

# Intra- and inter-specific effects of mast seeding on seed fates of two sympatric *Corylus* species

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**Abstract** We released seeds of two sympatric tree species, *Corylus mandshurica* (seed with thinner seed hull, higher nutrition) and *C. heterophylla* (seeds with thicker seed hull, lower nutrition) in the masting year of *C. mandshurica* in 2008, and *C. heterophylla* in 2009, respectively, to investigate how seed masting of the two sympatric *Corylus* species affects seed removal and dispersal fitness of the two species differently at both intra- and inter-specific levels. At intra-specific level, the authors found mast seeding of both *C. mandshurica* and *C. heterophylla* significantly reduced seed removal, seed consumption, but increased seed dispersal distance and seed dispersal fitness of the released seeds. Mast seeding of *C. mandshurica* increased seed caching of *C. mandshurica*. At inter-specific level, the authors found mast seeding of *C. mandshurica* reduced seed removal of *C. heterophylla*, but mast seeding of

*C. heterophylla* did not significantly reduce seed removal of *C. mandshurica*. Mast seeding of *C. mandshurica* reduced seed consumption of *C. heterophylla*, while mast seeding of *C. heterophylla* reduced seed consumption of *C. mandshurica*. We found mast seeding of *C. mandshurica* significantly reduced seed dispersal distance of *C. heterophylla*, while mast seeding of *C. heterophylla* significantly increased seed dispersal distance of *C. mandshurica*. We found that mast seeding of *C. mandshurica* significantly increased seed dispersal fitness of *C. heterophylla*, while mast seeding of *C. heterophylla* did not significantly increase seed dispersal fitness of *C. mandshurica*. More studies are needed to reveal the ecological consequences of mast seeding at inter-specific or community-level. Seed traits may attribute the differences of mast seeding at inter-specific level. Because seeds with thinner seed hull and higher nutrition were more harvested and eaten by rodents, mast seeding of *C. mandshurica* might have reduced seed removal and seed consumption, but increased dispersal fitness of *C. heterophylla* (seeds with thicker seed hull, lower nutrition). Therefore, synchrony among species is, or is not, selectively beneficial to the focus species depends on seed traits which determine gains from mast seeding at inter-specific level.

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## Introduction

Many studies have demonstrated that animals have great influences on tree regeneration of large-seeded trees (Wenny and Levey 1998; Theimer 2001; Jansen et al. 2004; Youngsteadt et al. 2008, 2009). Animals often scatter- or larder-hoard foods for later use to overcome food shortage (Vander Wall 1990). Scatter hoarding of animals is more beneficial to seedling regeneration of forests (Vander Wall 1990; Chambers and Macmahon 1994).

Many tree species produce massive seeds at irregular intervals (Jansen et al. 2004; Xiao et al. 2005; Li and Zhang 2007). Mast seeding usually affects seed dispersal and hoarding behaviors of small rodents (Kelly 1994). Previous studies have shown that seed removal speed become lower in mast seeding year (Crawley and Long 1995; Theimer 2001; Jansen et al. 2004; Xiao et al. 2005; Li and Zhang 2007), probably caused by the predator satiation effect (Kelly 1994). Rodents were seen to increase efforts of caching seeds in years of high food availability (Theimer 2001; Jansen et al. 2004; Zhang et al. 2008a). Empirical studies show that seeds are dispersed further in the mast seeding year (Janzen 1971; Jansen et al. 2002, 2004; Vander Wall 2003; Xiao et al. 2004), indicating that dispersal distance can also be influenced by seed abundance (Li and Zhang 2007; Moore et al. 2007).

Though mast seeding has been found to benefit forest regeneration at both population level (Li and Zhang 2007) and individual level (Zhang et al. 2008a), it is not clear if and how mast seeding of one tree species affect seed dispersal fitness of other sympatric tree species at inter-specific level; although, synchrony of mast seeding is selectively favored among *Dipterocarp* trees (Curran and Leighton 2000; Curran and Webb 2000) and *Chionochloa* grasses (Kelly et al. 2000, 2008). Here, we hypothesized that (1) synchrony in seed masting among species may or may not benefit each other, depending on whether one species has fitness gains from masting by the other species due to difference in seed traits; (2) differences in seed traits among species may influence the inter-specific effects of seed masting. Seeds of some tree species which are more likely eaten by rodents may help protect seed survival of the other tree species.

