

Dispersal Mechanisms of the Invasive Alien Plant Species Buffalobur (*Solanum rostratum*) in Cold Desert Sites of Northwest China

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Dispersal mechanisms of the alien plant species buffalobur during its invasion of cold desert areas in Xinjiang, northwestern China, were investigated. Seeds and fruits were readily moved by water in irrigation canals in the transition zone between natural desert and a farmed oasis. Maximum flotation time in moving canal water was ~ 4 h for seeds and > 48 h for fruits, and water moved fruits 279 m in 10 min. Also, 100% of the seeds remained viable during 8 wk of flooding in the laboratory. Mean dispersal distance was 3.4 m by wind-driven rolling of detached plants and 0.5 m by ants. Retention time for 50% of fruits on wool of live sheep was ~ 4 h. Seeds and fruits that fall into the canals (which are without irrigation water from mid-October to April) are cold-stratified during winter, and then during canal cleaning in spring soil and germinable seeds are deposited along the sides of the canals. The disturbed soil is a highly favorable site for plants to grow. The local spread of buffalobur away from the sides of canals is facilitated by sheep, wind, and ants. We conclude that water in the irrigation canals is the primary dispersal agent for seeds of this invasive species and that the best way to control its spread is to prevent plants growing beside the canals from setting seed.

Nomenclature: Buffalobur, *Solanum rostratum* Dunal SOLRO.

Key words: Cold desert, invasive species, seed dispersal.

Effective plant dispersal involves the movement of asexual or sexual propagules from the site where the mother plant grows to another site where conditions are suitable for germination, growth, and reproduction (Eriksson 1992; Figueira and Del Sarto 2007; Harper 1977; Nathan 2001). Asexual propagules include tubers, corms, bulbs, bulbils, rhizomes, and ramets, whereas seeds are sexual propagules that may be distributed while retained in fruits or infructescences (i.e., multiple fruits borne on a common stem). Both asexual and sexual propagules can result in rapid proliferation and expansion of individual species. However, only the maternal genotype is dispersed via asexual propagules (Figueira and Del Sarto 2007; Wang et al. 2008), whereas a new combination of maternal and paternal genes is dispersed by sexually produced seeds. Dispersal of sexual propagules may determine the level of gene flow within and among populations, thus affecting adaptation, specialization, and life-history evolution (Arnaud et al. 2003; Dieckmann et al. 1999; Rasmussen and Brodsgaard 1992; Zheng et al. 2004).

Dispersal of propagules can be achieved by wind, water, or animals, and it is a key event in the invasion of alien plants into new geographical regions and in spreading alien species throughout the new region after initial introduction (Kowarik and Säumel 2008; Richardson et al. 2000; Saura-Mas and Lloret 2005). Exotic plants often reach new habitats through intentional or unintentional activities of humans, after which dispersal is facilitated by natural or human-induced conditions such as disturbance (Cohen and Carlton 1998; Myers et al. 2004; Pyšek and Hulme 2005). The method and speed of spread of an alien plant species depend at least partially on the

dispersal capability of propagules (Good 1974; van der Pijl 1982), and dispersal ability is often a good predictor of whether or not an exotic plant will become invasive (Moody and Mack 1988; Neubert and Caswell 2000). Thus, an understanding of the interactions of propagule characteristics, such as propagule morphology/structure, quantity, and longevity, with local environmental conditions potentially will improve predictions of the spread of alien species (Skarpaas and Shea 2007). However, dispersal of an alien plant species into and throughout an area usually has not been documented, and mechanisms of long-distance (to new site) and short-distance (within a site) dispersal are not known.

Buffalobur is native to the Neotropics and southwestern United States, but it is now widely distributed in the Americas, Europe, Asia, Africa, and Australia (Bassett and Munro 1986; Cho and Kim 1997; Wei et al. 2009, 2010). In China, buffalobur was first reported in Liaoning Province in 1982, but currently it occurs in six additional provinces: Jilin, Hebei, Beijing, Shanxi, Xinjiang, and Inner Mongolia (He et al. 2011; Lin and Tan 2007; Wei et al. 2007). Thus, clearly its distribution is increasing in China. Buffalobur is an occasional or abundant annual weed in open disturbed sites such as roadsides, waste dumps, and overgrazed pastures (Bah et al. 2004; Rushing et al. 1985). It has a strong reproductive capability, and up to 7.85×10^4 seeds are produced per plant (Lin and Tan 2007). After dormancy is broken, seeds germinate over a wide range of temperatures in both light/dark and darkness (Wei et al. 2009; Shalimu et al. 2012). Seedlings grow rapidly if soil water is available (Gao et al. 2005).

