

A test of baker's law: breeding systems of invasive species of Asteraceae in China

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Abstract Invasive alien plant species are frequently characterized by a high fecundity. However, because suitable pollinators and/or mates may be absent in the new range, it is not clear how they achieve high seed production. According to Baker's Law, species capable of uniparental reproduction are more likely to establish after long-distance dispersal than species that rely on suitable mates and pollinators. To test whether self-compatible species, and particularly species capable of autonomous seed set, are more likely to establish and spread, we experimentally assessed the breeding systems of 12 species of Asteraceae that are invasive in China. Among these 12 species of Asteraceae, the percentages of self-compatible species (66.7%) and species capable of autonomous seed set (83.3%), which included self-fertilizing and apomictic species, were

significantly larger than expected from the percentages of such species in global data sets of Asteraceae (36.8% and 46.0%, respectively). Furthermore, the number of Chinese provinces in which the invasive alien species occur was significantly positively correlated with the proportion seed set on bagged capitula (i.e. with the degree of autonomous seed set). Among 36 species of Asteraceae that are invasive in China and for which we found breeding-system data in the literature, we also found a higher than expected percentage of self-compatible species (65.7%), and that these self-compatible species are more widespread in China than self-incompatible species. These results support the predictions of Baker's Law that self-compatible species, and particularly those capable of autonomous seed production, are more likely to establish and spread in a new range. Therefore, breeding systems of plants should be included as one of the key elements in risk assessment protocols for plant invasiveness.

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Introduction

Biological invasions pose a threat to biodiversity and ecosystem functioning, and can have large economic costs (Mooney et al. 2005). Therefore, one of the major aims in invasion biology is to find species

attributes that contribute to invasiveness and can be used to inform risk assessment (Daehler and Strong 1993; Rejmánek 1996; Rejmánek and Richardson 1996; Groves et al. 2001; Daehler 2003; Richardson and Pyšek 2006; van Kleunen and Richardson 2007). Obviously, introduced alien species can only become invasive if they manage to reproduce (Richardson et al. 2000). Indeed, high fecundity is frequently associated with invasive alien plant species (Pyšek and Richardson 2007; Mason et al. 2008; van Kleunen et al. 2010). However, it is less clear how invasive alien plants achieve a high reproductive output, particularly because they may lack suitable pollinators and/or suitable mates in the new range.

Baker (1955) pointed out that species capable of uniparental reproduction should be more likely to establish after long-distance dispersal than species that rely on suitable mates and pollinators. Therefore, self-compatible species, which do not suffer from mate limitation, and particularly species capable of autonomous seed set, which do not suffer from mate and pollinator limitation, are likely to be superior colonizers. This hypothesis, which is better known as Baker's Law (Stebbins 1957; also frequently referred to as Baker's rule), is likely to apply to both the initial establishment of alien plants after a long-distance dispersal event and to their subsequent spread in a new range (see Pannell and Barrett 1998; van Kleunen and Johnson 2005). Even in the presence of suitable mates and pollinators, autonomous self-fertilization might increase seed production (e.g. Rodger et al. 2010), and therefore, result in higher propagule pressure and invasiveness (e.g., Lockwood et al. 2005; Colautti et al. 2006).

Several multi-species studies have shown that autonomous seed production is frequently associated with naturalized and invasive plant species (Rambuda and Johnson 2004; van Kleunen and Johnson 2007; van Kleunen et al. 2008). Nevertheless, because there are also examples of highly invasive self-incompatible species, such as *Centaurea solstitialis* (Sun and Ritland 1998), *Senecio squalides* (Brennan et al. 2002), *Mikania micrantha* (Hong et al. 2007) and *Senecio inaequidens* (Lafuma and Maurice 2007), and highly invasive dioecious species (Cronk and Fuller 2001), there is still considerable skepticism regarding the applicability of Baker's Law to plant invasions. Therefore, we need more studies, particularly on multiple species, before we can conclude

that self-compatibility and the ability for autonomous seed reproduction are generally associated with invasiveness.