Both *Corylus mandshurica* and the sympatric tree species *C. heterophylla* are characterized by seed masting without some overlap in seed rain. In 2008,

there was a high level of seed crop of *C. mandshurica* but a very low level of seed crop of *C. heterophylla*, while in 2009 there was a high level of seed crop of *C. heterophylla* but an extremely low seed crop of *C. mandshurica* in our study areas, which provided an opportunity to study the effect of mast seeding of one tree species on its own seed dispersal fitness and on that of the sympatric tree species of the same genus. Seeds of both the species become mature from mid-August to early September, and are favorite food of small rodents (Yi and Zhang 2008). The fresh seed mass of *C. heterophylla* ( $1.18 \pm 0.28$  g,  $n = 12$ ) is larger than *C. mandshurica* ( $0.73 \pm 0.08$  g,  $n = 12$ ), and its seed hull ( $0.24 \pm 0.03$  cm,  $n = 11$ ) is thicker than that of *C. mandshurica* ( $0.11 \pm 0.01$  cm,  $n = 10$ ). The caloric value of per *C. mandshurica* seed ( $6.21 \pm 0.02$  kJ,  $n = 24$ ) is larger than that of *C. heterophylla* ( $4.30 \pm 0.03$  kJ,  $n = 22$ ). We released tagged seeds of *C. mandshurica* and *C. heterophylla* in a *C. mandshurica* dominated forest in 2008, and in a *C. heterophylla* dominated forest in 2009. Seeds were released late July with no seed rain (we defined it as “the pre- period” of seed rain), mid-August with little seed rain (we defined it as “the early period of seed rain”), late August with large amount of seed rain (we defined it as “the peak-period” of seed rain) and early September with little seed rain (we defined it as “the end-period” of seed rain), to investigate how seed masting (across the early, peak-, and end-period of seed rain) of the two sympatric *Corylus* species affects seed removal and dispersal fitness of the two sympatric *Corylus* species, respectively, by comparing the results obtained in pre-period (non-seed rain). The study aimed to examine whether the inter-specific effect of seed masting on is species-specific and seed trait-dependent for two sympatric tree species of *Corylus*. Besides, the intra-specific effects of mast seeding were also investigated for comparisons.

## Materials and methods

### Study site

The study was conducted from July to October of 2008 and 2009 in the Dongfanghong Forestry Center (elevation averaged at 750 m,  $45^{\circ} 58' N$ ,  $129^{\circ} 08' E$ ) in the Dailing District, Yichun City, Heilongjiang

Province, northeast China. The climate of the experimental site is dominated by the north temperate zonal monsoon with severe and long winters but short warm summers. The annual average air temperature is 1.4°C with extremes of 35°C and –40°C. The average annual precipitation is 660 mm, and 80% of which falls in the short growing season from May to September (Wang and Meng 2005). The vegetation is characterized by the secondary broad-leaved and conifer mixed forest. In the experimental region, dominant or common canopy tree species included *Betula platyphlla*, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurese*, *Acer mono*, and *Tilia amurenensis*, beneath the tree species, shrubs such as *C. mandshurica*, *C. heterophylla*, *Fructus schisandrae*, and *Acanthopanax senticosus* dominated. Small seed-hoarding mammals are *Apodemus peninsulae*, *Clethrionomys rufocanus*, and *Eutamias sibiricus*. Eurasian jay, *Garrulus glandarius* were potential agents for seed dispersal, but they are less important for the two species of *C. mandshurica* and *C. heterophylla* with relatively hard seed hull.

