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Effects of disperser abundance, seed type, and interspecific seed availability on dispersal distance

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Abstract Seed dispersal distance is influenced by a variety of seed properties and functional responses of dispersers. However, to our knowledge, how and why seed dispersal distances are determined remains poorly understood. In the present study, seeds of sympatric tree species, *Pinus koraiensis*, *Corylus mandshurica*, *Corylus heterophylla*, and *Quercus mongolica* were released to investigate the effects of rodent abundance, seed type, and seed availability on seed dispersal. Our results showed that seeds of *P. koraiensis* were dispersed further than those of *C. heterophylla* and *C. mandshurica* regardless of the ambient rodent and seed abundances, reflecting a consistent effect of seed type on seed dispersal distances. Seed dispersal distance was greatly facilitated by lower per-capita seed abundance (the ratio of seeds to rodents); however, seed caching and cache survival were benefited from higher per-capita seed abundance. Although seed dispersal and seed caching of a particular tree species can be enhanced by its own seed availability, no consistent influence was detected at interspecific levels, reflecting different interspecific effects of seed availability on seed dispersal of sympatric seed species. Our results provide evidences that the effect of seed availability on seed dispersal should be evaluated in terms of per-capita seed abundance and interspecific effects, rather than the independent influence of seed or disperser abundances.

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Introduction

Large seeds usually rely on a variety of animal dispersers for their movement and seedling establishment in forests (Vander Wall 1990; Chambers and Macmahon 1994; Xiao et al. 2005a; Li and Zhang 2007). Seed dispersal by animals has some potential advantages to plants as adult trees can locally reduce the seed survival and seedling recruitment of conspecifics (Janzen 1970). These benefits may include transport away from the proximity of parent trees, escape from conspecific pathogens and herbivores (Janzen 1970), reduced risk of density-dependent mortality (Wilson and Janzen 1972), and seedling establishment in favorable environments (Howe and Smallwood 1982). Seeds transported far from the parent trees are generally more likely to survive (Vander Wall 1990) and seed dispersal plays a critical role in the recruitment and spatial distribution of plant communities within many ecological systems (Jordano and Godoy 2002; Li and Zhang 2007; Moore et al. 2007; Yi et al. 2011). However, seeds may be less likely to germinate and establish seedlings if they are not dispersed or cached by scatter hoarders (Vander Wall 2010). How far seeds are dispersed determines the maintenance of genetic diversity within and among plant populations (Hamrick et al. 1993; Hovestadt et al. 1999; Jordano and Godoy 2002; Moore et al. 2007). Therefore, it is useful to explore the factors influencing dispersal distances or consequent outcome of seed dispersal in animal-dispersed tree species.

Seed dispersal distance is affected by a number of ecological factors and is not currently predicted by a general rule (Brewer 2001; Theimer 2003a; Xiao et al. 2004, 2005b; Li and Zhang 2007; Moore et al. 2007; Yi and Yang 2011).

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Various studies reveal a positive relationship between dispersal distance and seed size within a species (e.g., Jansen et al. 2002, 2004; Xiao et al. 2004, 2005b) and among different plant species (Stapanian and Smith 1978, 1984; Hurly and Robertson 1987; Vander Wall 1995; Forget et al. 1998; Xiao et al. 2005b). However, other studies show that seeds with large size are less likely to be dispersed for many plant species (e.g., Greene and Johnson 1993; Jordano 1995; Brewer 2001; Theimer 2003a; Yi and Yang 2011). The relative profitability of seed species plays another important role in seed dispersal by small rodents, through a trade-off between foraging investment and rewards (Hurly and Robertson 1987; Cao et al. 2006; Yang et al. 2012). Seeds with higher nutritional value and greater attractiveness to dispersal agents are usually dispersed at greater distance (Stephens and Krebs 1986; Grubb and Burslem 1998; Jansen et al. 2004; Moore et al. 2007). However, seed size and animal's body size can be more important than seed nutrient in determining seed dispersal and caching (Muňoz and Bonal 2008; Wang and Chen 2009). Furthermore, the effect of seed traits on cache distances can be inferred by high levels of food abundance (Moore et al. 2007) and interspecific effects of seed availability (Yi et al. 2011).

According to the optimal cache spacing model (Stapanian and Smith 1978, 1984; Clarkson et al. 1986), caching effort represents a trade-off between the costs of transporting caches away from the source and the costs of distance- or density-dependent cache loss. However, Moore et al. (2007) suggest that, when food is superabundant, dispersal distance is more likely to be determined by minimizing energy cost of caching than by minimizing pilfering rates. Although low-rodent density increases scatter hoarding and dispersal distances (Li and Zhang 2007), Clarkson et al. (1986) show that in areas with more conspecifics, pilfering rates are more strongly depended on cache density and dispersal distances, reflecting the controversial role of rodent abundance on seed dispersal.

In addition, the animal-mediated seed dispersal hypothesis suggests that plants benefit from improved dispersal when large seed crops are produced (Kelly 1994). Recent studies show that seeds are more likely to be dispersed at greater distance in seed-rich years (Vander Wall 2002, 2003; Xiao et al. 2005a; Li and Zhang 2007), because greater distance are required to maintain optimal cache densities as more seeds are cached (Stapanian and Smith 1978; Vander Wall 2002). Contrary to predictions of these conventional models, several studies have found that seeds are not moved further when food is abundant (Theimer 2001; Jansen et al. 2004; Moore et al. 2007). Per-capita seed abundance seems to provide a better explanation of most variation of seed removal (Levine 2000; Carlo et al. 2003), and better represents a functional response of predators to variation in seed availability (Theimer 2003b). Previous studies on seed dispersal distances by small rodents

are not entirely consistent; therefore, further investigations are required to elucidate the interacting factors affecting seed dispersal distances, one of the key seed dispersal parameters.

