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ORIGINAL PAPER

Alien dandelion reduces the seed-set of a native congener through frequency-dependent and one-sided effects

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Abstract In conservation biology, increasing numbers of studies have focused on reproductive interference (RI) between a native species and related aliens. However, few studies have examined the frequency dependence of RI, despite of its key importance to invasiveness. Here, we report for the first time frequency-dependent RI in a pair of native and alien dandelions: *Taraxacum japonicum* and *T. officinale*, respectively. *Taraxacum japonicum* has been displaced rapidly by the alien congener *T. officinale* in Japan and its causal mechanism are still poorly understood. Field observations revealed that the seed-set of natives decreased substantially as the proportion of alien neighbors increased. Subsequently, in a field experiment, the removal of alien flowers only greatly increased the seed-set of natives. We synthesized these results with existing theoretical models of RI and concluded that RI, which is mediated by strong frequency dependence, is presumably responsible for the displacement of *T. japonicum* by *T. officinale*.

Keywords Frequency dependence · Interspecific pollen transfer · Alien congener · Reproductive interference

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Introduction

The invasion of non-indigenous species is one of the most serious threats to biodiversity (Vitousek et al. 1996). Many studies have shown that invasive species can cause a decrease in the abundance of native species, sometimes displace them, and consequently drive them to extinction. Of the main factors relevant to this process, much research has focused on direct interactions such as predation or grazing (Fritts and Rodda 1998; Kats and Ferrer 2003) and competition for resources (e.g., nutrients, water, and light; Grace and Wetzel 1981, 1982; Delph 1986; Wardle et al. 1994; Weihe and Neely 1997), and indirect interactions such as effects via predators (Courchamp et al. 2000), parasites, and diseases (Combes 2001; MacNeil et al. 2003). These factors basically target the survival and individual growth of native species, although they may consequently affect reproductive success in some cases.

In addition to effects on survival and development, the reproductive process can also be affected by invasive species. Reproductive interference is one such effect on reproduction and is defined as an interfering interaction among sibling species in mating or reproductive processes (Kuno 1992). According to some theoretical studies, competitive displacement can be brought about more easily by reproductive interference than by ordinary resource competition (Kuno 1992). The key aspect of reproductive interference that makes it a powerful competitive interaction is its frequency dependence (Levin and Anderson 1970; Kuno 1992). This is because the chance of inter-specific mating is expected to vary proportionally to the relative frequency of the hetero-species. When two species exert reproductive interference on one another, the more abundant species exerts a more intense adverse effect on the reproductive success of the other and then becomes more abundant. Consequently, such species cannot co-exist, even if the interference is subtle (Ribeiro and Spielman 1986; Yoshimura and Clark 1994; Kuno 1992).

In plants, inter-specific interactions in pollination such as competition for pollinators and inter-specific pollen transfer (e.g., Waser 1978a, b) can work as concrete mechanisms of reproductive interference. In particular, some early theoretical studies emphasized the frequency dependence of inter-specific pollen transfer and its ecological importance (e.g., Levin and Anderson 1970; Waser 1978b). Recent empirical studies examined interactions during pollination as the source of adverse effects imposed by alien on native plant species (reviewed in Bjerknes et al. 2007); some studies have found a significantly negative effect of aliens (Grabas and Laverty 1999; Brown et al. 2002; Chittka and Schürkens 2001). However, most studies examined the negative effects of alien flowers on pollinator visitation and/or the seed-set of native species. Few studies have examined a key aspect of reproductive interference, frequency dependence. To evaluate the ecological importance of inter-specific interactions during pollination, this key aspect should be examined.

We present here one of the first reports of field observations and experiments examining the effects of frequency dependence in reproductive interference between a native and an alien species using two dandelion species distributed in western Japan. One species is a common exotic dandelion, *Taraxacum officinale* F. H. Wigg. It was originally distributed in Europe, was introduced to Japan in the early 1900s (Ogawa 2002), and now is found almost throughout the country (Ogawa 1979; Ogawa and Mototani 1985). The other species is *T. japonicum* Koidz., a native Japanese dandelion that is thought to have decreased in number (Ogawa and Mototani 1985). Many studies have attempted to elucidate the mechanisms behind the replacement of native dandelions by the alien species, but thus far have failed to find intense inter-specific interactions. Therefore, it is now generally thought that human activities have played a key role in the replacement by diminishing habitats suitable for natives and allowing aliens to colonize these areas (Sawada et al. 1982; Ogawa and Mototani 1991).