The invasion of buffalobur into new areas in Xinjiang Uyghur Autonomous Region (hereafter Xinjiang) in northwest China provides a good system to investigate long- and short-distance dispersal mechanisms in this invasive species. Although the number of populations is increasing, it does not yet occur in all the sites that appear to be suitable for its growth. Thus, the broad objective of this study was to gain a better understanding of dispersal characteristics of buffalobur in Xinjiang. Such information would help forecast the potential risk for invasion and formulate appropriate invasion prevention and control strategies. This study addresses the

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following questions: (1) What is the dispersal unit (seed, fruit, or infructescence)? (2) How are these units dispersed, and what are the dispersal distances for different dispersal agents?

Materials and Methods

Study Site. Xinjiang, China, has five distribution areas of buffalobur: Ürümqi County, Changji City, Shihezi City, Turpan City, and Toksun County (Song et al. 2013). Among these areas, the population of buffalobur in the transition zone between natural desert and the farmed oasis of Sangong Town of Changji City is larger than those in other areas and was selected for this study. The study site is located in the southern suburbs of Changji City (43.52°N, 87.09°E, 790 m above sea level) and has a typical cold desert climate with a mean annual temperature of 7 °C (1971 to 2000, Yang and Wang 2007). Mean temperatures of the coldest (January) and hottest (July) months are -15 and 25 °C, respectively. Average annual precipitation including both rain and snow is 194 mm, and the smallest (January) and largest (May) amounts of monthly precipitation are 7 mm and 25 mm, respectively (Shalimu et al. 2012). The type of soil at the study site is gray desert soil (Agricultural Bureau of Uygur Autonomous Region of Xinjiang, Soil Survey Office of Uygur Autonomous Region of Xinjiang 1996).

Two main irrigation canals provide water for farmlands in the study site. They are nearly parallel to each other and straight, and the distance between them is about 7 to 10 m. The width of the two canals is about 2 m, the slope of both sides is almost 90°, and the bed contains sand particles with diameters of 0.5 to 2 mm. The irrigation water in the canals comes from the same diversion point of the Toutun River and is intermittently present from early April to mid-October. During the rest of the year, the only water in the canals is from rain or snow. Water in both canals is turbid, and water flow rate was about 0.45 m s⁻¹ during our experimental period. Water depth in both canals is about 15 cm and 20 cm. Buffalobur is distributed along both sides of the canals, and its main plant associates include *Heliotropium ellipticum* Ledeb., harmel (*Peganum harmala* L.), prostrate knotweed (*Polygonum aviculare* L.), *Salsola affinis* CA Mey., *Salsola brachiata* Pall., spiny cocklebur (*Xanthium spinosum* L.), and siberia cocklebur (*Xanthium sibiricum* Patr. ex Widd.).

Livestock, mostly sheep but also cattle and camels, are present in the study site from early April to late November. The animals graze up to 3 km away from the canals and come to them at noon and at night, when they drink water and eat the tender leaves but not the fruits of buffalobur. The rodents grey hamster (*Cricetulus migratorius* Pall.), *Meriones erythrumus* Gray, house mouse (*Mus musculus* L.), and brown rat (*Rattus norvegicus* Berkenhout) have been reported in the study site (Li et al. 1991). In our field surveys, seven ant species including *Cataglyphis aenescens* Nyl., red barbed ant (*Formica rufibarbis* F.), *Formica cunicularia* Latr., *Messor clivorum* Ruzs., *Preformica epinotalis* K.-Ug., pavement ant (*Tetramorium caespitum* L.), and *Tetramorium turcomanicum* Emery and an unidentified lizard species also were found in the study site; no birds were observed during our field observation period.

Study Species. Buffalobur is a summer annual plant. In the study site, seeds usually germinate from late April to June, and

plants flower from mid-May to mid-October. Mean plant height is 43 ± 1 cm ($n = 100$), and except for flowers the whole plant is covered by sharp spines (1.08 ± 0.05 cm long, $n = 30$). Stems are erect, and they are extensively branched and slightly lignified near the base. The fruit is a berry that is spherical, and it is green when immature but turns brown or black as it matures. Berries ripen from late September to early October, at which time they are 1.11 ± 0.02 cm ($n = 30$) in diameter. The spiny calyx that covers a berry gradually dehydrates and becomes hard and splits open as plants dry. There are 65 ± 2 seeds per fruit ($n = 30$), and seeds are black, 2.5 to 3.1 mm long and 1.9 to 2.8 mm wide. Mass of 100 seeds is 0.33 ± 0.06 g ($n = 10$).