Here, we released seeds of sympatric tree species, *Pinus koraiensis*, *Corylus mandshurica*, *Corylus heterophylla*, and *Quercus mongolica* in 4 years with different seed and rodent abundances, to investigate the relationship between seed dispersal and seed type, seed abundance, and disperser abundance. We hypothesized that (1) there would be a consistent effect of seed type on seed dispersal distances because seed trait represents a trade-off between energy investment and nutrition rewards to small rodents; (2) seed disperser abundance would be more important than seed abundance in affecting seed dispersal because seed availability exerts different interspecific effects on seed removal of sympatric species (Yi et al. 2011); and (3) seed masting may be an antipredator strategy (through foraging satiation) in which seed crop occurs at alternative years, reducing the probability of seed being eaten. However, as food supply begins to overwhelm the predator's ability to consume and process it, seeds are expected to be less dispersible. Therefore, we predicted that predation satiation effects on seed dispersal would be an integrated consequence of per-capita (per predator) seed abundance (the ratio of seeds per rodent), rather than the independent influence of seed availability.

Materials and methods

Study site

The study was conducted in 2007, 2008, 2009, and 2010 in the Dongfanghong Forestry Center (average elevation 750 m, 45° 58′ N, 129° 08′ E) in Heilongjiang Province, Northeast China. The climate is dominated by the north temperate zonal monsoons, with severe long winters and short cool summers. The annual average air temperature is 1.4 °C (−40 to 37 °C). Annual precipitation averages 650 mm, with 80 % falling between May and September (Yi et al. 2011). The zonal vegetation is characterized by secondary broad-leaved and mixed conifer forest. At our study sites, common canopy tree species include *Betula platyphlla* (Betulaceae), *Juglans mandshurica* (Juglandaceae), *Q. mongolica* (Fagaceae), *P. koraiensis* (Pinaceae), *Fraxinus mandshurica* (Oleaceae), *Phellodendron amurese* (Rutaceae), *Acer mono* (Aceraceae), and *Tilia amurensis* (Tiliaceae). Dominant understory shrubs are *C. mandshurica*, *C. heterophylla* (Betulaceae), *Fructus schisandrae* (Magnoliaceae), and *Acanthopanax senticosus* (Araliaceae). The dominant rodent species are *Apodemus peninsulae* (Muridae), *Clethrionomys rufocanus* (Cricetidae), and *Tamias sibiricus* (Sciuridae), with *A. peninsulae* and *T. sibiricus* as important seed disperser. Seed falls of the four studied species (*P. koraiensis*, *C. mandshurica*, *C.*

heterophylla, and *Q. mongolica*) begin at the end of August and cease late September.

Seed tagging

Experimental mature seeds of *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* were obtained in the market because they were economic food items. Acorns of *Q. mongolica* were collected from more than ten adult trees during their seed falls to provide composite samples that incorporate seed trait variations. Seed mass of *C. heterophylla*, *P. koraiensis*, *C. mandshurica*, and *Q. mongolica* was 1.18±0.28, 0.73±0.05, 0.73±0.08, and 2.86±0.21 g, respectively (Yang et al. 2012). Caloric value of the focal seed species was estimated at 13.45±0.11, 29.77±0.19, 17.74±0.05, and 9.52±0.44 KJ/g, respectively. Sound seeds were selected and labeled using methods by Zhang and Wang (2001) with minor modifications. A tiny hole of 0.3 mm in diameter was drilled through the hull at the umbilici of each seed, avoiding any damage to the embryo. A white flexible plastic tag (2.5×3.5 cm, <0.3 g) fastening a 10-cm thin steel thread was tied through the hole in each seed. In order to easily relocate and identify each released seed, each tag on the seed was consecutively and discriminatively numbered. Small rodents usually scatter-hoard the tagged seeds in the soil or under tree leaves, but leave the tags on the ground surface, making them easy to locate (Zhang and Wang 2001). Plastic tagging appears to have a negligible effect on seed removal and caching by small rodents (Xiao et al. 2006).

Seed release

Seed stations were spaced at 20–30 m apart on six parallel transects each 200–300 m long at the experimental site. To explore the effects of per-capita seed abundance on seed dispersal distances, we established 60 seed stations for *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* with each seed species of 20 seed stations. The same stations were used to release seeds in 2007, 2008, 2009, and 2010. We released 30 conspecific-tagged seeds within each seed station with an area of 1 m² in mid July (preperiod of seed fall). We repeated the study across the 4 years (2007, 2008, 2009, and 2010) to explore the effects of rodent abundances on seed dispersal. A total of 1,800 seeds were released prior to the seed fall of local tree species in each year. Because seeds of the focal tree species usually began to fall at the end of August (Yi et al. 2011), seed fall period will not be overlapped with our survey period (<10 days). The released seeds were expected to be the most accessible food source for local rodent species;
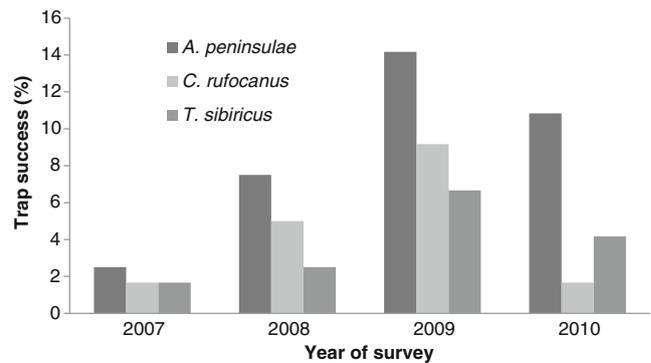
Fig. 1 Trap success of seed dispersers in 2007, 2008, 2009, and 2010

therefore, the per-capita seed abundance across the 4 years were relatively estimated as the number of released seeds/trap success of rodents.