Recently, competition for pollination between the native and alien dandelions was suggested (I. Kandori, unpublished data). Additionally, recent studies (Watanabe et al. 1997a, b; Hamaguchi et al. 2000; Shibaike and Morita 2002; Shibaike et al. 2002) have indicated that hybrids of *T. officinale* and *T. japonicum* exist in the wild. However, it is still not clear whether these reproductive effects have contributed to the displacement of native dandelions. Therefore, our aims were to examine reproductive interference between the native and alien dandelions in the field through observations and experiments, focusing on frequency dependence, and to compare the reproductive effect to resource competition in other organs (i.e., leaves or roots). We first calculated the proportion of alien species adjacent to native individuals and its effect on the reproductive success of the native species to detect an adverse effect of alien species and frequency dependence. We then removed alien flowers and observed the effects on seed development in the native species to confirm reproductive interference by the alien species.

Methods

Study species

We used dandelion species (*Taraxacum* spp.) and their hybrids. The indigenous *T. japonicum* is native to the lowlands of western Japan, but has recently been decreasing in number, particularly in developed areas (Ogawa and Mototani 1985). *Taraxacum japonicum* flowers in spring; each scape has one head inflorescence that consists of many (several dozen to 100) light-yellow ligulate florets. This species is a self-incompatible sexual diploid (Morita et al. 1990) and thus requires pollen transfer from another individual for fertilization.

The non-indigenous congener *T. officinale* is an agamospermous triploid. It is morphologically similar to *T. japonicum*, but has reflex bracts in the outer involucre whorl, which is quite different from the appressed bracts of *T. japonicum*. This species is native to Europe, is thought to have been introduced to northern Japan in the early 1900s (Ogawa 2002), and is now distributed throughout Japan, especially in urban areas (Ogawa and Mototani 1985). *Taraxacum officinale* reproduces asexually by agamospermy (Mogie and Ford 1988), but its flowers produce large amounts of pollen. In addition, three types of hybrid (triploid, tetraploid, and androgynous) occur between *T. officinale* and *T. japonicum* in the wild (Shibaike et al. 2003). The pure *T. officinale* and hybrids with *T. japonicum* are morphologically similar and have long been confused. Because we focused on the reproductive success of the genuine native dandelion, we needed to discriminate natives from aliens not by genetics, but by the degree of interference. Therefore, we considered genuine *T. officinale* and hybrids as "putative alien species" and divided them into two groups based on pollen production. One group was aliens that produce pollen, presumably consisting of the genuine species and the triploid hybrid. The other group was aliens that do not produce pollen, mainly the tetraploid and/or androgynous hybrids. Although some androgynous hybrids are reported to produce pollen (Shibaike 2005), the amount of pollen is usually conspicuously small. We observed no distinct variation in the amount of pollen for either native or alien dandelions.

Study site

We used four sites for observations and/or experiments. The first site was a grassland in the Nature Experiment and Observation Garden at Tsurumi Park (34°42′32″N, 135°34′55″E; abbreviated OT below), Osaka, Japan. Although the surrounding environment is a well-developed urban area, this site retains the native flora of western Japan because the topsoil and plants were transplanted from a neighboring rural area (Wakayama) for environmental education and civic amenity in 1998. Still, the site has suffered from the immigration of many exotic plants, including *T. officinale*. The second site was the plum garden at Osaka Castle Park (34°41′9″N, 135°31′43″E; OC), Osaka, Japan. This site has been constantly managed as a plum garden from 1974 to the present and is located approximately 5 km from OT. The third and fourth sites were Ikadachi (35°7′53″N, 135°54′30″E; SI) and Kamiryuge (35°9′26″N, 135°52′52″E; SK), Shiga, Japan. These sites are surrounded by rice fields that have been managed traditionally. SI and SK are located approximately 2 km apart. The sites in Osaka (OT and OC) and those in Shiga (SI and SK) are located >50 km apart.

