

# Domestic goat grazing disturbance enhances tree seed removal and caching by small rodents in a warm-temperate deciduous forest in China

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## Abstract

**Context.** Grazing by large herbivores may have a considerable influence on ground vegetation as well as on the species composition and abundance of granivores (e.g. small rodents) and this may affect forest regeneration. Very few studies have focussed on the effects of herbivore disturbance on forest regeneration by looking at the modified seed-hoarding behaviour of small rodents.

**Aims.** To test the indirect effects that grazing disturbance by domestic animals has on seed dispersal through the modified seed-hoarding behaviour of small rodents.

**Methods.** We looked at the differences in seed removal and caching of Liaodong oak (*Quercus liaotungensis*) by small rodents between a plot that was grazed and a plot that was ungrazed by domestic goats in a warm-temperate forest in northern China in 2006 (a non-mast-seeding year) and 2008 (a mast-seeding year).

**Key results.** Seed removal and caching by small rodents were significantly higher in the grazed plots, especially in the mast-seeding year (2008). Significantly more seeds were buried in soil during the mast-seeding year (2008) compared with the non-mast-seeding year (2006).

**Conclusions.** Grazing-induced disturbance might stimulate hoarding efforts by seed-caching rodents. Mast seeding benefits seed survival and forest regeneration.

**Implications.** The presence of large herbivores is likely to benefit early seed dispersal in forests by increasing the hoarding activities of rodents.

**Additional keywords:** forest regeneration, large herbivores grazing, rodent abundance, seedbank, seed survival.

## Introduction

It is well recognised that wild and domestic herbivores may exert considerable influence on the structure and composition of ground vegetation and tree regeneration (Adler *et al.* 2001; Rossell *et al.* 2005; Manier and Thompson Hobbs 2006; Darabant *et al.* 2007; Hufford *et al.* 2008). Large herbivores may directly affect the growth rates, fecundity, mortality and seed fates of the plants on which they feed by eating and trampling them, and these animals may indirectly influence plant communities by changing species interactions, soil structure and the nutrition cycle (Gill 1992; Peterson and Pickett 1995; Kirby 2001; Arsenault and Owen-Smith 2002; Darabant *et al.* 2007; Gill and Fuller 2007; Baraza and Valiente-Banuet 2008).

The grazing habits of large herbivores may also indirectly affect the species composition and abundance of small rodents, by modifying shelters, microclimates and food resources (Keesing 1998; Smit *et al.* 2001; Steen *et al.* 2005; Evans *et al.* 2006; Ogada *et al.* 2008).

Small rodents are generally considered important seed consumers and dispersers in forests, and they can have a significant impact on the seedling establishment of tree species and thus on vegetation succession (Vander Wall 1990; Jansen and Forget 2001; Zhang *et al.* 2005). Seed-hoarding rodents are often sensitive to the potential pressures of seed loss posed by competitors, and this causes rodents to adopt different tactics to maximise seed occupancy (Sanchez and Reichman 1987;

Vander Wall and Jenkins 2003; reviewed by Dally *et al.* 2006). For instance, seed-hoarding rodents may attempt to occupy more seeds by increasing seed-removal activities and by caching seeds immediately when potential competitors are present (Vander Wall and Jenkins 2003; reviewed by Dally *et al.* 2006). As potential food competitors, large herbivores might pose a pressure of seed loss on seed-eating rodents by eating seeds and trampling them into soil, which subsequently affects the seed survival of seed trees by influencing the seed-removal and -caching behaviours of small rodents. Besides, the presence of large herbivores may alter ground vegetation and thus influence seed hoarding of small rodents. However, very few studies have investigated this situation in forests.

Liaodong oak (*Quercus liaotungensis*) is a dominant tree species that is widely distributed in forests and shrublands in the Donglingshan Mountains, northern China. Acorns of *Q. liaotungensis* mature and fall in autumn and develop into seedlings during the following spring. Fresh acorns are the preferred food items of seed-eating rodents, and these acorns are largely dependent on rodents for their dispersal (Wang *et al.* 1999; Li and Zhang 2003; Lu and Zhang 2004, 2005; Zhang *et al.* 2008). Domestic animals (e.g. cattle and goats) also partially contribute to the loss of fresh acorns of *Q. liaotungensis*, by eating them or by trampling them into the soil (Li and Zhang 2003).