We experimentally assessed the breeding systems of 12 species of Asteraceae that are invasive in China. In addition, we compiled breeding system data of 36 such species from the literature. We chose the Asteraceae, because it is the largest dicotyledonous family and because it is notorious for its invasive species (Wu and Wang 2005; Zhu et al. 2005). Species of Asteraceae are proportionally overrepresented among invasive plant species worldwide (Pyšek 1998; but see Daehler 1998). Particularly in China, the percentage of invasive species of Asteraceae (c. 20%; Xu and Qiang 2004; Weber et al. 2008) is much larger than the percentage of Asteraceae in the global flora (8.4%; Pyšek 1998). Moreover, although most tribes of Asteraceae have both self-compatible and self-incompatible taxa (Ferrer and Good-Avila 2007), a minority of Asteraceae—at least the ones with known breeding systems—are fully or partially self-compatible (36.8%; Ferrer and Good-Avila 2007), and less than half (46.0%) are capable of autonomous seed set (including autogamous and apomictic species; Fryxell 1957). Thus, if self-compatibility and autonomous seed set are prevalent among invasive species of Asteraceae, this would be strong support for Baker's Law.

We used the breeding-system data of Asteraceae to address the following specific questions. (1) Is self-compatibility and ability for autonomous seed set among invasive Asteraceae in China more frequent than predicted from global breeding-system data of Asteraceae? (2) Is size of the invaded range positively associated with the degree of autonomous seed set among the invasive Asteraceae in China? We discuss the importance of our findings for the development of risk-assessment protocols for invasiveness.

Materials and methods

Study species and plant material

In China, 44 (Xu and Qiang 2004) to 53 (Weber et al. 2008) species of Asteraceae are considered invasive. These invasive species occur predominantly in urban and rural areas, but most of them also invade natural habitats, and cause damage to native species, habitats,

or to the economy (Weber et al. 2008). We selected all invasive species of Asteraceae that we could find near the city of Nanjing in the Jiangsu province of China, which resulted in 11 species. In addition, we selected *Ageratina adenophora*, which is invasive in the south-western parts of China, because we had it growing in our greenhouse. The 12 species differ in their regions of origin, life-form and range size in China (Table 1). Although for most of these species some information on their breeding systems is already available in the literature (Table 1), the ability for autonomous seed set was unknown for most of the 12 species.

In the springs of 2005 and 2006, we excavated 6–35 plants of each species from naturalized populations near Nanjing (except for *A. adenophora*, which we had already in our greenhouse), transplanted them into pots, and placed them in a greenhouse of the Nanjing Agricultural University. The greenhouse was open on all sides, which allowed access of pollinators to the plants. We watered the plants as needed.

Breeding-system assessment

To test whether our 12 study species are capable of autonomous seed set, we excluded pollinators from flowers by enclosing several capitula on each plant in paper bags. To test for non-pseudogamous apomixis (agamospermy), we cut off all anthers and stigmas of several capitula on each plant during the bud stage. As controls, we left several capitula on each plant for open pollination. We used five to 32 plants per species (Table 1), and each treatment included 6–70 capitula per species (more information on sample sizes per treatment and per species are given in Appendix S1—Electronic supplementary material). Experiments on the species were done in the years 2005, 2006 or 2008. For two of the species, *C. sumatrensis* and *S. asper*, we did the experiments in 2 years. We calculated seed set as the proportion of florets in a capitulum that developed achenes. If necessary, we used a dissecting microscope to assess whether achenes had developed.

Because species that are not capable of autonomous seed production could nevertheless be self-compatible, we tested self-pollen-stigma compatibility for seven of the 12 species (Table 1). The self-incompatibility response of Asteraceae usually takes place at the

stigmatic surface, and in an incompatible pollen-stigma interaction, pollen grains do not germinate or growth of pollen tubes is arrested at the stigmatic surface (Hiscock 2000). For each of the seven species, we collected two to three flowering capitula that had been enclosed in paper bags since the bud stage to prevent cross-pollination. We examined the germination of self-pollen grains and growth of their pollen tubes using the aniline-blue-fluorescence microscopy method (Currier 1957).

We considered a species as capable of autonomous seed production if it produced seeds on bagged capitula. In case a species capable of autonomous seed production also produced seeds on decapitated capitula, we considered it as apomictic, and otherwise as autogamous. The latter automatically means that the species is self-compatible. Because our breeding-system experiments did not include selfing and outcrossing treatments, which are virtually impossible in Asteraceae, we could not assess whether selfing results in similar levels of seed production as outcrossing, and also not whether genotypes of a species differ in self-compatibility. Therefore, we did not differentiate between fully and partially self-compatible species. For species not capable of autonomous seed production (and also for apomictic species), we considered them as self-incompatible if self-pollen did not germinate or if pollen tubes did not grow into the style.