### Seed tagging

Experimental mature seeds of last autumn were obtained in the market because they were economic food items. Sound seeds of *C. mandshurica* and *C. heterophylla* were selected and tagged using methods slightly modified from Zhang and Wang (2001). A tiny hole of 0.3 mm in diameter was drilled on the top of each seed with an electrical drill. Seeds were tied with a small, light plastic-tag (length  $\times$  width, 2.5 cm  $\times$  3.5 cm, <0.3 g) through the hole using a thin steel wire 10-cm long, each tag was coded with a serial number for easy identification. When small rodents bury the tagged seeds in the soil, the tags are often left on the ground surface, making them easily re-located. The effects of tagging on seed removal and caching by rodents are neglectable (Zhang and Wang 2001; Forget and Wenny 2005).

### Seed release and seed removal

In 2008, 40 seed stations spaced at 25–30-m apart were established along four transect lines because almost all seeds of *C. mandshurica* and *C. heterophylla* were confined in an area with a radius of

10 m (Yi and Zhang 2008). The first seed release was conducted on 21 July with no seed rain of *C. mandshurica* (pre-period of seed rain). 600 tagged seeds were released at 20 seed stations for *C. mandshurica* and *C. heterophylla*, respectively. The second release of 600 tagged seeds of each species was conducted on 19 August with little seed rain (early period of seed rain), the third release of 600 tagged seeds of each species was conducted on 28 August with large amount of seed rain (peak-period of seed rain), and the fourth release of 600 tagged seeds of each species was conducted on 9 September with little seed rain (end-period of seed rain). The pre-period was taken as control group for comparison with mast seeding group, while the early period, peak-period, and end-period were taken as group of mast seeding. In 2009, the seed release procedure in *C. heterophylla* dominated forest was similar to that in 2008. The seed release date was 21 July, 16 August, 27 August, and 12 September respectively. The same stations were used for all seed releases at different dates unless stations were occupied by previous released seeds when releasing. Then, alternative seed stations were established 10-m far away from the previous ones. After seed release, we searched the area around each station (radius, <20 m) through daily visits with equal efforts of 10 min for two people each visit at the first 10 days, looking for the tagged seeds removed from seed stations and recording seed fates by small mammals. Seed fates of the released seeds in each station were measured as: intact in situ (IS), eaten in situ (EIS); eaten after removal (EAR), intact after removal (on surface) (IAR); cached after removal (in soil) (CAR); missing (in burrow or not seen) (M). According to our observation, missing seeds were mostly moved into burrows and could not develop into seedlings. We pooled EAR, IAR, CAR, and M as removed seeds (R) by small rodents. EIS and EAR were pooled together to be eaten seeds (E) by small rodents. Afterward, seeds remained in stations and cached seeds were checked at regular time intervals. We define the dispersal fitness as the proportion of the survived intact cached seeds by the last survey (30 days after each release) according to Zhang et al. (2008b). The dispersal fitness is calculated as follows:  $F = N_S/N_0$ , here  $F$  denotes the dispersal fitness,  $N_S$  and  $N_0$  represent the total number of survived intact cached seeds at the last survey and the

total number of tagged seeds initially released, respectively. The dispersal distances were measured as the linear length from the center of released stations to the sites where tagged seeds were located.

#### Abundance and species composition of small rodents

In the experimental site, we used live trapping cages (width  $\times$  height  $\times$  length: 9 cm  $\times$  10 cm  $\times$  25 cm) baited with peanuts to investigate small rodent species and their relative abundances. Four transects adjacent to release areas were selected and 40 trap stations were set at 5-m intervals for three consecutive nights before each of seed release tests. The captured animals were measured and then released at the same trapping sites. The trapping procedures were conducted with permission of the Henan University of Science and Technology.

#### Data analyses

Data analyses were performed using SPSS 16.0. Cox regression was used to compare differences of seed removal level from seed stations among the different release periods (in the pre-, early, peak-, and end-periods of seed rain) (Xiao et al. 2005). We emphasized our data interpretation on comparisons of results in pre-period with those in the other three periods for detecting the effects of mast seeding. General Linear Model (GLM), which is more robust than ANOVA to the data distribution, was used to test differences in seed fates (following arc-sin transformation), the total dispersal fitness, and dispersal distances among the four seed release periods. The error distribution was specified using Levene's Test. If the error variance is equal, LSD Test was used, otherwise, Tamhane Test was used. Significant difference in rodent trap success was tested using Chi-square test.