In the study site, buffalobur grows in the farmland fields of cotton, corn, watermelon, sunflower, and other crops and on both sides of the canals, as well as in farmland adjacent to small canals that flow from main canals. It is abundant in loose soil that is piled along the sides of canals when they are cleaned.

Wind Dispersal. Seed dispersal of buffalobur mainly occurs in October and November, when the spiny calyx opens. Further, some whole plants or branches may be dislodged when the wind blows, and thus fruits, seeds, branches, and plants are scattered on the soil surface (Gunn and Gaffney 1974; Wei et al. 2009) or into the main irrigation canals. To estimate the frequency of whole-plant detachment and the distance they were moved by wind during the dispersal period, 100 randomly selected buffalobur plants were marked by tying red strings on them on October 10, 2009, and a number was fixed to the top and to the bottom of each plant. On April 25, 2010, before seed germination began, the number of broken stems was recorded. If the broken piece of stem could be found, the distance it had been moved by wind was measured and recorded.

Water Dispersal. Flotation in Canal. Because the two main irrigation canals are very similar (see study site subsection above), only one main canal was selected for this experiment. On October 10, 2011, 150 seeds and 150 fruits with seeds in them each were subdivided into five replicates of 30 and used in field trials to determine duration of floating in canal water. Five mesh baskets were fixed in the water at mid-canal, and then seeds and fruits were placed on the water surface in the basket to determine flotation capacity of seeds and fruits. Number of floating seeds and fruits was counted every 30 min for 12 h and then at 12-h intervals until 48 h from the beginning of the experiment or until all propagules sank. In another floating trial, 15 fruits of buffalobur were selected and put in the middle of the canal on the water surface. After 10 min, the distance fruits had floated on the water was measured. One-way ANOVA was used to assess statistical differences among treatments, and means were compared using Tukey post hoc tests.

Flotation in Laboratory. This experiment was conducted on October 15, 2011 following the method of Truscott et al. (2006). Fifty freshly collected seeds were placed in each of 15 200-ml beakers containing 100 ml of canal water. Beakers were allocated at random to one of three shaker speeds (rpm), 50 min⁻¹, 100 min⁻¹, and 150 min⁻¹, to reduce the influence of surface tension and to simulate water movement.

Seeds were exposed to each speed for 96 h. The number of floating seeds was counted after 1, 2, 4, and 8 h and then at 8-h intervals until 96 h from the beginning of the experiment. The effects of water agitation on seed flotation were compared using a two-way ANOVA, with observation time and shaker speed as main effects.

Influence of Submergence Time on Seed Germination. The method of Kowarik and Säumel (2008) was followed for this simulation experiment. Two thousand seeds were placed in each of four beakers and covered with distilled water to a depth of 15 cm (100 ml) for 0 (control) and 8 wk at room temperature. To facilitate oxygen exchange of water in beakers, each beaker was shaken five times each day at a shaker speed (rpm) of 100 min^{-1} for 5 min. Water in each beaker was replaced daily. After treatment, four replicates of 25 seeds each were incubated in Petri dishes on two sheets of filter paper moistened with distilled water at four temperature regimes (15/2, 20/10, 25/15, and 30/15 C) in cool white fluorescent light (light = 12 h each day, ca. $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$, 400–700 nm) for 28 d. At the end of the experiment, nongerminated seeds were checked for germination (viability) by incubating them in Petri dishes on two sheets of water-moistened filter paper at the same temperature regime at which they were incubated for 14 d. One-way ANOVA was used to assess statistical differences among time and temperature treatments, and mean comparisons were made using Tukey post hoc tests.

Livestock Dispersal. Diaspore Attachment to Sheep Dummy. This experiment was conducted on October 5 and November 5, 2010 following the method of Mouissie et al. (2005). A sheep dummy was used to investigate the kinds and numbers of diaspores likely to be dispersed by sheep. The size of dummy sheep skin was the same as that of adult sheep moving in the study site. Thirty experimental field plots, each 1 m wide by 15 m long, were established in a buffalobur population that was 2 m wide and 530 m in length. A piece of polyvinyl chloride tube 1 m long and 16 cm in diameter was covered with 9-cm-thick sheep wool held in place with thin wire. The sheep dummy was attached to a bicycle in a horizontal position at a height of 40 cm. Then, the bicycle was pushed through each plot at a speed of $\approx 3.6 \text{ km h}^{-1}$, after which all diaspores were removed from the wool and counted.