Because our sample of 12 species might not be representative for all 44 (Xu and Qiang 2004) or 53 (Weber et al. 2008) species of Asteraceae considered invasive in China, we additionally compiled breeding-system data from the literature for as many of these species as possible. This resulted in breeding-system data for 36 invasive species of Asteraceae in China (Appendix S2—Electronic supplementary material).

Statistical analyses

To test whether average seed set per capitulum per plant differed significantly at $P < 0.05$ between open-pollinated, bagged and decapitated treatments, we used Tukey's multiple-comparison tests for each species separately (statistical software: JMP 7.0; SAS Institute Inc., Cary, NC, USA).

To test whether the frequencies of self-compatible species among the 12 invasive Asteraceae in China used

Table 1 The 12 species of Asteraceae that are invasive in China, and were used in our breeding-system experiments

Species	Life form	Native range	Range size in China ^b	No. of plants in experiment	Inferred breeding system	Breeding system reported in literature	Reference ^d
<i>Ageratina adenophora</i> ^a (<i>Eupatorium adenophorum</i>)	Perennial shrub	Mexico	8	10	Self-incompatible, apomixis	Apomixis	1, 2, 3, 4, 5
<i>Ageratum conyzoides</i>	Annual	South and Central America	24	29	Self-compatible, autogamous, some apomixis	Self-compatible, self-incompatible, some apomixis	5, 6, 7, 8
<i>Aster subulatus</i>	Annual	North America	20	11	Self-compatible, autogamous.	–	–
<i>Bidens pilosa</i> ^a	Annual	Tropical America	22	10	Self-compatible, autogamous	Self-compatible	5, 7, 9
<i>Conyza bonariensis</i>	Annual or winter-annual	South America	21	5	Self-compatible, autogamous	–	5
<i>Conyza canadensis</i>	Annual or winter-annual	North America	34	10	Self-compatible, autogamous	Self-compatible	5, 10, 11
<i>Conyza sumatrensis</i>	Annual or winter-annual	South America	21	15, 32 ^c	Self-compatible, autogamous	Self-compatible	12
<i>Coreopsis lanceolata</i> ^a	Perennial herb	North America	13	12	Self-incompatible	–	5
<i>Erigeron annuus</i> ^a	Annual or winter-annual	North America	31	11	Self-incompatible, apomixis	Apomixis	3, 13, 14
<i>Solidago canadensis</i> ^a	Perennial herb	North America	14	14	Self-incompatible	Self-incompatible or partial self-incompatible	5, 10, 13, 15, 16, 17
<i>Sonchus asper</i> ^b	Annual or winter-annual	Europe	34	13, 10 ^c	Self-compatible, autogamous	Self-compatible	5, 18, 19, 20
<i>Sonchus oleraceus</i> ^a	Annual or winter-annual	Europe	34	11	Self-compatible, autogamous	Self-compatible or self-incompatible	5, 17, 18, 19

The table reports for each species the life form, the native range, the size of the invaded range in China, the number of plants used in the breeding-system experiment, the breeding system inferred from our experiments, and the breeding system of the species that were reported in the literature

^a These seven species were also included in the tests for self-pollen-stigma compatibility

^b Range size of a species was measured as number of invaded provinces in China, which also includes Taiwan and the special administrative region of Hong Kong and Macao (total is 34)

^c The breeding system experiments on *Conyza sumatrensis* and *Sonchus asper* were done in 2 years with different sample sizes

^d References 1, Baker 1965; 2, Auld and Martin 1975; 3, Nogler 1984; 4, Rambuda and Johnson 2004; 5, Ferrer and Good-Avila 2007; 6, Pullaiah 1982; 7, McMullen 1987; 8, Ming 1999; 9, Grombone-Guaratini et al. 2004; 10, Mulligan and Findlay 1970; 11, Weaver 2001; 12, Hao et al. 2009; 13, Fryxell 1957; 14, Noyes and Rieseberg 2000; 15, Werner et al. 1980; 16, Melville and Morton 1982; 17, Bertin 1993; 18, Hutchinson et al. 1984; 19, Mejias 1992; 20, Van Kleunen and Johnson 2007