It was a seed-rich year for *C. mandshurica* in 2008 (19.48±6.34 seeds per clone), while *Q. mongolica* experienced a moderate crop in 2009 (6.20±2.09 acorns/m²) and a big mast in 2010 (26.67±10.22 acorns/m²). Extreme low seed availability of the other focal tree species was found in 2007, 2008, 2009, and 2010 in the study plot. To detect the effects of seed availability on seed dispersal distances, we deployed the same method of releasing seeds of *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* at early (19 August) and end periods (7 September) of seed fall of *C. mandshurica* in 2008; while at early (25 August) and peak periods (5 September) of seed fall of *Q. mongolica* in 2009 and 2010, respectively. We explored any interspecific effects of seed masting on seed dispersal distances by further releasing 600 acorns of *Q. mongolica* evenly in 20 seed stations at early and peak periods of its seed fall in 2009 and
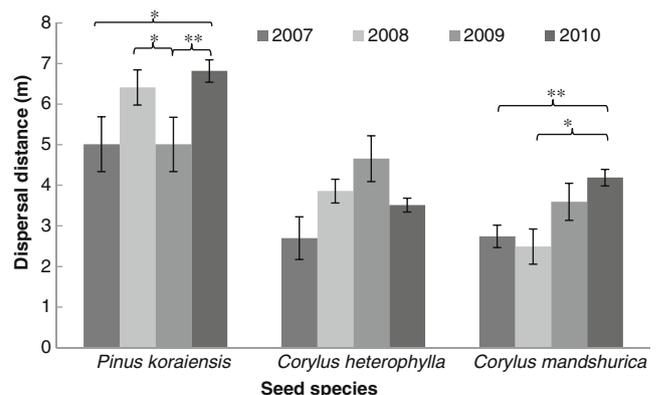
Fig. 2 Seed dispersal distances of *P. koraiensis*, *C. heterophylla*, and *C. mandshurica* in the four consecutive years with different disperser abundances. Data are expressed as mean ± SE. *$P<0.05$, **$P<0.01$, and ***$P<0.001$, significant differences between seed dispersal distance, respectively, indicated by histograms. The *asterisks* indicating significant differences in dispersal distances are within each species across the years

Table 1 Two-way ANOVA summary of distances seeds transported in 2007, 2008, 2009, and 2010 with different rodent abundances

Source	Sum of squares	df	Mean square	F	Sig.
Corrected model	2,423.118[a]	11	220.283	14.344	0.000
Intercept	13,194.651	1	13,194.651	859.196	0.000
Rodent abundance	195.293	3	65.098	4.239	0.005
Seed species	979.822	2	489.911	31.902	0.000
Rodent abundance × seed species	334.348	6	55.725	3.629	0.001
Error	19,933.357	1,298	15.357		
Total	50,905.590	1,310			
Corrected total	22,356.475	1,309			

[a] R^2=0.108 (adjusted R^2=0.101)

2010 in the same areas, respectively. Therefore, a total of 9, 600 (7,200+2,400) seeds (or acorns) were released during seed fall of *C. mandshurica* and *Q. mongolica*. After seed release, we checked the fate of seeds (eaten, removed, and cached) every day for 10 days around each seed station. Based on the dispersal kernels of the focal seed species in this study (Yi and Zhang 2008; Yi et al. 2008, 2011), we searched for tagged seeds or tags surrounding each station (radius, ≈20 m). Removed seeds were categorized as (1) buried or unburied and uneaten by small rodents (excluding those intact in the seed stations); (2) eaten after removal, and (3) missing. Dispersal distances were measured as the linear lengths from the center of seed sources to the locations where the tagged intact seeds were found.

Seed disperser survey

We monitored small rodent populations at the end of the seed release trials. Trapping sites were located in

Table 2 Multiple comparisons between dispersal distances seeds transported in 2007, 2008, 2009, and 2010 with different rodent abundances

		Mean difference	SE	Sig.	95 % Confidence interval	
					Lower bound	Upper bound
Releasing years	Releasing years					
2007	2008	−1.6818[a]	0.44610	0.000	−2.5570	−0.8067
	2009	−0.9996[a]	0.43446	0.022	−1.8519	−0.1473
	2010	−1.3989[a]	0.38970	0.000	−2.1634	−0.6344
2008	2007	1.6818[a]	0.44610	0.000	0.8067	2.5570
	2009	0.6823	0.35704	0.056	−0.0182	1.3827
	2010	0.2829	0.30098	0.347	−0.3075	0.8734
2009	2007	0.9996[a]	0.43446	0.022	0.1473	1.8519
	2008	−0.6823	0.35704	0.056	−1.3827	0.0182
	2010	−0.3993	0.28344	0.159	−0.9553	0.1567
2010	2007	1.3898[a]	0.38970	0.000	0.6344	2.1634
	2008	−0.2829	0.30098	0.347	−0.8734	0.3075
	2009	0.3993	0.28344	0.159	−0.1567	0.9553
Seed species	Seed species					
P. koraiensis	*C. heterophylla*	2.4978[a]	0.25688	0.000	1.9938	3.0017
	C. mandshurica	2.5663[a]	0.27172	0.000	2.0332	3.0994
C. heterophylla	*P. koraiensis*	−2.4978[a]	0.25688	0.000	−3.0017	−21.9938
	C. mandshurica	0.0685	0.27054	0.800	−0.4622	0.5993
C. mandshurica	*P. koraiensis*	−2.5663[a]	0.27172	0.000	−3.0994	−2.0332
	C. heterophylla	−0.0685	0.27054	0.800	−0.5993	0.4622