## Results

### Rodent species and abundance

In 2008, a total of 74 animals of three small rodent species were captured over 480 trap-nights including 51 *Apodemus peninsulae*, 18 *Clethrionomys rufocanus*, and 5 *Eutamias sibiricus*. No significant difference

was found in trap success (capture probability of traps, ranged from 10 to 17.5%) among the four surveys on 17 July, 15 August, 25 August, and 5 September ( $\chi^2 = 0.855$ ,  $df = 3$ ,  $P = 0.836$ , Chi-square test). In 2009, a total of 48 animals of three small rodent species were captured over 480 trap-nights including 32 *Apodemus peninsulae*, 13 *Clethrionomys rufocanus*, and 3 *Eutamias sibiricus*. No significant difference was found in trap success among the four surveys ( $\chi^2 = 0.874$ ,  $df = 3$ ,  $P = 0.858$ , Chi-square test).

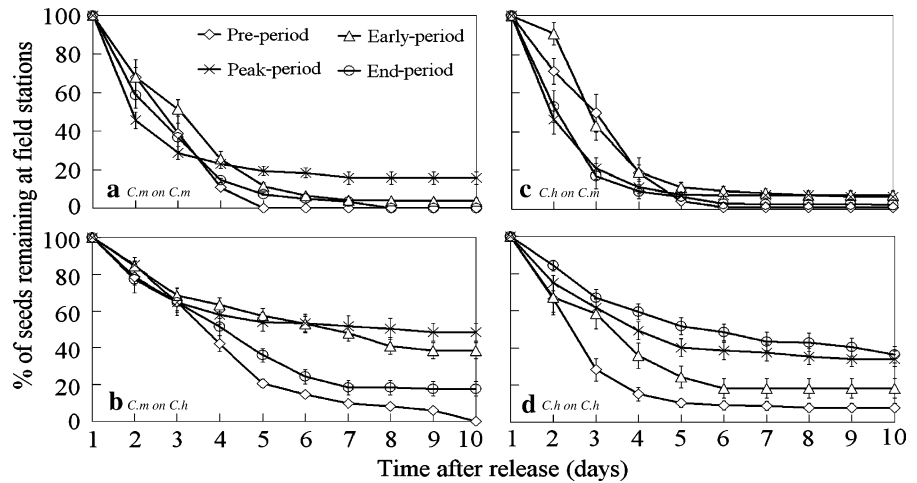
### Seed removal level

Cox regression analysis revealed no significant effects of seed rain of either mast seeding of *C. mandshurica* or *C. heterophylla* on seed removal level of *C. mandshurica* (Wald = 2.550,  $df = 3$ ,  $P = 0.446$ ; Wald = 2.477,  $df = 3$ ,  $P = 0.480$ ) (Fig. 1a, c). However, mast seeding (early, peak-, and end- periods) of *C. mandshurica* tended to decrease removal level of *C. heterophylla* (Wald = 16.770,  $df = 3$ ,  $P = 0.001$ ) (Fig. 1b), while mast seeding of *C. heterophylla* tended to decrease removal level of *C. heterophylla* (Wald = 18.698,  $df = 3$ ,  $P < 0.0001$ ) (Fig. 1d). Seed removal level of *C. heterophylla* in the pre-period seed rain of *C. mandshurica* was significantly higher than those in the early, peak-, and end- periods (Wald = 9.222,  $df = 1$ ,  $P = 0.002$ ; Wald = 8.915,  $df = 1$ ,  $P = 0.003$ ; Wald = 5.117,  $df = 1$ ,  $P = 0.024$ ). Seed removal level of *C. heterophylla* in the pre-period of its own seed rain was significantly higher than those in the early, peak-, and end- periods (Wald = 4.408,  $df = 1$ ,  $P = 0.036$ ; Wald = 6.370,  $df = 1$ ,  $P = 0.012$ ; Wald = 8.521,  $df = 1$ ,  $P = 0.003$ ).