in our breeding-system experiments and among the 36 invasive Asteraceae in China for which we found breeding-system data in the literature are larger than expected, we compared them to the frequency of self-compatible species in a data set of 571 species of Asteraceae from around the world (Ferrer and Good-Avila 2007). To the best of our knowledge, this is the largest data set on self-compatibility of Asteraceae that is available. This data set does not give information on the ability for autonomous seed set (i.e. autogamy and apomixis) of species. Therefore, to test whether the frequency of species with autonomous seed set among our 12 species of Asteraceae that are invasive in China is larger than expected, we compared it to the frequency of species with potential for autonomous seed set in a data set of 139 species of Asteraceae from around the world (Fryxell 1957; also see Rambuda and Johnson 2004). A similar analysis was not possible for the 36 invasive Asteraceae in China for which we collected breeding-system data from the literature, because for most of these species we had no information on autonomous seed set. Fryxell (1957) categorized breeding systems of species within a triangle between strictly self-incompatible, strictly apomictic and strictly autogamous. The latter two categories are capable of autonomous seed set, but also some of the intermediate categories in Fryxell's classification system might be capable of this. Therefore, we categorized all species that are not strictly self-incompatible in Fryxell's data set as species with autonomous seed set. This is most likely an overestimate, which makes our comparison more conservative. We tested the significance of deviations of frequencies of self-compatible species and of species capable of autonomous seed set among our invasive species from the frequencies in the global data sets with two-tailed χ^2 -squared tests or, when some of the raw counts in a cell were <5 , with Fisher's exact-probability tests (statistical software: VassarStats; <http://faculty.vassar.edu/lowry/VassarStats.html>).

To test whether the degree of autonomous seed production of the 12 species in our breeding-system experiments is associated with size of the invaded range in China, we calculated the Pearson correlation coefficient between the number of Chinese provinces in which the species occurs and proportion seed set on bagged capitula (statistical software: R, version 2.9.1; R Development Core Team 2009). For the 36 invasive Asteraceae in China for which we collected breeding-system data from the literature, we used

Tukey's multiple-comparison tests to test whether the number of Chinese provinces differs significantly at $P < 0.05$ between self-incompatible, partially self-incompatible, self-compatible and apomictic species (statistical software: JMP 7.0; SAS Institute Inc., Cary, NC, USA).

Results

Breeding systems of invasive Asteraceae in China

Ten of the 12 invasive species of Asteraceae in our breeding-system experiments were capable of seed production when pollinators were excluded with paper bags (for all ten species seed set was $>40\%$; Fig. 1). Two of the ten species with autonomous seed set, *Ageratina adenophora* and *Erigeron annuus*, had similar seed set on decapitated capitula as on bagged capitula (seed set $>40\%$; Fig. 1), indicating that these two species are highly apomictic, and that the other

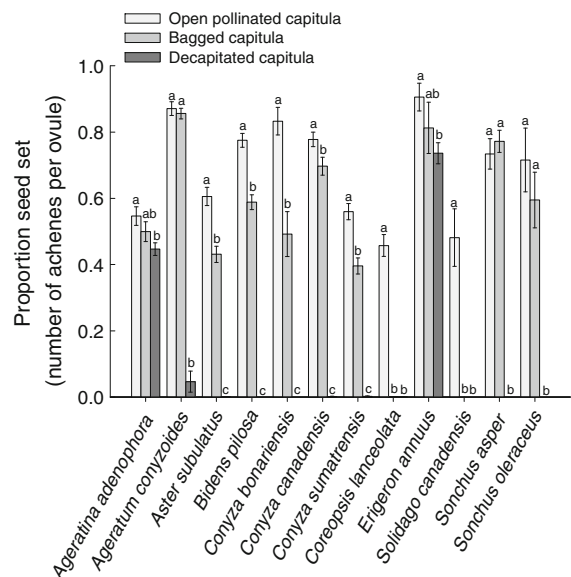


Fig. 1 Mean (\pm SE) seed set of 12 invasive alien species of Asteraceae in China for open-pollinated, bagged and decapitated capitula. Seed set was measured as the number of seeds divided by the number of ovules per capitula. Seed set on bagged capitula indicates autonomous seed set, and seed set on decapitated capitula indicates apomixis. Significant differences ($P < 0.05$; based on Tukey multiple-comparisons tests) in seed set between treatments are indicated by different letters above the bars for each species separately

eight species are autogamous and thus self-compatible. In addition, one of the autogamous species, *Ageratum conyzoides*, also showed a low degree of apomixis (Fig. 1).