Based on observed means. The error term is mean square (error)=15.357

[a] The mean difference is significant at the 0.05 level

the same habitat as the seed placement experiments (within 1 km of experimental area), to ensure similar rodent species compositions and abundances in the animal trapping and seed release plots (Li and Zhang 2007). Ten transects (50 m in length, 10 m apart) were established and trap stations were set at 5 m intervals along each transect. Captured animals were identified and then released. Trapping occurred for 3 days and 3 nights in each trial. Trap success was estimated according to Cheng et al. (2005): trap success = total number of trapped animals/number of traps.

Statistical analyses

Data were analyzed using Statistic Package for Social Science 16.0. Seed dispersal distances of the all seed stations in each bout were pooled together to detect their differences across years with different rodent abundances and among seed rain periods with different seed abundances (Xiao et al. 2004, 2005b; Xiao and Zhang 2006; Zhang et al. 2008; Chou et al. 2011). Because rodent abundance varied greatly in the four consecutive years, the effect of rodent abundance can be evaluated across the years (Xiao et al. 2005b; Li and Zhang 2007). Therefore, two-way analysis of variance (ANOVA) under general linear model (GLM) was used to detect the effects of per-capita seed abundance and seed type on the dispersal distances over the four consecutive years (with dispersal distance being the dependent variable and per-capita seed abundances and seed type being the independent variables) and the effects of seed availability (i.e., seed rain period) and seed type on the dispersal distances at different periods of seed fall of C. mandshurica and Q. mongolica (with dispersal distance being the dependent variable and seed availability and seed type being the independent variables). To determine whether the dependent variable was normally distributed for each combination of the levels of the two independent variables, Levene's test was used. If significant effects of seed type were detected, the effects of rodent abundance or seed abundance on dispersal distances of each seed species were further tested using multiple comparisons (least significant difference or Student–Newman–Keuls). One-way ANOVA of univariate GLM was applied to test the effect of seed availability of Q. mongolica on its own acorn dispersal distances. GLM was also used to detect the effect of per-capita seed abundance or seasonal seed availability (C. mandshurica and Q. mongolica) on seed caching and cache survival (P. koraiensis, C. mandshurica. and C. heterophylla), respectively. Chi-square test of non-parametric tests was used to detect the differences in

trap success of small rodents and per-capita seed abundances (see Xiao et al. 2006).
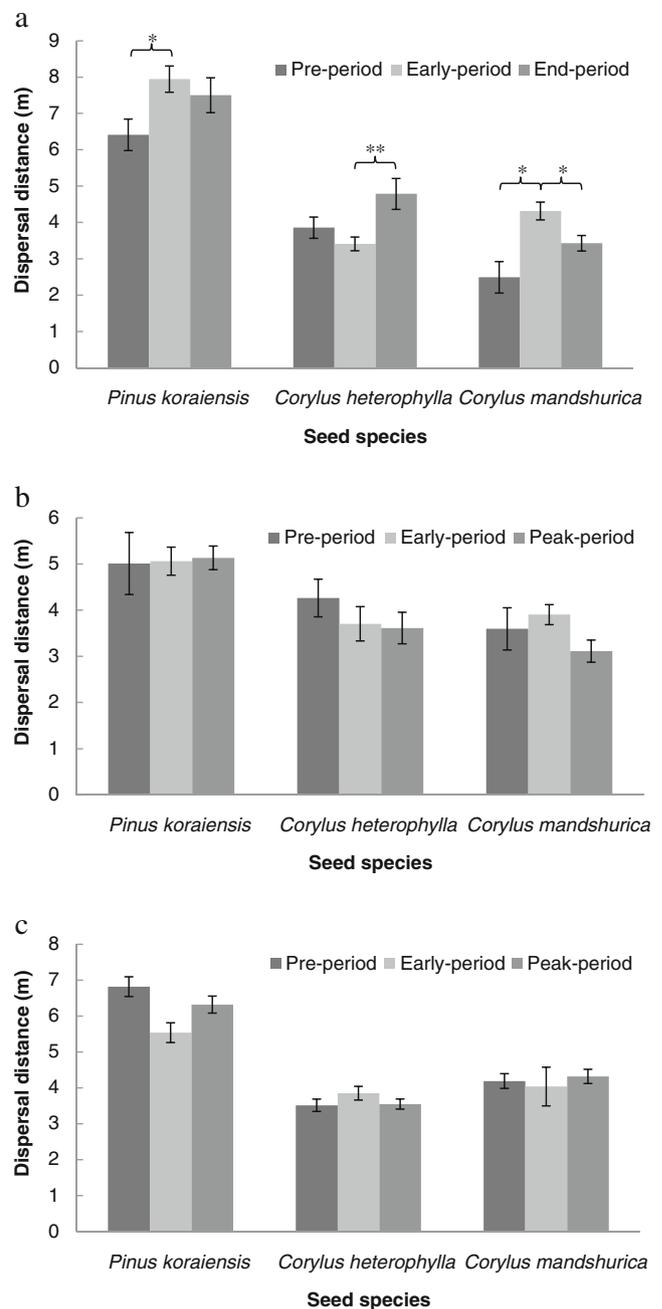
Fig. 3 Seed dispersal distances of P. koraiensis, C. heterophylla, and C. mandshurica during different periods of seed fall of C. mandshurica in 2008 and Q. mongolica in 2009 and 2010. a Dispersal distances of P. koraiensis, C. heterophylla, and C. mandshurica during the different periods of seed fall of C. mandshurica in 2008. b Seed dispersal distances of P. koraiensis, C. heterophylla, and C. mandshurica during the different periods of seed fall of Q. mongolica in 2009. c Seed dispersal distances of P. koraiensis, C. heterophylla, and C. mandshurica during the different periods of seed fall of Q. mongolica in 2010. Data are expressed as mean ± SE. *P<0.05, **P<0.01, and ***P<0.001, significant differences between seed dispersal distance indicated on histograms, respectively