To understand the indirect effects that grazing disturbance by domestic animals has on the seed dispersal of *Q. liaotungensis* through the modified seed-hoarding behaviour of small rodents, we studied the differences of seed removal and caching of *Q. liaotungensis* by small rodents between a plot that was grazed and a plot that was ungrazed by domestic goats in a secondary forest in the Donglingshan Mountains, northern China, in 2006 (a non-mast-seeding year) and in 2008 (a mast-seeding year).

## Methods

### Study area

The present study was conducted at the Liyuanling field station (40°00'N, 115°30'E, ~120 km north-west of Beijing city, China) at an altitude of 1140 m. The station is located in the Donglingshan Mountains of northern China. The location has a temperate continental monsoon climate, with 500–650 mm of annual precipitation, and the annual temperature ranges from 5 to 11°C (Wang *et al.* 1999). Shrublands, secondary forests and abandoned farmlands are the dominant landscapes in the study area and have been heavily disturbed by cultivation and grazing by domestic animals in recent decades. Forests and shrublands are dominated by *Q. liaotungensis* as well as wild walnut (*Juglans mandshurica*), wild apricot (*Prunus armeniaca*) and wild peach (*Amygdalus davidiana*) trees (Wang *et al.* 1999; Li and Zhang 2003, 2007; Lu and Zhang 2004). *Q. liaotungensis* is widely distributed in the study area in scattered forests and shrublands. Because of its high contents of crude protein (11.5%) and crude starch (34.1%) and its relatively high caloric value (14.2 KJ per seed), a fresh acorn of *Q. liaotungensis* (~13.3 ± 2.1 mm width, 17.8 ± 2.7 mm length and 2.0 ± 0.9 g weight,  $n = 50$ ) is a favourite food item of seed-eating rodents (Wang *et al.* 1999; Lu and Zhang 2008; Zhang and Zhang 2008). Chinese white-bellied rats (*Niviventer confucianus*), Korean field mice

(*Apodemus peninsulae*), striped field mice (*A. agrarius*), great long-tailed hamsters (*Tscheskia triton*), Père David's rock squirrels (*Sciurotamias davidianus*) and Siberian chipmunks (*Tamias sibiricus*) are common rodent species in this area and are mainly responsible for the removal and consumption of *Q. liaotungensis* acorns (Li *et al.* 2004; Lu and Zhang 2004, 2005, 2008; Zhang and Zhang 2008; Zhang *et al.* 2008). There were four herds of domestic goats (~300 goats per herd) rotationally grazing in the secondary forests and shrublands in the study area all year around. These goats have caused a great loss of both seeds and seedlings of *Q. liaotungensis* by eating and trampling (H. Zhang, pers. obs.).

### Experimental design and data collection

The experiment was conducted during the seedfall period (from the beginning of August to the beginning of October) of *Q. liaotungensis* in 2006, and it was repeated in 2008. It was not conducted in 2007 because too few *Q. liaotungensis* acorns were produced.

A pair of plots, one grazed and one ungrazed, was selected for the experiments in two secondary forests. The plots were separately located on two hills, ~500 m apart (horizontal distance). Both plots comprise an area of ~3.0 ha on north-east-facing slopes, with an incline gradient of 45–60°. The study sites were dominated by *Q. liaotungensis* trees (which accounted for more than 50% of all tree species in the study area), with some *P. armeniaca* and Prince Rupprecht's larch (*Larix principis-rupprechtii*) being scattered among them. Except for *Q. liaotungensis*, there were nearly no seed crops of other tree species in either plot during the study period. The average canopy coverage was more than 90% in both plots. The understorey was composed of shrubs, grass, leaf litter and bare ground. We did not determine the ground vegetation in 2006 and 2008. However, we had some ground-vegetation data of the two plots determined in 2005, for the purpose of other studies. Fifty quadrats (2.0 × 2.0 m, 10 m apart) were located along two horizontal transects (250 m in length and 30 m apart) in each plot for measurement of coverage (%) of ground shrubs and grass in September 2005 (compared with leaf litter or bare ground).