Microscopy showed that self-pollen of the two highly apomictic species did not develop on their stigmas, indicating that they are self-incompatible or have low pollen viability. For the two species not capable of autonomous seed set, *Coreopsis lanceolata* and *Solidago canadensis*, self-pollen also did not develop on their stigmas, indicating that they are also self-incompatible. On the other hand, for the three species capable of autonomous seed set, *Bidens pilosa*, *Sonchus asper* and *S. oleraceus*, tubes of self-pollen grew into their styles, confirming self-compatibility of these species.

Breeding systems of species of Asteraceae invasive in China and of those in global data sets

Ferrer and Good-Avila (2007) reported data on self-compatibility of 571 Asteraceae from around the world of which 361 species (63.2%) were categorized as strictly self-incompatible. The others are fully (154 species) or partially self-compatible (56 species). Among our 12 species of Asteraceae that are invasive in China, the percentage of self-compatible species (66.7%) was significantly higher than expected from the percentage of fully and partially self-compatible species in the global data set of Ferrer and Good-Avila (36.8%; Fisher exact test, $P = 0.040$). For the invasive Asteraceae in China for which we found breeding-system data in the literature, the percentage of self-compatible species (65.7%) was also significantly higher than expected from the global data set of Ferrer and Good-Avila ($\chi^2 = 11.67$, $df = 1$, $P = 0.0006$).

Fryxell (1957) reported breeding system information on 139 Asteraceae from around the world of which 75 species (54.0%) were categorized as strictly self-incompatible (i.e. not capable of autonomous seed-set). Among our 12 species of Asteraceae that are invasive in China, the percentage of species capable of autonomous seed set (83.3%) was significantly larger than expected from the percentage of such species in the global data set of Fryxell (46.0%; Fisher exact test, $P = 0.016$).

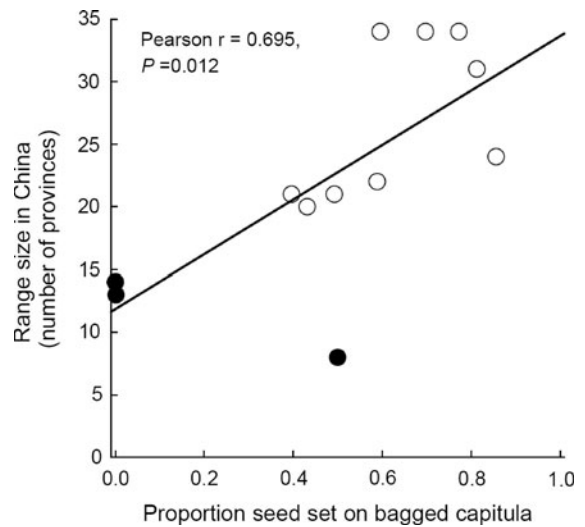


Fig. 2 Correlation between degree of autonomous seed set (i.e. seed set on bagged capitula) and invaded range size of 12 invasive alien species of Asteraceae in China. Open symbols are annual species, and closed symbols are perennial species (see Table 1). We plotted a regression line ($y = 11.9 + 21.8x$, $R^2 = 0.48$) to emphasize the significant positive correlation

Degree of autonomous seed set and spread of invasive species in China

The number of Chinese provinces in which the 12 invasive alien species used in our breeding-system experiments occur was significantly positively correlated with the proportion seed set on bagged capitula ($r = 0.695$, $P = 0.012$; Fig. 2). Among the 36 invasive alien species for which we found breeding-system data in the literature, self-incompatible species occurred in the smallest number of provinces whereas the fully self-compatible species occurred in the largest number of provinces (Fig. 3).

Discussion

We assessed breeding systems of 12 species of Asteraceae that are invasive in China to test whether—as predicted from Baker's Law (Baker 1955)—self-compatibility and ability for autonomous seed set are associated with invasiveness. We found that ten of the 12 species are capable of autonomous seed set when pollinators were excluded. In two of the species, autonomous seed set was solely through apomixis, in seven species solely through autogamy,