### Seed fates

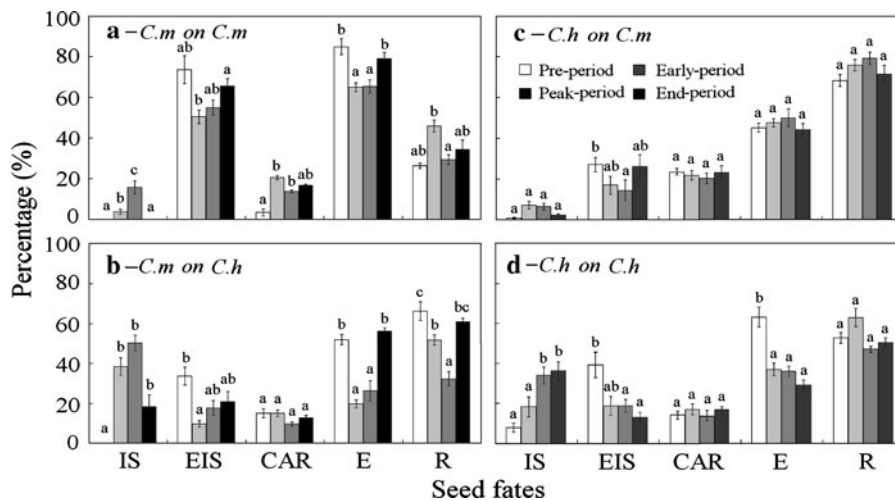
In Fig. 2a, there were significantly more tagged seeds of *C. mandshurica* remained in situ (IS) in the early period ( $P = 0.030$ ) and peak-period ( $P = 0.005$ ); significantly more seeds cached after removal (CAR) in the early period ( $P < 0.0001$ ) and peak-period ( $P = 0.015$ ); but significantly less seed eaten (E) in the early period ( $P < 0.0001$ ) and peak-period ( $P = 0.001$ ) than in pre-period of seed rain of *C. mandshurica*. These results indicated that mast seeding of *C. mandshurica* increased seed caching, but reduced seed removal and seed consumption of *C. mandshurica*.

**Fig. 1** Effects of mast seeding of *C. mandshurica* and *C. heterophylla* on seed removal level of *C. mandshurica* and *C. heterophylla*. Data were expressed as mean ± SE. **a, b** Effect of mast seeding of *C. mandshurica* on *C. mandshurica* and *C. heterophylla*, respectively. **c, d** Effect of mast seeding of *C. heterophylla* on *C. mandshurica* and *C. heterophylla*, respectively



In Fig. 2b, there were significantly more tagged seeds of *C. heterophylla* remained in situ (IS) in the early period ( $P < 0.0001$ ), peak-period ( $P < 0.0001$ ), and end-period ( $P = 0.007$ ); but there was significantly less seed eaten in situ (EIS) in the early period ( $P = 0.002$ ); less seed eaten (E) in the early period ( $P < 0.0001$ ) and peak-period ( $P < 0.0001$ ); less seeds removed (R) in early period ( $P = 0.042$ ) and peak-period ( $P < 0.0001$ ) than in the pre-period of seed rain of *C. mandshurica*. These results indicated that mast seeding of *C. mandshurica* reduced both seed removal and seed consumption of *C. heterophylla*.

In Fig. 2c, there were significantly less tagged seeds eaten in situ (EIS) of *C. mandshurica* in the peak-period ( $P = 0.014$ ) than in the pre-period of seed rain of *C. heterophylla*. In Fig. 2d, there were significantly more tagged seeds remained in situ (IS) of *C. heterophylla* in the peak-period ( $P < 0.0001$ ) and end-period ( $P < 0.0001$ ); but significantly less seeds eaten in situ (EIS) in the peak-period ( $P = 0.041$ ) and end-period ( $P = 0.004$ ); less seeds eaten (E) in the early period ( $P < 0.0001$ ), peak-period ( $P < 0.0001$ ), and end-period ( $P < 0.0001$ ) than in the pre-period of seed rain of *C. heterophylla*. These results indicated



**Fig. 2** Effects of mast seeding of *C. mandshurica* and *C. heterophylla* on seed fates of *C. mandshurica* and *C. heterophylla*. Data were expressed as mean ± SE. **a, b** Effect of mast seeding of *C. mandshurica* on *C. mandshurica* and *C. heterophylla*, respectively. **c, d** Effect of mast seeding of

*C. heterophylla* on *C. mandshurica* and *C. heterophylla*, respectively. Different letters indicate significant differences between seed rain periods according to General Linear Model analyses,  $P < 0.05$ , while bars sharing the same letter do not differ significantly at  $P = 0.05$

that mast seeding of *C. heterophylla* reduced seed consumption of both *C. heterophylla* and *C. mandshurica*, and also reduced seed removal of *C. heterophylla*.