Domestic goats were excluded from accessing the ungrazed plot by the shepherders all-year-round, whereas in the grazed plot the goats were present rotationally (two or three times per month, but not while making observations).

Two horizontal transects ~200 m in length and 30 m apart were established in each experimental plot. Ten seed stations at intervals of 20 m were located along each transect for seed placement. Thirty fresh and intact acorns of *Q. liaotungensis* were placed on the ground surface of each seed station at the beginning of seedfall (5 September in 2006 and 2 September in 2008 for seed placement). In total, 20 seed stations were located and 600 seeds released in each experimental plot, to measure seed-removal speed. All of the released seeds were collected in *Q. liaotungensis* forests outside the experimental plots at the beginning of seedfall (2 September in 2006 and 31 August in 2008 for seed collection). During the 20 days following seed placement, each seed station was checked every morning (0900–1100 hours), and the number of remaining acorns (acorns that were still at the seed stations) was recorded.

Twenty 1 × 1 m quadrats (~20 m apart) were located along another horizontal transect to survey seed status in the seedbank of each plot at the end of seedfall (1 October in 2006 and 2 October in 2008). Seed status in each quadrat was recorded according to the following three categories: (1) on ground surface – acorns were on the ground surface of the quadrat; (2) under leaf litter – acorns were covered by leaf litter; or (3) buried in soil – acorns were buried in decomposed leaf litter or in soil <5 cm deep as defined by previous studies (e.g. Li and Zhang 2003; Lu and Zhang 2005). Previous studies in this area have demonstrated that the buried acorns were mainly cached by small rodents (e.g. Wang *et al.* 1999; Li and Zhang 2003; Lu and Zhang 2005; Zhang *et al.* 2008). A few acorns might also have been buried unintentionally by other animals (e.g. roe deer, *Capreolus capreolus*, and hog badger, *Arctonyx collaris*) when they walked over the area; however, these effects were neglected because population densities of these animals are very low in this area (Li and Zhang 2003).

Live trapping was conducted for three consecutive days to determine the composition and abundance of rodent species within the study plots at the end of seedfall (1 October to 3 October in 2006; 30 September to 2 October in 2008). Twenty live traps (made of steel wire, 12 × 12 × 25 cm, baited with peanuts) were placed along each seed-placement transect at an interval of 5 m. All traps were checked twice per day, at sunrise and at sunset. After identification of species, we released the captured animals (not marked) immediately *in situ*. Forty traps were placed in each plot. There was a total of 120 trap days (40 traps × 3 days) in each plot. We defined rodent abundance by trap success (%), as follows: total number of captured animals/total number of live traps × 100%.

#### Data analysis

SPSS for Windows (ver. 13.0; SPSS Inc., Chicago, IL) was used for data analysis. Data were tested for normality of distribution by using the Shapiro–Wilks test (see also Darabant *et al.* 2007), and when necessary, log-transformed to achieve normal distribution. Life Tables, a convenient tool for depicting the mortality process of a population, was used to calculate median survival time of released seeds *in situ*, in each plot or year (see also Lu and Zhang 2004, 2005; Zhang and Zhang 2008; Zhang *et al.* 2008). Cox regression was used to test for differences in seed-removal speed between experimental plots and between years, and for interactions between the plots

and years (see also Xiao *et al.* 2004, 2005, 2006; Zhang and Zhang 2008; Zhang *et al.* 2008). GLM-multivariate test (MANOVA) was used to test the main effects of year and plot and their interactions on each seed status (on the ground surface, under leaf litter, and buried in soil) by using the number of seeds for each seed status as a dependent variable (see also Sassi *et al.* 2006; Zhang *et al.* 2008). Because data were independent between plots and between years, Mann–Whitey *U* (one of the ‘two independent samples tests’ in SPSS) was used to test the frequency differences of each seed status between years and between plots, with the number of seeds for each seed status as a test variable (see also Lu and Zhang 2004). Student’s *t*-test was used to test for differences in rodent abundance between plots and between years, with the trapping success (%) as the test variable; this test was also used to test the different coverage of ground shrubs and grass between grazed and ungrazed plots.