Seed density in each of the 30 1-m by 15-m plots was estimated using 10 1-m by 1-m subplots that were randomly located in each of the above 1-m by 15-m field plots. First, we counted the number of infructescences in each subplot. Next, 10 infructescences were randomly selected, and the number of fruits in each infructescence was counted and then averaged. Finally, 10 fruits were randomly selected, and the number of seeds in each fruit was counted and then averaged. The number of seeds in each subplot was the mean numbers of seeds per fruit by mean number of fruits per infructescence by number of infructescences. The mean number of seeds in all 10 subplots was used to estimate seed density for each of the 30 1-m by 15-m plots. Attachment probability of seeds, fruits, or infructescences in a 1-m^2 area (P_{attach}) was calculated as

$$P_{\text{attach}} = D_f / D_v \quad [1]$$

where D_f is the number of seeds, fruits, or infructescences found in 1 m^2 of fur. In our study, however, seeds, fruits, or

infructescences in the 1 m^2 of fur were collected after pushing the sheep dummy in the 15-m by 1-m plots. Thus, mean number of seeds, fruits, or infructescences in a 1-m by 1-m area was equal to 1/15 of the total number. D_v is the seed, fruit, or infructescence density in 1 m^2 of vegetation. One-way ANOVA was used to assess statistical differences among fruits and infructescences, and mean comparisons were made using Tukey post hoc tests. The relationship between the number of seeds attached to the sheep dummies and seed density in the vegetation was tested using linear regression models.

Retention Time. To investigate retention time of infructescences and fruits on the wool of live sheep, we followed the method of Eichberg et al. (2005). On November 6, 2010, 50 buffalobur fruits or 50 infructescences were gently pressed onto the wool of each of five sheep with a wool depth of 8 to 11 cm. Then, the sheep were allowed to walk around in an open area where no shrubs grew. Retention time was determined by counting the number of fruits and infructescences remaining in the wool at 1-h intervals until all of them had become detached. One-way ANOVA was used to assess statistical differences among treatments, and mean comparisons were made using Tukey post hoc tests.

Feces. Only one herd of livestock, consisting of sheep, cattle, and camels, grazed in the study site, and the animals never were observed feeding on the fruits of buffalobur. To further determine if seeds were passed through animals, 2000 piles of feces for sheep and 500 piles each for cattle and camels were collected at three field locations in the study site on November 7, 2010. In the laboratory, each pile of feces was examined to determine the number of buffalobur seeds present. During the entire period of time livestock were grazing the area, buffalobur fruits from the previous year were readily available; in addition, new plants were produced. Thus, seeds and fruits were available for livestock consumption.

Ant Dispersal. Our field observations indicated that of the seven ant species in the study site, only *M. clivorum* dispersed the seeds of buffalobur. To determine the distance that *M. clivorum* move buffalobur seeds, we followed ants of this species naturally dispersing seeds from the site where they collected a seed back to their nest. Then, we measured the distance that seeds had been moved by ants with a tape measure (Leal et al. 2007; Zhang 2006). Observations were made from 10:30 A.M. to 7:30 P.M. for three consecutive days, starting October 3, 2009, at each of three field locations. After seeds are dispersed by ants, they may be completely or partly predated, or they may not be damaged at all. To learn more about how *M. clivorum* interacts with buffalobur seeds, a study was conducted in a field where no buffalobur plants occurred. One thousand intact seeds (five replications \times 200 seeds per replication) were placed on the soil surface and covered with a screened cage to prevent rodents, birds, and other seed predators from removing seeds but allowed ants free access to the seeds. The number of seeds removed by ants was determined after 2 d. We also assessed the fate of these ant-removed seeds. At 1-wk intervals for 2 wk after introduction of buffalobur seeds, we surveyed all ant mounds in the area to determine if buffalobur seeds were present on the soil surface. If seeds were present, we examined them for evidence of predation.

Dispersal of Rodents, Birds, and Other Animals. To further determine if rodents or birds transport seeds of buffalobur, 50 seeds were placed on a white-board (12 cm by 14 cm) seed tray. The white board was painted around the edges with sticky liquid glue to prevent ants from removing seeds. However, the glue did not prevent rodents or birds from removing seeds. Observations were made at 7:00 A.M. and 7:00 P.M. for three consecutive days, starting October 9, 2009, and the number of seeds removed was recorded. Ten white boards were located at each of three field locations. To determine if other animals such as lizards dispersed seeds, the same board (with glue around the edges to prevent ants from taking the seeds) was covered with a screen to prevent rodents and birds from removing seeds.