### Dispersal distances

The dispersal distance of tagged seeds of *C. mandshurica* was significantly larger in the early period ( $P = 0.006$ ) than that in the pre-period of seed rain of *C. mandshurica* (Fig. 3a). The dispersal distances of tagged seed of *C. heterophylla* were significantly lower in the peak-period ( $P = 0.044$ ) and end-period ( $P < 0.0001$ ) than that in the pre-period of seed rain of *C. mandshurica* (Fig. 3b). The dispersal distances of tagged seeds of *C. mandshurica* were significantly larger in the early period ( $P < 0.0001$ ), peak-period ( $P < 0.0001$ ), and end-period ( $P < 0.0001$ ) than that in the pre-period of seed rain of *C. heterophylla* (Fig. 3c). The dispersal distances of tagged seeds of *C. heterophylla* were significantly larger in the early period ( $P < 0.0001$ ), peak-period ( $P < 0.0001$ ), and end-period ( $P < 0.0001$ ) than that in the pre-period of seed rain of *C. heterophylla* (Fig. 3d). These results indicated that mast seeding of *C. mandshurica* significantly increased seed dispersal distance of *C. mandshurica*, but reduced seed dispersal distance of *C. heterophylla*, while mast seeding of *C. heterophylla*

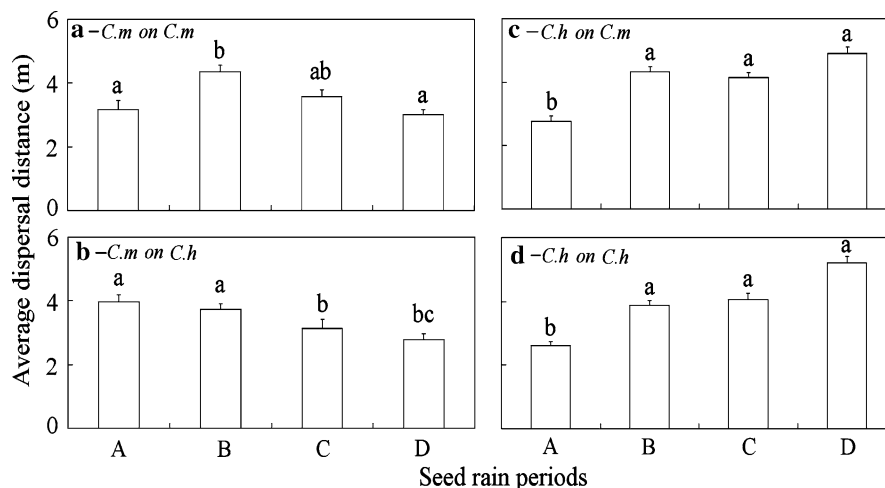
significantly increased seed dispersal distance of both *C. mandshurica* and *C. heterophylla*.

### Dispersal fitness

The dispersal fitness of tagged seeds of *C. mandshurica* was significantly higher in the early period ( $P = 0.044$ ) and peak-period ( $P = 0.002$ ) than that in the pre-period of seed rain of *C. mandshurica* (Fig. 4a). The dispersal fitness of tagged seeds of *C. heterophylla* were significantly higher in the early period ( $P = 0.003$ ) than that in the pre-period of seed rain of *C. mandshurica* (Fig. 4b). The dispersal fitness of tagged seeds of *C. heterophylla* was significantly higher in the peak-period ( $P < 0.0001$ ) than that in the pre-period of seed rain of *C. heterophylla* (Fig. 4d). These results indicated that mast seeding of *C. mandshurica* significantly increased seed dispersal fitness of both *C. mandshurica* and *C. heterophylla*, while mast seeding of *C. heterophylla* only significantly increased seed dispersal fitness of *C. heterophylla*.