#### Results

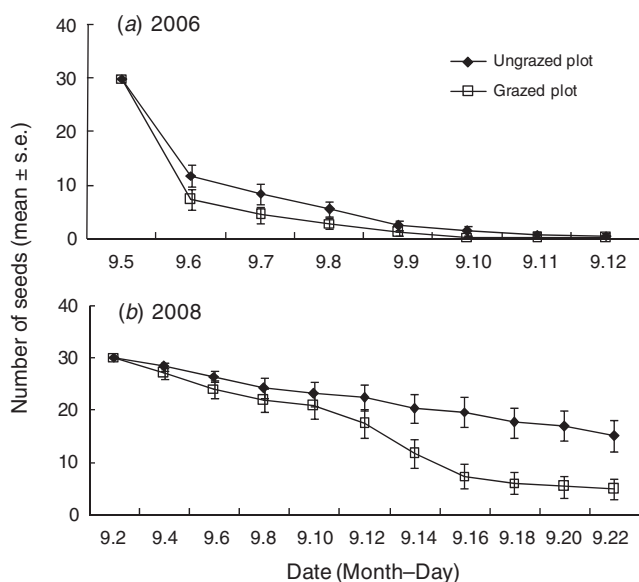
In September 2005, the average cover of shrubs and grasses was significantly lower in the grazed than in ungrazed plot (21.5 ± 9.5% in the grazed plot, 28.6 ± 10.5% in the ungrazed plot,  $t = -3.510$ , d.f. = 98,  $P = 0.001$  for shrubs; 35.6 ± 14.2% in the grazed plot, 45.4 ± 15.4% in the ungrazed plot,  $t = -3.318$ , d.f. = 98,  $P = 0.001$  for grasses, mean ± s.d.,  $n = 50$ , *t*-test).

Results for rodent species and their abundance are listed in Table 1. Trapping success (%) of rodent species was not significantly different between the plots (all  $P > 0.05$  for all species, *t*-test), although it was significantly higher in 2006 than in 2008 (all  $P < 0.05$  for all species, *t*-test). Both *N. confucianus* and *A. peninsulae* had higher trapping success than did other species in both plots during the 2 years (Table 1).

Seed-removal speed was significantly affected by year (Wald = 481.473, d.f. = 1,  $P = 0.000$ ; Cox regression), plot (Wald = 19.496, d.f. = 1,  $P = 0.000$ ; Cox regression) and their interaction (Wald = 63.648, d.f. = 1,  $P = 0.000$ ; Cox regression). In 2006, the median survival time for released seeds was 2.1 days in the ungrazed plots and 1.5 days in the grazed plots, and this difference was significant (Wald = 4.834, d.f. = 1,  $P = 0.026$ ; Cox regression) (Fig. 1a). In 2008, the median survival time for released seeds was 21.0 days in the ungrazed plots and 11.7 days in the grazed plots, with the difference here also being significant (Wald = 145.653, d.f. = 1,  $P = 0.000$ ; Cox regression) (Fig. 1b). These results suggest that grazing by

**Table 1.** Number of rodents of each species captured and abundance estimation (trap success (%) in 120 trap-days) in the grazed and ungrazed plots  
Proportion (%) denotes the proportion of the number of captured individuals of a species to all species captured that year

| Year | Plot           | <i>Niviventer confucianus</i> | <i>Apodemus peninsulae</i> | <i>Sciurotamias davidianus</i> | <i>Tscheskia triton</i> | Total     |
|------|----------------|-------------------------------|----------------------------|--------------------------------|-------------------------|-----------|
| 2006 | Grazed plot    | 4 (3.3)                       | 6 (5.0)                    | 3 (2.5)                        | 2 (1.7)                 | 15 (12.5) |
|      | Ungrazed plot  | 5 (4.2)                       | 4 (3.3)                    | 2 (1.7)                        | 3 (2.5)                 | 14 (11.7) |
|      | Total          | 9 (7.5)                       | 10 (8.3)                   | 5 (1.7)                        | 5 (4.2)                 | 29 (24.2) |
|      | Proportion (%) | 31.0                          | 34.5                       | 17.2                           | 17.2                    | 100       |
| 2008 | Grazed plot    | 3 (2.5)                       | 1 (0.8)                    | 1 (0.8)                        | 1 (0.8)                 | 6 (5.0)   |
|      | Ungrazed plot  | 3 (2.5)                       | 0 (0.0)                    | 2 (1.7)                        | 0 (0.0)                 | 5 (4.2)   |
|      | Total          | 6 (5.0)                       | 1 (0.8)                    | 3 (2.5)                        | 1 (0.8)                 | 11 (9.2)  |
|      | Proportion (%) | 54.5                          | 9.1                        | 27.3                           | 9.1                     | 100       |



