



## Original article

# A herbivory-induced increase in the proportion of floating seeds in an invasive plant



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## ABSTRACT

It is important to determine the factors prompting seed dispersal because for plant species seed dispersal is the only opportunity to disperse into a new habitat. Previous studies showed that the maternal stress, such as high density and low nutrient levels, induces the adaptive plastic increase of the dispersal ability in seed heteromorphic plants. In this study, we examined whether herbivory can change the relative proportion of dispersal-related seed heteromorphism (floating or non floating seeds) in an invasive weed *Ambrosia artemisiifolia*. Because *A. artemisiifolia* often distributes in the riparian habitat, floating seeds might contribute to the long distance dispersal by hydrochory. Floating ability and seed weight were compared between plants damaged by a specialist herbivore *Ophraella communa* and undamaged plants. The damaged plants produced lighter and more likely floating seeds than the undamaged plants. However, multi-regression analysis revealed that the probability of floating was affected by seed weight but was not affected by herbivore treatment (damaged vs. undamaged plants). These results suggest that the increased proportion of floating seeds was not a direct response to the herbivore signal but an indirect response through the herbivore's effect on the reduction of seed weight. Plants damaged by herbivores might not only decrease seed production and quality but also increase the dispersal ability. These responses in dispersal ability against the herbivores might contribute to the spread of invasive plants.

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## 1. Introduction

Dispersal is a key process for understanding the colonization, gene flow and population dynamics. In plant species, the seed offers the only opportunity to disperse into a new habitat. Hence it is important to investigate environmental factors affecting the seed dispersal ability of plants. For example, abiotic environmental gradients, types and abundance of seed dispersal vectors, and seed predators can influence seed dispersal (Howe and Smallwood, 1982; Nathan and Muller-Landau, 2000; Ozinga et al., 2004). Maternal experiences may also change the seed dispersal ability. Several theoretical studies predicted that plants in stressful conditions could facilitate seed dispersal, when the stressful condition for mother plant is associated with those for the condition for the progeny (Levin et al., 1984; McPeck and Holt, 1992).

Several studies showed that stressful condition change the seed dispersal ability in plants that possess seed heteromorphism (the

production of different types of seeds by a single individual). For example, Baker and O'Dowd (1982) showed that *Hypochoeris glabra* (Asteraceae) increase the proportion of peripheral achenes over central achenes in response to an increasing maternal density. They suggested that the plastic change in the proportion of peripheral achenes contributes to the increased dispersal distance because peripheral achenes appear to have greater dispersal ability than central achenes in this species. Imbert and Ronce (2001) also found that low nutrient levels induce the increased proportion of central achenes in *Crepis sancta*. Central achenes provide a greater dispersal ability than peripheral achenes in this species. They suggested that the increased proportion of central achenes in *C. sancta* were induced by the low nutrient condition as an adaptive phenotypic change to disperse seeds away from mother plants.

In addition to the high density and low nutrient levels, herbivory is another major stressful condition for plants. The damage caused by herbivores could therefore induce the increased seed dispersal ability in order to disperse the seeds further away from mother plants. Until now, however, a few studies have examined the effect of herbivory on plastic change in the seed dispersal

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related characters (Imbert and Ronce, 2001; Weinig et al., 2003). Here, we assess the effect of herbivory on the dispersal-related seed heteromorphism in an invasive weed *Ambrosia artemisiifolia*.

*A. artemisiifolia* (Asteraceae) is an annual, wind pollinated weed, native to North America (Bassett and Crompton, 1975). It grows in open, disturbed habitats such as wastelands, roadsides, or riverbanks (Bassett and Crompton, 1975; Friedman and Barrett, 2008). *A. artemisiifolia* exhibits seed heteromorphism: floating and non-floating seed (Fumanal et al., 2007). A proportion of *A. artemisiifolia* seeds are able to float from less than 1 h to 12 h and the rest sink down immediately (Fumanal et al., 2007). Floating seeds are lighter, and more dormant than non-floating seeds. In the non-dormant seeds, floating seeds germinated faster than non-floating seeds (Fumanal et al., 2007). However, there are no particular morphological differences between floating and non-floating seeds. In riparian and aquatic plants, floating seeds can be dispersed over long distances by the river flow, while non-floating seeds may be moved only marginally from the parent (Williamson et al., 1999; Pollux et al., 2009). Although seed of *A. artemisiifolia* have been dispersed by human activities such as transportation of seed-contaminated soil (Bassett and Crompton, 1975), hydrochory could also play a key role in the colonization process because many populations are found in riversides (Bassett and Crompton, 1975; Fumanal et al., 2007). Therefore, the ability to float in this species probably contributes to the long-distance seed dispersal by hydrochory.