Data Analysis. Data were analyzed using SPSS for Windows, Version 16.0 (SPSS Inc., Chicago, IL 60606). All data were analyzed for normality and homogeneity of variance before analysis, and if normal and homogeneous they were subjected to further analysis. If data exhibited nonnormal distribution or if variances were not homogeneous, they were \log_{10} or square-root transformed before analysis to ensure homogeneity of variance. Significant differences among treatment means were identified by Tukey's test at the 0.05 level of significance.

Results and Discussion

Wind Dispersal of Detached Plants. On April 25, 2010, 67 of the 100 plants marked in autumn 2009 were located in the study site. Thirty-eight of the 67 plants (57%) did not have a broken stem and were still present in situ. Twenty-six of the 29 (43%) plants that had become detached from stems were still present along the canal, but three were found in the canal ~ 240 m away from where they had grown the previous summer. Because the three plants in the canal may have been transported by water, we did not use them to compute the average distance that detached plants were moved by wind. Thus, for the 26 plants that had been dispersed by wind, average dispersal distance was 3.4 ± 0.8 m with a range of 0.1 to 14.9 m. Each of these plants acted as a "tumbleweed," a phenomenon in which the dead plant breaks near the base and is rolled by the wind. As plants roll across the landscape, seeds fall from them (Borger et al. 2007; Mehlman 1993; Stallings et al. 1995). Rolling of detached buffalobur plants across the landscape by wind greatly increases seed dispersal distance compared with seeds falling from stationary plants.

Water Dispersal. Flotation in Canal. In the first floating trial, all fruits were still floating on the water surface in the canal after 48 h, when the experiment ended, whereas only 51 ± 2 , 29 ± 6 and $13 \pm 6\%$ of seeds floated for 1, 2, and 3 h, respectively (Figure 1A). Mean dispersal distance of fruits allowed to disperse on canal water for 10 min was 279 ± 2 m ($n = 15$). These results and the frequent occurrence of buffalobur populations along irrigation canals in Xinjiang suggest the potential for seed dispersal by water.

Flotation in Laboratory. In the 96-h seed buoyancy trials, there was a significant time-by-treatment interaction ($P < 0.001$). The proportion of seeds that remained floating in the 150 rpm/min shaker treatment was lower than that for both the

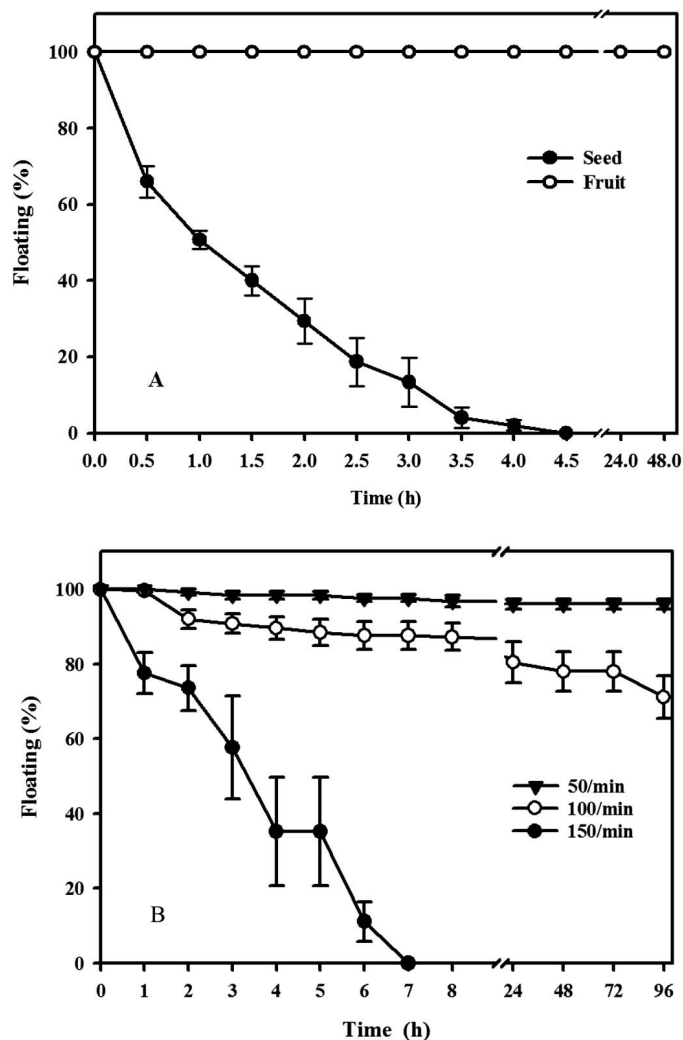


Figure 1. Ability of fruits and seeds to float on canal water in the field (A) and on canal water agitated at various speeds (rpm/min) in the laboratory (B).