Local alien proportion and seed-set

To investigate the frequency-dependent effects of putative alien dandelions on the reproductive performance of the native species, we first calculated the local alien proportion, defined as the proportion of putative alien dandelion individuals within a 2 m radius, at each study site. Two meters is the average distance for effective pollen transfer in dandelions (Takakura et al. unpublished). At OT, alien frequency was calculated three times: on 5 and 23 April 2005 and 20 April 2007. At SI, OC, and SK, the calculations were done once, on 30 April, and 1 and 5 May 2007, respectively. We used two methods to determine seed-set: direct observation at OT and OC, and indirect observation at SI and SK. At OT and OC, we arbitrarily chose native dandelions and then counted the number of native individuals and pollen-producing alien individuals within a 2 m radius. When counting, we also arbitrarily selected one flower head for each sample and tagged its scape. Two weeks after counting, the flower heads were collected, taken to the laboratory, and carefully dissected with forceps to count the number of normally developed and undeveloped seeds. Seed-set was defined as the proportion of normally developed seeds to the total number of seeds for each *T. japonicum* flower head. At SI and SK, we counted native and alien dandelions in the same way, but measured seed-set differently. We did not wait

2 weeks until the samples bore fruit, but collected fruiting scapes on the same day that we counted individuals because the pollen-producing dandelions in Shiga headed toward the end of the flowering season and there was a risk that we would not be able to evaluate the influence of aliens correctly. Instead, we counted native and alien individuals at the same phenological stage to avoid mismatching their interaction. After collecting the fruiting scapes, we surveyed seed-set for the Shiga samples using the same procedure as for the Osaka samples.

The relationship between the local alien proportion and seed-set was analyzed using a generalized linear mixed model (GLMM; Wolfinger and O'Connell 1993) with a binomial error structure and a logit link function. In this analysis, the response was the normal development of seeds, and the explanatory variables were the local alien proportion and the total number of *Taraxacum* plants. We used the total number of *Taraxacum* in the analytical model to reflect the general quality of the local habitat (e.g., light, water, and nutrient availability). Individual flower heads were also incorporated to the model as a random effect. All analyses used R version 2.4.0 (Ihaka and Gentleman 1996).

Experimental removal of alien flowers

To experimentally control for interference by *T. officinale* and its hybrids on *T. japonicum*, flowers and buds of putative aliens were removed by hand. This experiment was done at OT in 2005. We removed all flower buds that occurred on 8 April and all blooming flowers that occurred on 14 April. Only the flower head was removed; neither the leaf nor root was removed. These treatments were expected to reduce the interference effect on *T. japonicum* individuals that flowered on 14 April, but not to reduce the effect on individuals that flowered on other days. Therefore, individual *T. japonicum* flowering on 5 April and 23 April were categorized as representing the early and late control periods, respectively, and those flowering on 14 April were categorized as the treatment. Flower heads of *T. japonicum* were collected 2 weeks after flowering. As described above, seed-set was calculated for each flower head.

The difference in seed-set among periods was analyzed using GLMMs. First, analyses were conducted using two analytical models. One model included treatment (period) and individual flower head as fixed and random effects, respectively, and the other included the random effect only. A likelihood ratio test between these two models examined the significance of the treatment. Second, we created three subsets of data containing two out of the three periods (i.e., treatment, and early and late controls). Subsequently, we applied GLMMs to these subsets and compared seed-set between the two periods. The probabilities of the significance level were adjusted using Holm's method (Holm 1979).

Flowering phenology in Tsurumi

In the experiment described above, we counted the number of individuals that were flowering in the study site during the three experimental periods (on 5, 14, and 23 April 2005). We divided putative aliens into two groups based on pollen production. We then counted the number of individuals in each group: aliens with pollen and aliens without pollen.