Seed dispersal ability can be closely related to the invasiveness of introduced plants. In the process of plant invasion, seed dispersal is often a key process because invasive plants spread rapidly to new sites by long-distance seed dispersal (Lonsdale, 1993; Myers et al., 2004; Von der Lippe and Kowarik, 2007). To understand the spread of invasive species, it is important to investigate environmental factors affecting the seed dispersal. *A. artemisiifolia* is one of the most invasive plants introduced in Japan. From 1890's to 1950, they spread throughout the Japanese islands (Hisauchi, 1950). The Japanese populations of *A. artemisiifolia* have suffered severe damage by accidentally introduced native specialist herbivore *Ophraella communa* (Coleoptera: Chrysomelidae) since 1996 (Fukano and Doi, 2013; Miyatake and Ohno, 2010; Yamazaki et al., 2000). Herbivory by *O. communa* for mother plants of *A. artemisiifolia* may be associated with the herbivory for their neighbor progeny because *O. communa* spend all their life stages on the host plant and decrease their flight activity before diapauses (Tanaka and Yamanaka, 2009). Therefore, *A. artemisiifolia* may produce more floating seeds in response to herbivory by *O. communa* as an adaptive phenotypic change to disperse seeds away from the mother plant. Alternatively, the increase of floating seeds could be induced by the developmental constraint caused by herbivory. Herbivory by *O. communa* decreases the total seed production of *A. artemisiifolia* (Fukano et al., 2013). If herbivory decreases seed weight, the proportion of floating seeds can increase indirectly because floating seeds are lighter than non-floating seeds (Fumanal et al., 2007). Irrespective of the proximate mechanism (a direct response to herbivory or an indirect effect of decreased seed weight), the increase of floating seeds may contribute to the long-distance dispersal and invasiveness of *A. artemisiifolia*.

We examined whether *A. artemisiifolia* increase the proportion of floating seeds in response to herbivory by *O. communa*. We also investigated the proximal mechanism of the change of floatability. Specifically we asked the following questions. 1) Do damaged plants by *O. communa* increase the proportion of floating seeds relative to undamaged plants? 2) What factors (herbivore, seed weight, and maternal characters such as those mentioned by Donohue (1999)) are the main causes of the change in the proportion of floating seeds?

## 2. Materials and methods

### 2.1. Study species

Common ragweed, *A. artemisiifolia*, native to North America, is an invasive weed in many places in the world (Gaudeul et al., 2011). It germinates in spring and produces seeds in late summer. This invasive plant has a high seed production (up to 60,000) (Bassett and Crompton, 1975). *A. artemisiifolia* is particularly problematic because its wind-dispersed pollen can cause serious allergic responses (Meggs et al., 1996).

Ragweed beetle *O. communa* (Chrysomelidae) is also native to North America and was accidentally introduced to Chiba prefecture, Japan in 1996 (Takizawa et al., 1999). In Japan, *O. communa* is the only specialist herbivorous species of *A. artemisiifolia* (Yamazaki et al., 2000; Miyatake and Ohno, 2010). They consume leaves and reproductive organs but not seeds.

### 2.2. Field experiment and seeds collection

We used seeds of *A. artemisiifolia* collected from a previous study (Fukano et al., 2013). In the previous study, we germinated stocked seeds that were collected in 1998, 2000, 2002, 2006, and 2009. The collection year has no effect on the seed characteristics in this study. When seedlings had grown to approximately 10 cm height, we randomly selected and planted some of them into a plastic flowerpot filled with 3 L of garden soil. The transplanted seedlings were allocated randomly to one of 16 blocks of 20 m × 40 m in the experimental field of the National Institute for Agro-Environment Science (Tsukuba, Japan). Each block (4 m × 4 m) containing 5 × 5 plants was placed at a distance of 80 cm from each other. Half of the 16 blocks were sprayed with a dichlorvos insecticide (produced by Hokko Chemical Industry Co. Ltd, Japan) twice a month to prevent herbivory by *O. communa*. The other eight blocks were not sprayed. Plants were watered every two or three days. The percentage of consumed leaf area was estimated every ten days by eye in 10% increments. After seed maturation we recorded plant height and harvested infructescences of all plants. Harvested infructescences were dried in a green house for a month. Finally, we collected and counted the number of seeds per plant by seed counter (waver series IC-VA, AIDEX, co., LTD., Nagoya, Japan). Collected seeds were stocked at room temperature.

### 2.3. Floating experiment

Following the procedure described in Fumanal et al. (2007), we calculated the proportion of floating seeds of both damaged and undamaged *A. artemisiifolia* plants. We randomly selected 50 seeds from 40, both damaged and undamaged, mother plants and then put them in plastic cups containing 80 mL water at room temperature ( $n = 4000$ ). The water and seeds were agitated for 1 min with a magnetic stirrer. Six hours after the agitation, we recorded the number of remaining floating seeds (floating seeds), and sunken seeds (non-floating seeds). All seeds were crushed and checked if empty (without a living white embryo) to determine seed sterility.

To examine the effect of herbivory by *O. communa* on dried seed weight and seed water absorption, 30 randomly selected seeds from ten, both damaged and undamaged, mother plants were put in plastic cups containing 80 mL water at room temperature. Before the experiment, these seeds were confirmed to be filled by a strong pinch with tweezers. Six hours after the same agitation procedure described above, we measured wet seed weight of floating and non-floating seeds. All seeds were dried (35 °C with ventilation for 12 h) and weighed. We calculated water absorption of each seed by subtracting dry weight from wet weight. After the experiment, we

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