Table 3 Two-way ANOVA summary of distances seeds transported during seed rain periods of *C. mandshurica* in 2008

Source	Sum of squares	df	Mean square	F	Sig.
Corrected model	2,943.390[a]	8	367.924	27.009	0.000
Intercept	14,679.018	1	14,679.018	1.078E3	0.000
Seed rain periods	104.983	2	52.492	3.853	0.022
Seed species	2,068.254	2	1,034.127	75.915	0.000
Seed rain periods × seed species	246.037	4	61.509	4.515	0.001
Error	12,995.492	954	13.622		
Total	42,960.940	963			
Corrected total	15,938.882	962			

[a]$R^2=0.185$ (adjusted $R^2=0.178$)

Results

Seed disperser abundance and per-capita seed abundance

In 2007, three rodent species was trapped and the trap success was estimated at 6.00 %, representing a low level of rodent abundance (Fig. 1). The trap success was 15.33, 30.00, and 17.33 % in 2008, 2009, and 2010, respectively. Trap success in 2007 was significantly lower than those in 2008, 2009, and 2010 (chi-square test, $\chi^2=17.294$, $df=3$, $P=0.001$), representing high level of rodent abundances. Trap success was higher in 2009 than in 2008 and 2010 (chi-square test, $\chi^2=6.419$, $df=2$, $P=0.040$; Fig. 1). Three surveys carried out on 17 July, 15 August, and 4 September 2008 showed no significant difference in trap success ($\chi^2=0.824$, $df=2$, $P=0.662$, Chi-square test), therefore, we predicted no

significant variations in rodent abundance from late July to early September in 2009 and 2010. The per-capita seed abundances in 2007, 2008, 2009, and 2010 were 300, 117, 60, and 104, respectively, and showed significant difference ($\chi^2=232.115$, $df=3$, $P<0.001$).

Response of seed dispersal distances of *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* to per-capita seed abundances

We found 1,310 (18.2 % of the released seeds) dispersed seeds of *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* during primary dispersal at the preperiod of seed fall (July) in the four consecutive years with different per-capita seed abundances. Two-way ANOVA analyses indicated that dispersal distances varied significantly with per-capita seed abundances and seed

Table 4 Multiple comparisons between dispersal distances seeds transported during seed rain periods of *C. mandshurica* in 2008

Seed rain periods	Seed rain periods	Mean difference	SE	Sig.	95 % Confidence interval	
					Lower bound	Upper bound
Preperiod	Early period	−0.1198	0.29711	0.687	−0.7028	0.4633
	End period	−0.5073	0.34363	0.140	−1.1817	0.1670
Early period	Preperiod	0.1198	0.29711	0.687	−0.4633	0.7028
	End period	−0.3876	0.29015	0.182	−0.9570	0.1818
End period	Preperiod	0.5073	0.34363	0.140	−0.1670	1.1817
	Early period	0.3876	0.29015	0.182	−0.1818	0.9570
Seed species	Seed species					
P. koraiensis	*C. heterophylla*	3.3795[a]	0.27875	0.000	2.8325	3.9265
	C. mandshurica	3.1914[a]	0.29859	0.000	2.6055	3.7774
C. heterophylla	*P. koraiensis*	−3.3795[a]	0.27875	0.000	−3.9265	−2.8325
	C. mandshurica	−0.1881	0.32171	0.559	−0.8194	0.4433
C. mandshurica	*P. koraiensis*	−3.1914[a]	0.29859	0.000	−3.7774	−2.6055
	C. heterophylla	0.1881	0.32171	0.559	−0.4433	0.8194

Based on observed means. The error term is mean square (error)=13.622

[a] The mean difference is significant at the 0.05 level

Table 5 Two-way ANOVA summary of distances seeds transported during seed rain periods of *Q. mongolica* in 2009

Source	Sum of squares	df	Mean square	F	Sig.
Corrected model	380.317[a]	8	47.540	3.823	0.000
Intercept	12,439.178	1	12,439.178	1.003E	0.000
Seed rain periods	14.426	2	7.213	0.581	0.559
Seed species	333.137	2	166.596	13.426	0.000
Seed rain periods × seed species	32.672	4	8.168	0.658	0.621
Error	9,627.540	776	12.407		
Total	2,4536.270	785			
Corrected total	10,007.857	784			

[a] $R^2 = 0.038$ (adjusted $R^2 = 0.028$)

species, respectively (Fig. 2, Table 1). In addition, a significant interaction effect between seed species and per-capita seed abundances was observed. Multiple comparisons indicated that seeds released at lower per-capita seed abundances (in 2008, 2009, and 2010) were dispersed further than those at higher per-capita seed abundances (in 2007; Table 2). These facts showed that low per-capita seed abundance benefits seed dispersal. GLM analyses showed a significant effect of per-capita seed abundance on the dispersal distances of *P. koraiensis* ($F_{3, 457} = 3.770$, $P = 0.011$), *C. heterophylla* ($F_{3, 466} = 3.126$, $P = 0.026$) and *C. mandshurica* ($F_{3, 375} = 4.825$, $P = 0.003$; Fig. 2). These results indicated that seeds were more likely to be dispersed further at low per-capita seed abundances. Studies in the four consecutive years consistently showed seeds of *P. koraiensis* were dispersed further than those of *C. mandshurica* and *C.*

heterophylla; however, *C. mandshurica* and *C. heterophylla* exhibited similar dispersal distance (Table 2).