**Fig. 1.** Seed removal of *Quercus liaotungensis* acorns by small rodents in both the grazed and ungrazed plots in (a) 2006 and (b) 2008. The error bars denote s.e.

domestic goats might have significantly stimulated seed removal from seed stations by small rodents.

Multivariate tests (MANOVA) showed that seed status in the seedbanks were significantly affected by year (Wilks' value = 0.375,  $F_{3,74} = 41.157$ ,  $P = 0.000$ ), plot (Wilks' value = 0.618,  $F_{3,74} = 15.239$ ,  $P = 0.000$ ) and their interaction (Wilks' value = 0.721,  $F_{3,74} = 9.544$ ,  $P = 0.000$ ). Tests of between-subject effects show that the number of seeds on the ground surface, under leaf litter and buried in soil were significantly affected by year, plot and their interactions (Table 2). Mann–Whitey  $U$  analysis indicated that the number of buried seeds was significantly higher in the grazed than in the ungrazed plot in 2006 ( $Z = -2.114$ ,  $P = 0.037$ , Fig. 2a) and in 2008 ( $Z = -2.882$ ,  $P = 0.004$ , Fig. 2b). However, the total number of seeds was significantly lower in the grazed plot in 2008 ( $Z = -2.366$ ,  $P = 0.038$ , Fig. 2b) than in the ungrazed plot in the same year. These results suggest that grazing by domestic goats might have stimulated seed caching by small rodents.

Mann–Whitey  $U$  analysis indicated that, except for the number of buried seeds in the ungrazed plot ( $Z = -1.657$ ,  $P = 0.098$ ), the number of seeds for the two other seed status in 2008 were significantly higher than those in 2006 both in the ungrazed (on the ground surface:  $Z = -4.442$ ,  $P = 0.000$ ; under leaf litter:  $Z = -4.352$ ,  $P = 0.000$ ; total:  $Z = -4.509$ ,  $P = 0.000$ ) and grazed plot (on the ground surface:  $Z = -4.393$ ,  $P = 0.000$ ; under leaf litter:  $Z = -3.807$ ,  $P = 0.000$ ; buried in soil:  $Z = -3.297$ ,  $P = 0.001$ ; total:  $Z = -4.278$ ,  $P = 0.000$ ).