100 rpm/min ($P < 0.001$) and 50 rpm/min treatments ($P < 0.001$) at each time interval (Figure 1B), and the 100 rpm/min and 50 rpm/min treatments also were different ($P = 0.026$). In contrast, all fruits were still floating after 96 h for all three shaker treatments.

Water turbulence also affects seed flotation time, and in the laboratory flotation time increased as the rate of water agitation decreased. On the other hand, all fruits placed in the canal were still floating after 48 h, and all fruits remained floating after 96 h in the laboratory shaker experiments regardless of the shaker speed. Thus, both seeds and fruits could be moved relatively long distances by flowing water in canals with fruits having the potential to be moved farther than seeds.

Influence of Submergence Time on Seed Germination. Seeds submerged in distilled water for 8 wk germinated to only 0, 5 ± 2 , 0, and 0% after 8 wk of incubation at 15/5, 20/10, 25/15, and 30/15 C, respectively. However, nongerminated seeds were viable and thus germinated to 100% at all four temperature regimes after they were scarified.

From mid-October to April, water does not move through the canals, and any seeds and fruits that fall into the water during autumn overwinter in the moist soil at the canal

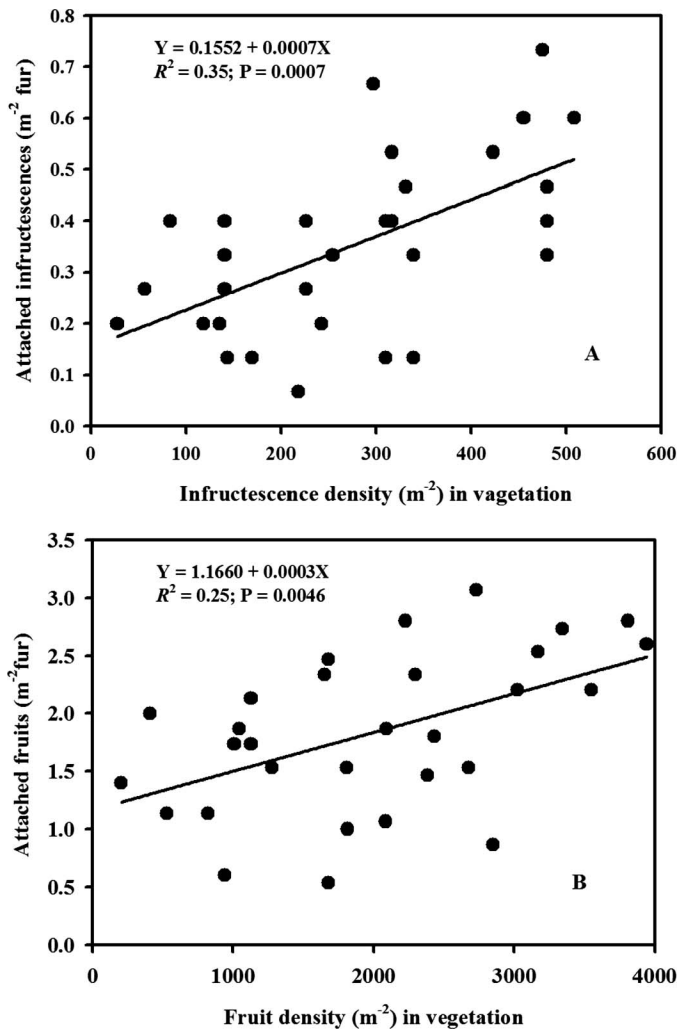


Figure 2. Number of infructescences (A) and fruits (B) that became attached to wool of a sheep dummy in relation to density of infructescences/fruits in natural buffalobur populations.

bottom. Seeds in the moist but nonflooded environment at the canal bottom would be cold-stratified during winter and thus should be ready to germinate in spring (Shalimu et al. 2012). In some years, canals are “cleaned” in early spring, and soil containing buffalobur seeds from the canal bottom is piled beside the canal. Consequently, nondormant seeds of buffalobur are placed alongside the canal, where they can readily germinate and grow in the freshly disturbed soil. Thus, canals potentially are not only an important agent of long-distance dispersal within the farming region, but the practice of removing soil from canals helps explain why dense populations of buffalobur are found beside canals.