Results

Local alien ratio and seed development

The results of GLMMs to analyze the seed-set of natives showed similar trends across study sites and seed collection dates. That is, all analyses showed significantly negative effects of alien ratio on native seed-set (Table 1). This trend occurred even when only the alien ratio was taken into account (Fig. 1). The effect of the total number of individuals was consistently positive, but was marginally or not significant in some cases (Table 1). At OT, data were collected twice in 2005. The absolute coefficient of the local alien proportion was larger in the second collection than in the first (−2.09 and −2.59, respectively; Table 1), although the difference was slight.

Experimental removal of alien flowers

Seed-set differed significantly among flowering periods ($\chi^2 = 12.62$, df = 3, $P < 0.001$), and differences between pairs of periods were also significant

Table 1 Results of GLMMs for the analysis of seed-set

Study site		Coefficient ± SE	
Date	df	Total number of *Taraxacum*	Local alien ratio
OT			
5 April 2005	4,923	0.01 ± 0.009 n.s.	−2.09 ± 0.332***
23 April 2005	6,705	0.13 ± 0.009***	−2.59 ± 0.465***
20 April 2007	649	−0.01 ± 0.020 n.s.	−2.89 ± 0.820***
SI			
30 April 2007	713	0.00 ± 0.009 n.s.	−2.04 ± 0.766**
OC			
1 May 2007	845	0.03 ± 0.014*	−4.11 ± 1.217***
SK			
5 May 2007	563	0.01 ± 0.003*	−3.69 ± 1.562*

Estimated coefficients and standard errors (SE) are shown for the two explanatory variables: the total number of *Taraxacum* and the local alien ratio at 2 m. The symbols n.s., *, **, and ***, indicate not significant, $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

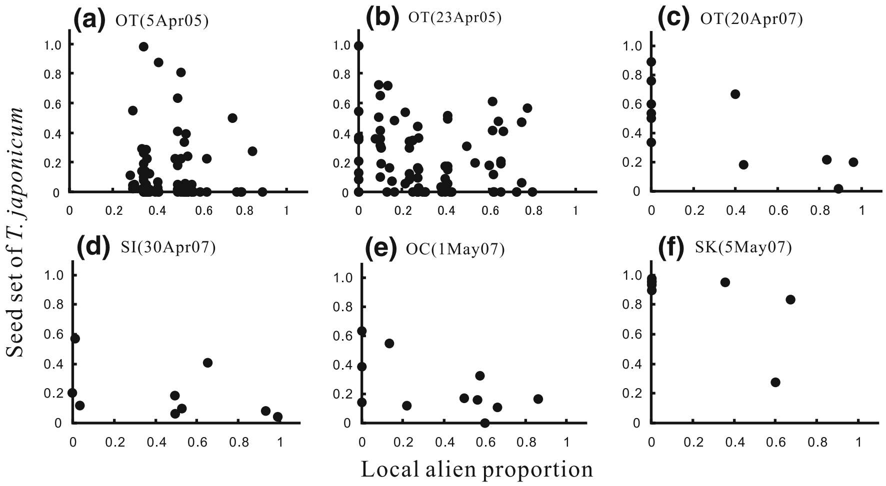

Fig. 1 The relationship between local alien proportion and seed-set (the proportion of normally developed seeds to the number of total seeds) at the four study sites: OT (**a**–**c**), SI (**d**), OC (**e**), and SK (**f**). Each plot represents one flower head. These plots are not weighted by the number of seeds in each flower head, although the total number is taken into account in GLMM analyses (see text). Dates in parentheses indicate the data collection dates

($P < 0.05$, paired GLMMs with Holm's adjustment). Seed-set was highest during the treatment period, followed by the late control period (Fig. 2).

Flowering phenology in Tsurumi

At the three observation times, the number of flowering individuals was approximately similar (Table 2), 52–77 and 23–32 for native and pollen-producing aliens, respectively. There were no data for alien species in the intermediate period because alien flowers were experimentally removed at that time. However, aliens that did not produce pollen flowered in the last period only (Table 2).