Seed dispersal distances in response to seed fall of *C. mandshurica* and *Q. mongolica*

Totally, 4,143 (27.6 % of the released seeds) dispersed seeds were found for primary dispersal during seed fall of *C. mandshurica* and *Q. mongolica*. Two-way ANOVA revealed significant effects of seed abundances of *C. mandshurica* on seed dispersal distances (Fig. 3a, Table 3). Multiple comparisons demonstrated significant effects of seed abundances on the dispersal distances of *P. koraiensis* ($F_{2, 433} = 3.239$, $P = 0.040$), *C. heterophylla* ($F_{2, 293} = 5.277$, $P = 0.006$), and *C. mandshurica* ($F_{2, 234} = 5.814$, $P = 0.003$), respectively (Table 4). However, we found different effects of seed availability of *C. mandshurica* on the dispersal

Table 6 Multiple comparisons between dispersal distances seeds transported during seed rain periods of *Q. mongolica* in 2009

Seed rain periods	Seed rain periods	Mean difference	SE	Sig.	95 % Confidence interval	
					Lower bound	Upper bound
Preperiod	Early period	−0.0695	0.30631	0.820	−0.6708	0.5318
	Peak period	−0.0803	0.30984	0.796	−0.6885	0.5279
Early period	Preperiod	0.0695	0.30631	0.820	−0.5318	0.6708
	Peak period	−0.0108	0.30783	0.972	−0.6151	0.5935
Peak period	Preperiod	0.0803	0.30984	0.796	−0.5279	0.6885
	Early period	0.0108	0.30783	0.972	−0.5935	0.6151
Seed species	Seed species					
P. koraiensis	*C. heterophylla*	1.1518[a]	0.29471	0.000	0.5773	1.7304
	C. mandshurica	1.5003[a]	0.31430	0.000	0.8833	2.1173
C. heterophylla	*P. koraiensis*	−1.1518[a]	0.29471	0.000	−1.7304	−0.5733
	C. mandshurica	0.3485	0.32767	0.288	−0.2948	0.9917
C. mandshurica	*P. koraiensis*	−1.5003[a]	0.31430	0.000	−2.1173	−0.8833
	C. heterophylla	−0.3485	0.32767	0.288	−0.9917	0.2948

Based on observed means. The error term is mean square (error)=12.407

[a] The mean difference is significant at the 0.05 level

Table 7 Two-way ANOVA summary of distances seeds transported during seed rain periods of *Q. mongolica* in 2010

Source	Sum of squares	df	Mean square	F	Sig.
Corrected model	2,667.433[a]	8	333.429	34.534	0.000
Intercept	26,546.381	1	26,546.381	2.749E3	0.000
Seed rain periods	22.741	2	11.370	1.178	0.308
Seed species	1,998.561	2	999.281	103.499	0.000
Seed rain periods × seed species	120.827	4	30.207	3.129	0.014
Error	16,316.930	1,690	9.655		
Total	57,456.400	1,699			
Corrected total	18,984.363	1,698			

[a] $R^2 = 0.141$ (adjusted $R^2 = 0.136$)

distances of the three seed species, i.e., seed dispersal distances were increased in *P. koraiensis* and *C. mandshurica*, but decreased in *C. heterophylla*. Seed dispersal distances varied greatly among the three seed species (Tables 3 and 4), reflecting the effect of seed type on seed dispersal. Although there was a significant difference in the seed crops of *Q. mongolica* between 2009 and 2010, seed dispersal distances of *P. koraiensis*, *C. heterophylla*, and *C. mandshurica* was not significantly influenced (Fig. 3b, c, Tables 5, 6, 7, and 8). However, seed dispersal distances of *Q. mongolica* were significantly enhanced by its own seed availability in 2009 ($F_{1, 293} = 48.411$, $P < 0.001$; Fig. 4), indicating different interspecific effects of seed availability of *Q. mongolica* on dispersal of sympatric seed species. Surprisingly, seed dispersal distances of *Q. mongolica* did not vary significantly during its own seed fall in a big

mast year of 2010 ($F_{1, 274} = 1.068$, $P = 0.302$; Fig. 4), suggesting that seed dispersal can not necessarily benefit from massive crops of seeds. Unlike seed abundance, seed type exhibited consistent effects on seed dispersal distances (Tables 1, 3, 5, and 7), i.e., seeds of *P. koraiensis* were dispersed further than those of *C. heterophylla* and *C. mandshurica*.

The ratio of seeds cached to eaten seeds of *C. heterophylla*, *C. mandshurica*, and *P. koraiensis* showed significant differences between the four consecutive years with different per-capita seed abundances ($F_{3, 12} = 8.356$, $P = 0.008$), with the ratios in 2010 and 2007 were much larger than those in 2008 and 2009, respectively ($P = 0.011$, $P = 0.039$; $P = 0.002$, $P = 0.008$; Table 9). However, the survived caches did not change significantly among the 4 years ($F_{3, 12} = 2.634$, $P = 0.112$). Seed abundances of *C. mandshurica* showed no effect on the ratio of cached seeds to eaten

Table 8 Multiple comparisons between dispersal distances seeds transported during seed rain periods of *Q. mongolica* in 2010