### Discussion

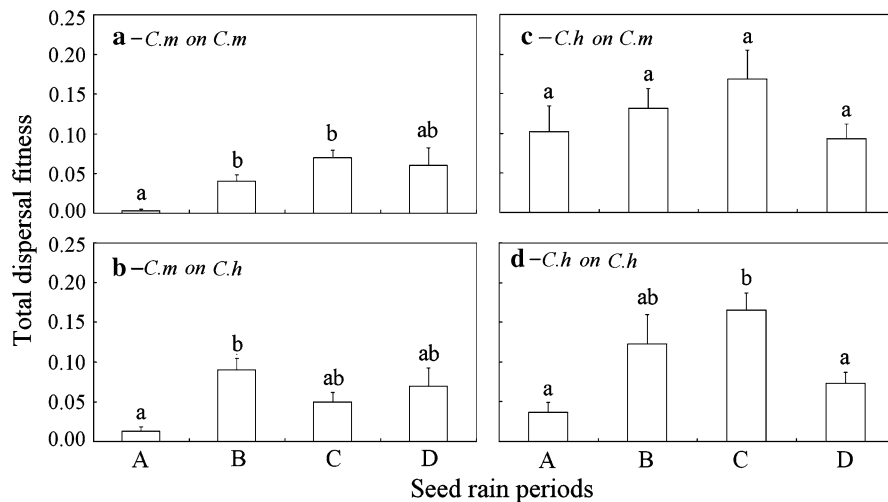
Our results demonstrated that seed masting of both *C. mandshurica* and *C. heterophylla* significantly



**Fig. 3** Effects of mast seeding of *C. mandshurica* and *C. heterophylla* on seed dispersal distance of *C. mandshurica* and *C. heterophylla*. Data were expressed as mean  $\pm$  SE. **a**, **b** Effect of mast seeding of *C. mandshurica* on *C. mandshurica* and *C. heterophylla*, respectively. **c**, **d** Effect of mast seeding of *C. heterophylla* on *C. mandshurica* and *C. heterophylla*,

respectively. Different letters indicate significant differences between seed rain periods according to General Linear Model analyses,  $P < 0.05$ , while bars sharing the same letter do not differ significantly at  $P = 0.05$ . Capital letters A, B, C, and D indicate pre-period, early period, peak-period, and end-period of seed rain, respectively





**Fig. 4** Effects of mast seeding of *C. mandshurica* and *C. heterophylla* on seed dispersal fitness of *C. mandshurica* and *C. heterophylla*. Data were expressed as mean  $\pm$  SE. **a**, **b** Effect of mast seeding of *C. mandshurica* on *C. mandshurica* and *C. heterophylla*, respectively. **c**, **d** Effect of mast seeding of *C. heterophylla* on *C. mandshurica* and *C. heterophylla*,

respectively. Different letters indicate significant differences between seed rain periods according to General Linear Model analyses,  $P < 0.05$ , while bars sharing the same letter do not differ significantly at  $P = 0.05$ . Capital letters A, B, C, and D indicate pre-period, early period, peak-period, and end-period of seed rain, respectively

reduced seed removal of their own released seeds, which is well in agreement with previous studies on the effect of seed masting (Janzen 1971; Crawley and Long 1995; Theimer 2001; Li and Zhang 2007). This observation is well explained by the predator satiation effect that it will take more time for animals to remove sufficient seeds in mast seeding year (Kelly and Sork 2002; Jansen et al. 2004). It is notable that, at inter-specific level, we found mast seeding of *C. mandshurica* reduced seed removal of *C. heterophylla*, but mast seeding of *C. heterophylla* did not significantly reduce seed removal of *C. mandshurica*. This is probably because *C. mandshurica* has higher nutrition and thinner seed hull than *C. heterophylla*, and were more likely harvested by rodents. Our previous studies demonstrated that seeds with hard hull are less selected, and then removed more slowly by rodents (Lu and Zhang 2005a, b; Yi and Zhang 2008; Zhang and Zhang 2008).