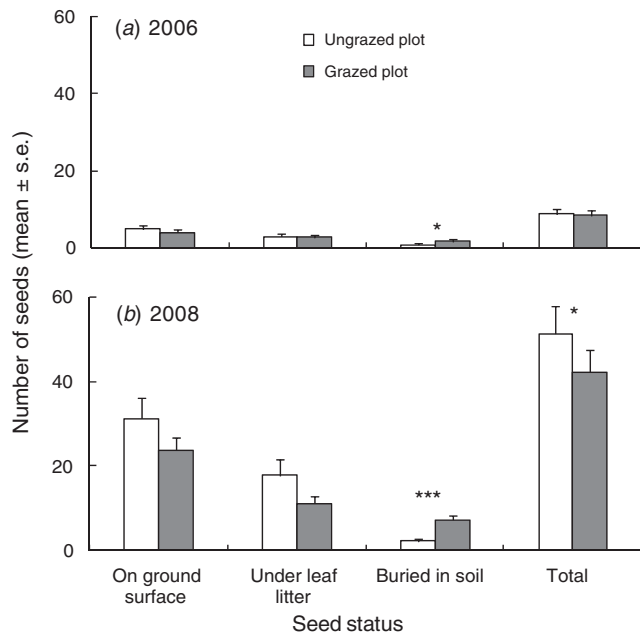
## Discussion

Grazing by large herbivores may affect plant composition as well as the species composition and abundance of granivores (e.g. birds and small rodents) (e.g. Keesing 1998; Gill and Beardall 2001; Gonnet 2001; Tabeni and Ojeda 2005; Evans *et al.* 2006; Gill and Fuller 2007; Ogada *et al.* 2008). Wada *et al.* (1995) reported a higher seed predation at grazed sites in the Thar Desert of India, owing to a higher density of small rodents. Sassi *et al.* (2006) reported that seed removal by small rodents showed no significant responses towards cattle grazing in the central Monte desert ecoregion in Argentina. Our results indicated that the speed of seed removal and the number of seeds buried in soil were significantly higher in the grazed than in the ungrazed plot in 2006 and 2008. These results suggest that the grazing behaviour by domestic goats might have stimulated enhanced hoarding efforts by seed-eating rodents. It is obvious that rodent abundance and species composition did not contribute to the observed difference in seed removal and caching because there was no significant difference either in the rodent abundance or species composition between the grazed and the ungrazed plot.

Domestic goats are potential food competitors of seed-eating rodents in our study area because they have been observed eating acorns of *Q. liaotungensis* and to trample them into soil (H. Zhang, pers. obs.). Previous studies demonstrated that seed-caching rodents often tend to remove and cache more seeds when potential competitors are present (Vander Wall and Jenkins 2003; reviewed by Dally *et al.* 2006). Therefore, small rodents in the grazed plot are likely to enhance their seed-removal and -caching efforts, to prevent the potential pressure of food competition brought on by the presence of domestic goats. Enhanced removal and caching were also observed in the presence of potential competitors in some small rodents. For instance, the presence of conspecific competitors induced

**Table 2.** Results of the MANOVA test, with the number of each seed status of *Quercus liaotungensis* acorns as the dependent variables, showing the effects of year, plot and their interactions ( $P < 0.05$ )

| Source             | Dependent variable | Type III sum of squares | d.f. | Mean square | $F$    | $P$      |
|--------------------|--------------------|-------------------------|------|-------------|--------|----------|
| Year               | On ground surface  | 14905.800               | 1    | 14905.800   | 90.079 | 0.000*** |
|                    | Under leaf litter  | 3125.000                | 1    | 3125.000    | 40.421 | 0.000*** |
|                    | Buried in soil     | 248.513                 | 1    | 248.513     | 22.198 | 0.000*** |
| Plot               | On ground surface  | 1394.450                | 1    | 1394.450    | 8.427  | 0.005**  |
|                    | Under leaf litter  | 378.450                 | 1    | 378.450     | 4.895  | 0.030*   |
|                    | Buried in soil     | 165.313                 | 1    | 165.313     | 14.766 | 0.000*** |
| Year $\times$ Plot | On ground surface  | 1095.200                | 1    | 1095.200    | 6.619  | 0.012*   |
|                    | Under leaf litter  | 328.050                 | 1    | 328.050     | 4.243  | 0.043*   |
|                    | Buried in soil     | 78.013                  | 1    | 78.013      | 6.968  | 0.010*   |



**Fig. 2.** Number of *Quercus liaotungensis* acorns in each seed-status category in the grazed and ungrazed plots in (a) 2006 and (b) 2008. The error bars denote s.e. \* $P < 0.05$ ; \*\*\* $P < 0.001$  (Mann–Whitey  $U$  test).

Edward's rats (*Leopoldamys edwardsi*) to cache significantly more seeds in semi-natural enclosures (Cheng *et al.* 2005); *Sciurotamias davidianus*, *A. peninsulae* and *N. confucianus* tended to remove and cache more seeds in enclosures when their cached seeds were removed artificially (Lu 2004); and both *A. peninsulae* and *N. confucianus* enhanced caching in semi-natural enclosures when hetero- and conspecific competitors were present in the study area (H. Zhang, unpubl. data). The frequent presence of domestic goats might stimulate seed removal and caching behaviours of small rodents in the grazed plots because these goats are potential food competitors.