Seed rain periods	Seed rain periods	Mean difference	SE	Sig.	95 % Confidence interval	
					Lower bound	Upper bound
Preperiod	Early period	0.2841	0.21336	0.183	−0.1344	0.7026
	Peak period	0.0414	0.16634	0.803	−0.2848	0.3677
Early period	Preperiod	−0.2841	0.21336	0.183	−0.7026	0.1344
	Peak period	−0.2427	0.21419	0.257	−0.6628	0.1774
Peak period	Preperiod	−0.0414	0.16634	0.803	−0.3677	0.2848
	Early period	0.2427	0.21419	0.257	−0.1774	0.6628
Seed species	Seed species					
P. koraiensis	C. heterophylla	2.7548[a]	0.17672	0.000	2.4082	3.1014
	C. mandshurica	2.1247[a]	0.19184	0.000	1.7484	2.5010
C. heterophylla	P. koraiensis	−2.7548[a]	0.17672	0.000	−3.1014	−2.4082
	C. mandshurica	−0.6301[a]	0.19033	0.001	−1.0034	−0.2568
C. mandshurica	P. koraiensis	−2.1247[a]	0.19184	0.000	−2.5010	−1.7484
	C. heterophylla	0.6301[a]	0.19033	0.001	0.2568	1.0034

Based on observed means. The error term is mean square (error)=9.655

[a] The mean difference is significant at the 0.05 level
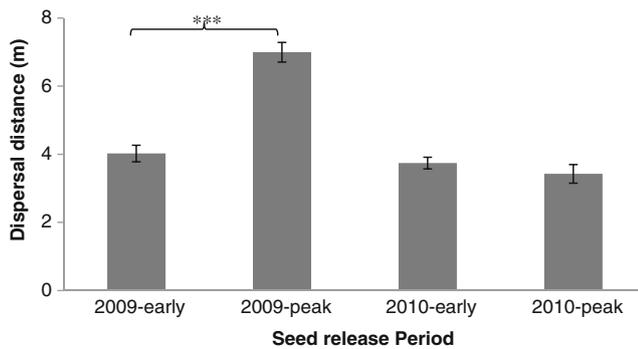
Fig. 4 Seed dispersal distances of *Q. mongolica* during its own early and peak periods of seed fall in 2009 and 2010. Data are expressed as mean ± SE. ***$P<0.001$, significant differences between seed dispersal distances indicated on histograms

seeds of *C. heterophylla*, *C. mandshurica*, and *P. koraiensis* ($F_{2, 9}=3.090$, $P=0.120$), however, significantly influenced the number of survived caches ($F_{2, 9}=10.616$, $P=0.011$), with more survived caches at the early period than at the pre- and end periods of the seed rain of *C. mandshurica* ($P=0.039$, $P=0.004$; Table 9). In 2009, seed abundances of *Q. mongolica* showed no effect on the ratio of cached to eaten seeds and the survived caches ($F_{2, 9}=1.714$, $P=0.258$; $F_{2, 9}=0.724$, $P=0.523$). However, in 2010, with high level of seed abundance, the ratio of cached seeds to eaten seeds was significantly influenced by seed availability of *Q. mongolica* ($F_{2, 9}=24.975$, $P=0.001$), more seeds were cached at the peak-period of seed rain of *Q. mongolica* ($P=0.002$, $P=0.001$). But, we found no effect on the survived caches ($F_{2, 9}=0.845$, $P=0.475$; Table 9).

Discussion

In general, our 4-year studies show that seed dispersal distances are seed type dependent. Seeds of *P. koraiensis* are consistently dispersed further in regardless of per-capita seed abundances, reflecting the dominant effects of seed types in determining seed dispersal. Seed dispersal distances are more likely to be influenced by rodent abundance than by seed abundance; low per-capita seed abundance seems to facilitate seed dispersal. The effects of seed availability on seed dispersal distances are not only determined by per-capita seed abundance but also seed types.

Effects of seed type on seed dispersal

Our results show that *P. koraiensis* seeds with smallest size (Yang et al. 2012) are always dispersed farther; while *C. heterophylla* seeds with the largest size are transported less far. These findings are not in agreement with the previous studies that larger seeds are transported further than smaller

ones (Stapanian and Smith 1978, 1984; Hurly and Robertson 1987; Vander Wall 1995; Forget et al. 1998; Jansen et al. 2002, 2004; Xiao et al. 2004, 2005b). Our results cannot deny the effect of seed size on dispersal distances, however, may reflect the main effect of seed nutrition on seed dispersal. Meanwhile, our results support the prediction that seeds with higher nutritional value are usually dispersed at greater distance and cached at lower densities (Grubb and Burslem 1998; Jansen et al. 2004; Moore et al. 2007; Yang et al. 2012). The differential effects of seed traits on seed dispersal distance are consistent with the fact that no significant correlation was found between seed size and seed nutrition ($r=-0.703$, $P=0.503$). The consistent responses of seed dispersal distances to seed species at different levels of seed and rodent abundances reflect the important role of seed types in determining seed dispersal in our study.

Effects of per-capita seed abundances on seed dispersal

Seeds on the ground surface are more likely to be removed by other competitors during seed caching processes (Vander Wall 2010); therefore, seed density is likely to be diluted at high abundances of seed dispersers. Regardless of seed species, seeds were transported further in 2008, 2009, and 2010 than in 2007 with high per-capita seed abundance in our study. Because our survey period of the effects of per-capita seed abundances was not overlapped with the seed fall period in the four consecutive years, it is reasonable to conclude that low per-capita seed abundances facilitate seed dispersal. We acknowledge that other food items (plant buds, insects, etc.) may serve as an alternative energy supply for local dispersers in different years. On the other hand, yearly variations in rodent composition are expected to influence seed dispersal, as large-bodied seed dispersers tend to disperse seeds further than those with small body (Yi's unpublished data). Despite these factors, our results support the previous observations (Clarkson et al. 1986; Jansen et al. 2002) that seeds are likely to be taken further at high level of disperser abundance. We also found more seeds were cached in 2007 and 2010 with higher per-capita seed abundance than in 2008 and 2009 with higher rodent abundances, indicating that low per-capita seed abundance may promote seed caching. However, low per-capita seed abundance may not benefit cache survival as no difference was detected in the survived caches of the focal tree species among the four consecutive years. This can be attributed to the high level of cache recovery rate and cache pilferage at low per-capita seed abundance.