Livestock Dispersal. *Diaspore Attachment to Sheep Dummy.* The mean number of fruits and infructescences attached to the wool of the sheep dummy after it was pushed through the 30 1-m by 15-m plots was 27.5 ± 1.9 ($n = 30$) and 5.2 ± 0.5 ($n = 30$), respectively. Estimated mean attachment probability (P_{attach}) of fruits and infructescences in the 30 1-m by 15-m plots was $1.7 \pm 0.3 \times 10^{-3}$ ($n = 30$) and $1.3 \pm 0.2 \times 10^{-3}$ ($n = 30$), respectively. Fruit and infructescence attachment to the sheep dummy was positively correlated to their density at the site (Figure 2).

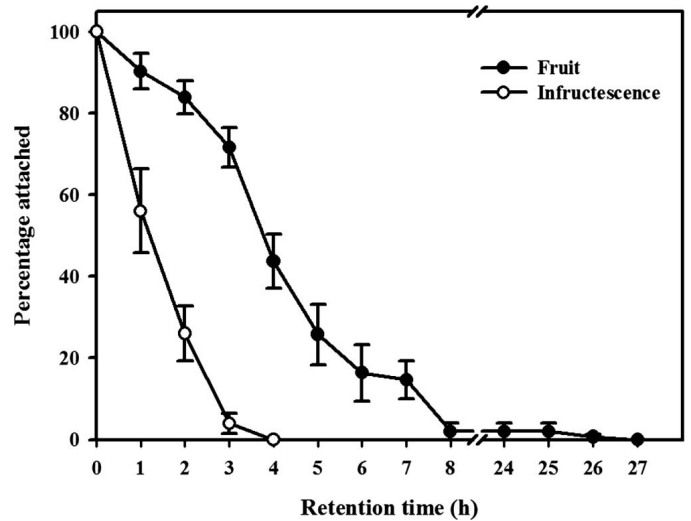


Figure 3. Depletion curves for retention time of infructescences and fruits in the wool of sheep.

Retention Time. Infructescences remained attached to moving sheep for a shorter period of time than fruits (Figure 3). On average, 50% of infructescences were lost in a little over 1 h, and ~ 50% of fruits were lost in a little less than 4 h. No infructescences were retained in wool for > 4 h. About 90% of the fruits were lost from the sheep’s wool within 6 h, but it took another 21 h for the remaining 10% of the fruits to become detached. One animal shook its body soon after reaching the paddock, causing a high portion of the fruits and infructescences to fall out. Infructescences and fruits also were lost from the wool due to contact between animals (e.g., during aggressive behavior) and through contact with the ground (e.g., lying or rolling on the ground).

Dispersal of seeds via attachment of fruits (and to some extent infructescences) to the wool of sheep appears to be an effective means of dispersal. Fruits more readily attached to wool than did infructescences, and they remained attached for longer periods of time. Approximately half of fruits placed on sheep were still on the animal after 4 h, and maximum retention time of fruits on sheep was 27 h, during which time a sheep potentially could walk a long distance or wander extensively back and forth over the same area. Seed dispersal of other plant species by sheep also has resulted in both short- and long-distance dispersal (Constible et al. 2005; Knight 1985).

Feces. No seeds of buffalobur were found in feces of sheep, cattle, or camels collected from natural habitats. Because fecal material from these animals did not contain any buffalobur seeds or seed fragments, they either did not eat the fruits, or seeds that were eaten were completely destroyed in the animal’s digestive system. Although we cannot definitively rule out complete digestion, buffalobur seeds are small and have firm seed coats, and seeds of other species with similar size and seed coat characteristics typically pass through the digestive system of livestock relatively intact (Ramos et al. 2006). Furthermore, neither rodents, birds, nor any other animal removed seeds from trays placed in the field. In contrast, fruits of other Solanaceae species are known to be eaten and dispersed by animals. For example, bittersweet nightshade (*Solanum dulcamara* L.) seeds are dispersed by

birds, mammals, and deer (Kollmann and Pirl 1995; White and Stiles 1992); *Solanum thomasiifolium* Sendtner seeds by birds, crab-eating foxes, lizards, and ants (Vasconcellos-Neto et al. 2009); and wolf apple (*Solanum lycocarpum* St. Hil.) seeds by maned wolf (Lombardi and Junior 1993). The presence of the spiny calyx around fruits of buffalobur probably is the reason why sheep, cattle, and camels do not eat them. In fact, sheep that were offered green branches of buffalobur touched the plant material once but did not attempt to eat it. Thus, dispersal of buffalobur seeds is not facilitated by animals eating fruits and then depositing seeds at new locations in their feces.