Discussion

The putative alien species exerted an adverse effect on the reproductive success of its native congener, and that effect was frequency dependent. The increased abundance of alien dandelions, especially in urban areas of Japan, has been documented since the 1960s (Ogawa 2002) and has caused concern that the alien species might outcompete the native species. Many studies have examined the competitive effects of alien dandelions on natives, but a direct and extensive competitive effect that excludes natives has not been found. At present, therefore, it is widely accepted that alien dandelions do not exclude native

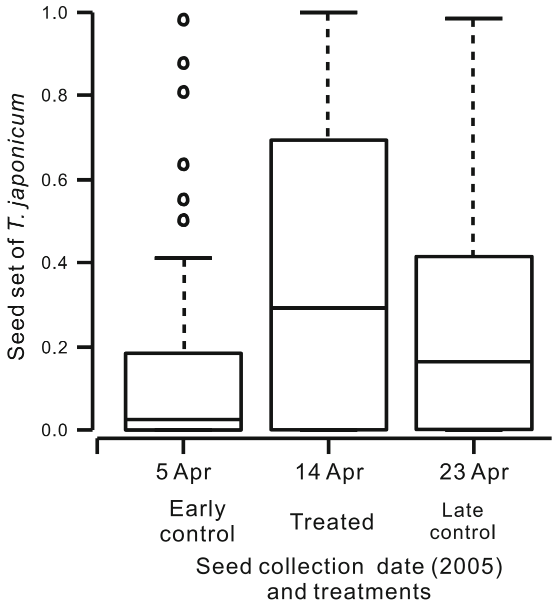

Fig. 2 Box-and-whisker plots displaying medians, quartiles, and ranges of seed-set for native dandelions flowering during the early control, treatment, and late control periods. The lines indicate the lower quartile, median, and upper quartile. The whisker lines extend to the most extreme data points or have a maximal length of 1.5 times the box height. Dots represent data points beyond the ends of the whiskers

species via direct resource competition and that habitat changes (i.e., urbanization) are the probable cause of the displacement (Ogawa 1979; Ogawa and Mototani 1985, 1991). However, those studies and others (e.g., Hoya et al. 2004) did not examine effects on reproductive success. Our study sheds new light on the displacement of native dandelions by aliens.

The experimental removal of alien flowers increased the seed-set of the native dandelion. In this field experiment, we removed only flower heads, not the leaves or roots of alien dandelions. This methodology and these results, therefore, suggest that the decreased seed-set in natives was not caused by competition for light, water, or nutrients, but was related to the reproductive process.

These findings strongly suggest that the native dandelion *T. japonicum* is affected by reproductive interference, a very powerful competitive effect, from the alien congener. In particular, it is noteworthy that the reproductive success of the native species decreased as the local alien ratio increased (Table 1, Fig. 2). This result indicates that the adverse effects of the alien species were frequency dependent, which is a key aspect of reproductive interference (Kuno 1992). Thus, reproductive interference among dandelion species should be a positive feedback process; the less abundant native species incurs a larger adverse effect from more abundant aliens, becomes even less abundant, and finally disappears. Additionally, the adverse effect was probably one-sided for these dandelion species because the self-incompatible native species requires out-crossing, whereas the alien species reproduces asexually and requires no pollen (Richards 1973; Morita et al. 1990). It is likely that the reproductive success of the apomictic alien species is not affected by pollen transfer, even when it is a minority in the early stages of invasion. These facts suggest that reproductive interference has perhaps played an important role in the displacement of native dandelions by aliens.

The results and estimated parameters demonstrate some interesting trends in reproductive interference among native, alien, and hybrid dandelions in Japan. First, there was a seasonal change in the intensity of reproductive interference. At OT in 2005, the effect of local aliens on native seed-set was analyzed twice. The negative slope per unit proportion of pollen-producing aliens was steeper in the second season than in the first (Table 1). A consistent trend can be observed throughout Table 1. The coefficients estimated from data collected in May were larger than those in April, although this comparison is not entirely appropriate (e.g., it is based on data from different study sites). This trend might indicate that the effect of reproductive interference increases as the temperature increases and pollinators become

Table 2 Flowering phenology of dandelions in 2005

Species or group	Number of flowering individuals on date		
	5 April	14 April	23 April
Taraxacum japonicum	52	77	60
Putative aliens with pollen	32	–	23
Putative aliens without pollen	0	–	22

See text for details of dandelion classification more active. Such a change is probable in entomophilous flowers.