Effects of seasonal seed availability on seed dispersal

Two-way ANOVA showed no significant difference in seed dispersal distances of *P. koraiensis*, *C. mandshurica*, and *C.*

Table 9 Ratio of cached seeds to eaten and cache survival of *C. heterophylla*, *C. mandshurica*, and *P. koraiensis* released at different time

Seed release time	Seed species	Ratio of cached seeds to eaten seeds	Survived caches
Preperiod of seed rain in 2010	*C. heterophylla*	0.73	53
	C. mandshurica	0.75	38
	P. koraiensis	0.56	73
Preperiod of seed rain in 2009	*C. heterophylla*	0.22	69
	C. mandshurica	0.15	40
	P. koraiensis	0.13	17
Preperiod of seed rain in 2008	*C. heterophylla*	0.04	31
	C. mandshurica	0.29	14
	P. koraiensis	0.56	27
Preperiod of seed rain in 2007	*C. heterophylla*	0.60	48
	C. mandshurica	1.11	62
	P. koraiensis	0.83	88
Early period of seed rain of *C. mandshurica* in 2008	*C. heterophylla*	0.32	37
	C. mandshurica	1.23	38
	P. koraiensis	1.42	49
End period of seed rain of *C. mandshurica* in 2008	*C. heterophylla*	0.28	12
	C. mandshurica	0.45	19
	P. koraiensis	0.39	2
Preperiod of seed rain of *Q. mongolica* in 2009	*C. heterophylla*	0.22	69
	C. mandshurica	0.15	40
	P. koraiensis	0.13	17
Early period of seed rain of *Q. mongolica* in 2009	*C. heterophylla*	0.06	43
	C. mandshurica	0.08	18
	P. koraiensis	0.36	29
Peak period of seed rain of *Q. mongolica* in 2009	*C. heterophylla*	0.52	40
	C. mandshurica	0.10	22
	P. koraiensis	0.62	9
Preperiod of seed rain of *Q. mongolica* in 2010	*C. heterophylla*	0.73	53
	C. mandshurica	0.75	38
	P. koraiensis	0.56	73
Early period of seed rain of *Q. mongolica* in 2010	*C. heterophylla*	0.26	52
	C. mandshurica	0.06	17
	P. koraiensis	0.18	62
Peak period of seed rain of *Q. mongolica* in 2010	*C. heterophylla*	1.01	40
	C. mandshurica	0.70	29
	P. koraiensis	0.83	40

heterophylla in response to seed fall periods of either *C. mandshurica* or *Q. mongolica*, consistent with the previous studies that seeds are not moved as far in seed-rich years as in seed-poor years (Theimer 2001; Faden and Parker, 2003; Jansen et al. 2004; Moore et al. 2007). These results indicate the effects of seasonal seed availability on seed dispersal seem to be stable. However, there were different interspecific effects of seed masting on the focal seed dispersal. Multiple comparisons indicate that seed abundance of *C. mandshurica* increases seed dispersal distances of *P.*

koraiensis and *C. mandshurica*, but decreases those of *C. heterophylla*. Nevertheless, seed abundance of *Q. mongolica* exhibits no significant influence on seed dispersal of the other three seed species both in 2009 and 2010. This implies that seed masting of one given tree species will generate different or even reverse effects on seed dispersal of other tree species. Our results seem to challenge the previous studies that dispersal distances will be greater when food is sufficient (Janzen 1970; Kelly 1994; Vander Wall 2002, 2003; Xiao et al. 2005a; Li and Zhang 2007). Although high

level of seed availability of *C. mandshurica* did not affect seed caching of the focal tree species, more seeds were survived in caches. In contrast, high level of seed abundance of *Q. mongolica* in 2010 significantly increased seed caching but not survived caches. These facts reflect different interspecific effects of mast seeding on seed dispersal (Yi et al. 2011). Our results imply that seed abundance of one specie do not necessarily incur predator satiation effect of interspecific seed species, which can be attributed to different attractiveness of seed species to seed dispersers. Seed abundance of *Q. mongolica* increased its own seed dispersal distances in 2009 but not in 2010, indicating that the effects of seed availability on seed dispersal are not consistent in different years. Difference in rodent abundance in 2009 and 2010 may partially explain this inconsistency. The lower per-capita seed abundance is supposed to be responsible for the increased seed dispersal distance in 2009, echoing to our yearly results. Therefore, it seems that massive crops (e.g., higher per-capita seed abundance) do not necessarily benefit seed dispersal (Jansen et al. 2004; Moore et al. 2007; but see Vander Wall 2002; Li and Zhang 2007).

Our study shows that seed dispersal distance is an integrated ecological consequence of seed abundance and rodent abundance (i.e., per-capita seed abundance). We also notice that the yearly seed masting shows different effects on the dispersal distances of the focal tree species, which might be caused by an interspecific impact of seed masting in different years. We argue that the predator satiation hypothesis should be tested on the basis of the interspecific effects of seed availability and the per-capita seed abundance.

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