Previous studies have demonstrated that seed masting or abundant seeds generally decrease the proportion of seeds eaten (e.g., Vander Wall 2003; Jansen et al. 2004; Xiao et al. 2004; Li and Zhang 2007; Yi and Zhang 2008; Zhang et al. 2008a). Our results indicated that mast seeding of *C. mandshurica* reduced seed consumption of both *C. mandshurica* and *C. heterophylla*, while mast seeding of *C. heterophylla* reduced seed consumption of both

*C. heterophylla* and *C. mandshurica*. The mast seeding effect on seed consumption of the same species observed in this study is well in agreement with that in the previous observations (e.g., Li and Zhang 2007; Zhang et al. 2008a). In this study, we first demonstrate that the inter-specific effect of mast seeding on seed consumption is similar to that intra-specific effect. The mast seeding effect on seed consumption can also be well explained by predator satiation hypothesis.

In this study, we found mast seeding of *C. mandshurica* increased seed caching of *C. mandshurica*, supporting some previous observations that more seeds were cached in masting years (e.g., Jenkins and Peters 1992; Li and Zhang 2007). Animals tend to quickly scatter-hoarded seeds surrounding seed resources in order to sequester and occupy more food resources (Jenkins and Peters 1992). However, we did not detect such significant effect in *C. heterophylla* or the inter-specific effect of mast seeding on seed caching.

Our studies indicated that, at the intra-specific level, mast seeding of both *C. mandshurica* and *C. heterophylla* significantly increased seed dispersal distance of their own seeds, supporting some previous observations (e.g., Stapanian and Smith 1978; Vander Wall 2002; Jansen et al. 2004; Li and Zhang 2007).

However, dispersal distance may be affected by several factors (Brewer and Webb 2001; Theimer 2003; Xiao et al. 2004). A few studies have reported that seeds were moved less far in seed-rich years than in seed-poor years (e.g., Theimer 2001; Jansen et al. 2004; Xiao et al. 2005; Moore et al. 2007). At the inter-specific level, we found mast seeding of *C. mandshurica* significantly reduced seed dispersal distance of *C. heterophylla*, while mast seeding of *C. heterophylla* significantly increased seed dispersal distance of *C. mandshurica*. This is also probably because more nutritional and hull-thinner seeds of *C. mandshurica* were more harvested than *C. heterophylla*, and they negatively affected the dispersal distance of the other species.

We found mast seeding of both *C. mandshurica* and *C. mandshurica* significantly increased seed dispersal fitness of their own seeds, supporting our previous studies (Li and Zhang 2007; Zhang and Zhang 2008). Because decrease in seed consumption and increase in seed caching in masting years, there would be more seeds survived the predation by rodents. This is also well explained by predator satiation hypothesis. At inter-specific level, we found that mast seeding of *C. mandshurica* significantly increased seed dispersal fitness of *C. heterophylla*, while mast seeding of *C. heterophylla* did not significantly increase seed dispersal fitness of *C. mandshurica*. This is likely that *C. mandshurica* seeds with higher nutrition but thinner seed hull are more likely eaten by rodents, which might increase the survival of *C. heterophylla* seeds. While *C. heterophylla* seeds with less nutrition and harder seed hull might not have such positive effect on seed survival of *C. mandshurica* seeds. Therefore, mast seeding may benefit seed dispersal fitness of itself, but may benefit, or not benefit, the seed dispersal fitness of the other species, depending on the seed trait of the focal species.

In summary, at intra-specific level, mast seeding of *C. mandshurica* and *C. heterophylla* significantly decreased seed removal, seed consumption, but increased dispersal distance, seed caching and dispersal fitness of their own seeds. At inter-specific level, the effects of mast seeding were different, probably due to differences in seed traits. Mast seeding of *C. mandshurica* seeds with thinner hull and higher nutrition significantly increased seed dispersal fitness but reduced dispersal distance of *C. heterophylla* seeds with harder hull and lower

nutrition rewards. We conclude that synchrony among species is, or is not, selectively beneficial to the focus species depends on whether one species has fitness gains from masting by the other species.

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