Additionally, sustained grazing has altered the spatial heterogeneity of ground vegetation in the grazed area (also see Hester *et al.* 1996; Adler *et al.* 2001; Rossell *et al.* 2005). Unfortunately, we did not determine the ground vegetation cover in the grazed and ungrazed plots in 2006 and 2008. However, because the grazing regimes were similar in this region, the measurement of ground vegetation in the grazed and ungrazed plots in 2005 may help understand the effect of grazing-induced vegetation on seed hoarding of rodents. The average cover of both shrubs and grasses (compared with leaf litter or bare ground) was significantly lower in the grazed plot. It is obvious that grazing significantly reduced the ground vegetation cover. Poor ground vegetation cover may enhance seed-removal and -caching behaviour in rodents. Our previous studies indicated that seed removal of *P. armeniaca* and *Q. liaotungensis* is higher in habitats with poor ground cover in the same study area (Lu and Zhang 2004, 2005). In habitats with a lower cover, the visibility of acorns that fall, or are placed, on the surface of the ground may be increased, and this may increase the probability of seed removal by the competitors (e.g. birds, goats) of small rodents. Rapid removal

and increased caching of seeds will decrease the risk of food competition posed by other foragers (Vander Wall 1993; Lu and Zhang 2004). However, because of the lack of replication of these observations in the grazed and the ungrazed plots as well as the lack of quantitative data on the difference of ground vegetation between the plots during the time of seed placement, our results need to be further tested in future studies.

It was expected that seed-removal speed would be significantly lower and that the total number of seeds in the seedbank would be significantly higher in 2008 than in 2006. The year 2008 was a mast-seeding year for common tree species, including *Q. liaotungensis*, *P. armeniaca*, *A. davidiana* and cultivated walnut (*Juglans regia*), and 2008 was also a year of a lower density of small rodents in the study area (see Table 1). Our seed-trap experiments showed that the densities of intact *Q. liaotungensis* acorns were  $1.5 \pm 0.6$  (mean  $\pm$  s.d.,  $n = 40$ ) seeds per trap ( $0.5 \text{ m}^2$ ) in 2006 and  $25.5 \pm 7.8$  seeds per trap in 2008 (H. Zhang, unpubl. data). The predator-satiation hypothesis proposes that massive crops of plants in mast-seeding years can satiate seed predators, and this allows more seeds to escape predation by animals and subsequently benefits seed survival and seedling establishment (Janzen 1970; Kelly *et al.* 2001; Kelly and Sork 2002; Schnurr *et al.* 2002). Massive seed crops of *Q. liaotungensis* and a low density of small rodents resulted in an obvious predator-satiation effect in 2008. Previous studies have also demonstrated that mast seeding could reduce seed-removal speed and increase seed caching by small rodents, as suggested by the predator-satiation hypothesis (e.g. Crawley and Long 1995; Kelly and Sork 2002; Jansen *et al.* 2004; Li and Zhang 2007). Our results indicated that mast seeding significantly reduced seed removal but increased seed caching by rodents in both the grazed and the ungrazed plot. This observation supports the predator-satiation hypothesis and is in agreement with the results of previous studies.

In summary, grazing by large herbivores may have important direct and indirect effects on plant communities. Large herbivores, through their grazing behaviour, may affect plant communities directly by eating and trampling vegetation and by dispersing seeds (e.g. Mitchell and Kirby 1990; Gill 1992; Rossell *et al.* 2005; Baraza and Valiente-Banuet 2008) and indirectly by changing the competition among the components of understorey vegetation, soil compaction, nutrient removal or input, susceptibility to drought and densities of granivores (e.g. rodents and birds) (e.g. Gill and Beardall 2001; Smit *et al.* 2001; Steen *et al.* 2005; Evans *et al.* 2006; Darabant *et al.* 2007; Gill and Fuller 2007; Ogada *et al.* 2008). Our results suggest that domestic goats, even though causing considerable damage to the ground vegetation in the study area, may benefit the early seed-dispersal fitness of *Q. liaotungensis* by enhancing the hoarding activities of small rodents. Therefore, we suggest that grazing by large herbivores is likely to be an important factor in facilitating seed dispersal by small rodents.

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