community succession theory (Sun et al., 1993), *C. duriuscula* is a pioneer species during the initial stages of succession. *C. duriuscula* has a thriving cushion-like root system, and rotten roots can modify the physical and chemical properties of the soil, consequently providing substantial nutrition for *L. chinensis* establishment. These results demonstrated that all exogenous successions (floods, fires, grazing, etc.) will come to fruition via endogenetic successions (the plant's own biological characteristics), and endogenetic succession is a universal succession mode in nature.

Our results indicated that the productivity of *L. chinensis* and contribution of *L. chinensis* bud banks to population persistence were higher than those of

C. duriuscula (Figure 1). Furthermore, the number of total *L. chinensis* buds between September 2003 and 2004 were nearly equal ($P>0.05$) (Table 1), and the number of total *C. duriuscula* buds in 2004 was significantly lower than those in 2003 (Table 2). In spite of both *L. chinensis* and *C. duriuscula* have long rhizomes, and *C. duriuscula* shoot is much shorter as well as its rhizome is much thinner than those of *L. chinensis.* These revealed that *L. chinensis* would become the dominant species and *C. duriuscula* would become an associated species in the restoration community again. At the same time, bud banks are very important to seasonal and yearly regeneration in our study.

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