Ants, Rodents, and Other Animal Dispersers. Dispersal distance of seeds moved by the ant *M. clivorum* ranged from 0.1 to 2.43 m, with 91% of seeds carried a distance of 0.1 to 0.71 m; mean dispersal distance was 0.48 ± 0.02 m ($n = 559$). During the 2-d ant-dispersal studies, ants took 992 (99 \pm 1%) of the 1000 intact seeds provided to them. After 1 and 2 wk, we retrieved $13 \pm 3\%$ and $22 \pm 3\%$ of the seeds, respectively, from around ant mounds. All of these retrieved seeds were intact and did not show any evidence of predation. We did not observe birds or rodents removing seeds from where we placed them, and no seeds were removed from the white-board seed trays with glue around the edges to prevent ant dispersal and a screened cage over the top to prevent rodent/bird dispersal.

Although many buffalobur seeds were collected by *M. clivorum*, mean dispersal distance was only 0.48 m. Thus, ant dispersal of seeds cannot account for long-distance dispersal of buffalobur. However, ants may affect local seed dispersal. First, $\sim 44\%$ of the seeds collected by ants subsequently were found near their nests, which likely increases the size of seed banks near ant mounds. Second, although we do not definitively know the fate of the remaining 56% of seeds collected by ants, another potential impact of ants may be to temporarily remove a portion of buffalobur seeds from the active seed bank and place them in sites safe from seed consumers. Thus, ants potentially alter the degree of seed aggregation, move seeds to nutrient-rich areas, and facilitate escape from predation and other hazards (Christian and Stanton 2004; Dean and Yeaton 1992; Holmes 1990; Moody and Mack 1988).

The first step in development of a new population of a species is movement of propagules to the new site. If a species has successfully invaded a new habitat, it obviously has an adequate dispersal mechanism to do so. However, we often know little about the dynamics of dispersal and see only the final result, i.e., a well-established, new population of plants. Clearly, buffalobur is invading new territory in Xinjiang, China, and our studies provide some insight into how this species is expanding.

Invasive plant species need to be capable of both long- and short-distance dispersal, with long-distance dispersal taking the species to new sites and short-distance dispersal filling the site with plants (Baker 1974; Pyšek et al. 2008). For buffalobur in the San Gong farming region of Xinjiang, the ability of fruits to float for at least several days and ability of seeds to tolerate flooding suggest that water dispersal is a likely mechanism for long-distance dispersal to new locations along irrigation canals and other waterways in the region. Long-distance dispersal on animal fur also is likely to occur as

animals move to waterways to drink, catch fruits in their fur, and then move away from the waterway to forage. Because flotation time for fruits is much greater than retention time in wool, one may conclude that waterways are more important for long-distance dispersal than are livestock in the farming region. However, the spread of buffalobur from Liaoning Province to other provinces in China (He et al. 2011; Wei et al. 2007) logically cannot be attributed to waterway dispersal. One possibility for buffalobur dispersal from one province to another is that humans transported sheep with buffalobur fruits in their wool.

In conclusion, the continuous spread of buffalobur in China since 1982 confirms that this exotic species has high invasive potential. Our studies on dispersal mechanisms of buffalobur indicate that this species has multiple ways to facilitate both long- and short-distance dispersal. However, to control the invasion of exotic species, the best time to use control techniques is when the species first appears in an area, i.e., after long-distance dispersal (Lin and Tan 2007). If an exotic plant is not eradicated when it first appears in an area, short-distance dispersal will begin to occur, and the population may become very large and difficult (perhaps impossible) to control. In the case of buffalobur in the San Gong region of Xinjiang, water appears to be the primary long-distance dispersal agent, with sheep, wind/gravity, and ants moving the seeds within sites. Thus, the best chance of controlling the spread of this species is to prevent plants growing along canals from setting seeds. After local dispersal via sheep, ants, and wind begins to occur, populations can quickly become too large to be easily controlled.

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