The second interesting trend is the effect of no-pollen aliens. At OT in 2005, as described above, the per-unit effect of pollen-producing aliens was slightly larger at the earlier than at the later data collection time, but the native seed-set was higher at the last collection than that at the first (Fig. 2). This was perhaps because there were fewer flowering pollen-producing aliens at the later collection than at the earlier collection (Table 2). In the later period, about half of the putative aliens did not produce pollen. Therefore, reproductive interference by pollen-producing aliens was apparently diluted by the aliens that did not produce pollen. These trends are unique to reproductive interference via pollen transfer, although we did not examine them thoroughly.

In general, alien species are one of the most important factors that damage native flora and fauna (Vitousek et al. 1996). Alien species are treated as serious threats mainly when they are predators, parasites, or competitors for resources needed by native species. The risk of reproductive interference has not been taken into account sufficiently. Evidence of a significant negative effect of aliens is relatively rare (Brown and Mitchell 2001; Brown et al. 2002; Bell et al. 2005), and evidence from field conditions is even more restricted (Grabas and Laverty 1999; Chittka and Schürkens 2001). As described above, the frequency dependence of reproductive interference is a key aspect that has not been examined in most cases. Researchers who study the effects of alien species on native biomes should examine reproductive interference and its frequency dependence more closely.

Being surrounded by alien congeners resulted in reduced reproductive success for a native dandelion. However, the detailed mechanisms leading to this phenomenon were not investigated. There are at least two mechanisms by which alien flowers could decrease the reproductive success of natives. The first possible mechanism is competition for pollinators. The size and number of flower heads of alien dandelions are generally larger than those of native species (Naito 1975). Therefore, alien flowers may attract more pollinators than natives, decreasing the pollination service that the native species would have received otherwise. Because the native dandelion is self-incompatible and requires outcrossing (Richards 1973), a decrease in pollination service could lead to a decrease in seed-set. The second hypothetical mechanism is inter-specific pollen transfer (IPT). An adverse effect of IPT has been observed in some plant species (e.g., Char 1977; Feinsinger and Tiebout 1991; Caruso 2000; Waites and Ågren 2004) and has been experimentally detected between native and alien loosestrife in the USA (Brown and Mitchell 2001; Brown et al. 2002). For dandelions, artificial pollen transfer from alien *T. officinale* to native *T. japonicum* rarely produces viable hybrids, and most ovules do not develop (Morita et al. 1990). IPT in the field might result in a similar phenomenon. The native seed-set was higher when approximately half of the flowering aliens produced no pollen than when all of the flowering aliens produced pollen (Table 1, Fig. 2). This might imply that IPT affected these dandelions. Virtually, the experimental IPT decreased the native seed-set (Takakura et al., unpublished data). However, more data are necessary to specify the mechanism behind the reproductive interference in dandelions.

The apparent alien dandelion has several hybrids between native and alien species: triploid, tetraploid, and androgynous (e.g., Shibaike et al. 2002). As discussed above, we roughly classified the putative aliens based on their pollen production and showed that reproductive interference was perhaps diluted by no-pollen hybrids. Even among pollen-producing hybrids, there might be a difference in the effects of reproductive interference. This issue should be examined in future research on reproductive interference in dandelions. When a sexual interaction exists between species, genetic invasion, hybridization, and introgression often attract attention (Rhymer 1996). It is feared that the alien species *T. officinale* will genetically assimilate native dandelions in Japan (Hoya et al. 2004) and the USA (Brock 2004). This concern is based on the existence of actual hybrid individuals from assimilation. However, the effect of reproductive interference does not appear threatening, especially in the field, because it leads to the absence of the viable offspring, and the absence itself is invisible. However, because of this invisible result, the effect of reproductive interference could be a serious threat for native species.

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