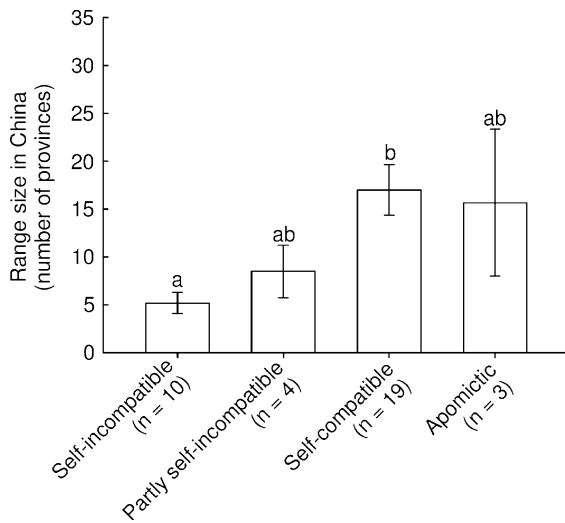


Fig. 3 Mean \pm SE number of invaded provinces in China for self-incompatible, partly self-incompatible, self-compatible and apomictic species of Asteraceae. Significant differences ($P < 0.05$; based on Tukey multiple-comparisons tests) between species of different breeding-system categories are indicated by different letters above the bars

and in one species through both mechanisms. The two species without autonomous seed set, *Coreopsis lanceolata* and *Solidago canadensis*, were self-incompatible. These two species are, however, capable of vegetative reproduction through vigorous rhizomatous growth. The breeding systems that we inferred from our experiments largely confirmed information that we found in the literature on self-compatibility and apomixis of the 12 species (Table 1), but added important information of the capacity for autonomous seed production. Overall, our results indicate that all 12 study species are capable of uniparental reproduction of some form, and that in most of these species this is through autonomous seed production.

On the basis of Baker's Law, we predicted that self-compatible species, and particularly those capable of autonomous seed production, should have a higher chance to become invasive than self-incompatible species. Therefore, the frequency of self-compatible species and of species capable of autonomous seed set should be higher among invasive species than among the potential source flora (Rambuda and Johnson 2004). Indeed, among our 12 species of Asteraceae that are invasive in China, the frequencies of self-compatibility and autonomous seed set were higher than the corresponding frequencies in global data sets of

Asteraceae. Similarly, among the 36 species of Asteraceae that are invasive in China and for which we found breeding-system data in the literature, the frequency of self-compatible species was also higher than expected. Although we do not have information on whether all species of Asteraceae in these global data sets have had the opportunity to become invasive in China (i.e. whether they have been introduced to China), these results are in line with the predictions of Baker's Law. Similarly, Rambuda and Johnson (2004) found that among 17 invasive alien species in South Africa, all were capable of autonomous seed set. Furthermore, van Kleunen et al. (2008) found that among 20 South-African species of Iridaceae, the ones capable of autonomous seed set were more likely to naturalize after introduction elsewhere in the world. Overall, our results add to the evidence that self-compatibility and autonomous seed set increase the likelihood of establishment after introduction.

Baker's Law would also predict that among the species that have become invasive, the ones capable of autonomous seed set should be more widely spread (van Kleunen and Johnson 2007). Indeed, among our 12 species of invasive alien Asteraceae in China, the number of provinces in which a species occurs was positively associated with seed set on bagged capitula. Furthermore, among the 36 species of Asteraceae that are invasive in China and for which we found breeding-system data in the literature, self-compatible species were more widespread than self-incompatible species. This indicates that autonomous seed set is not only associated with initial establishment of an alien species of Asteraceae in China but also with its subsequent spread. Similarly, van Kleunen and Johnson (2007) reported that among 361 European species naturalized in North America, the ones capable of autonomous seed set occur in more USA states. This opposes the findings of Sutherland (2004), who reported that among 142 species, invasive exotic weeds in the USA are less frequently self-compatible than non-invasive ones. This discrepancy could reflect that Sutherland (2004) used a categorical variable (invasive vs. non-invasive) instead of a continuous one (number of USA states), and that it was biased towards inclusion of invasive species that are perennials, particularly shrubs and trees, which are more frequently self-incompatible than annuals (Lloyd and Schoen 1992; Barrett et al. 1996). Other recent studies, however, found that among alien introduced species, the ones

capable of autonomous seed set are more widespread (Küster et al. 2008; Lambdon et al. 2008). Overall, our results add to the evidence that self-compatibility and autonomous seed set might promote spread of plant species.

Although our results and the results of previous studies (e.g. Rambuda and Johnson 2004; van Kleunen and Johnson 2007; Küster et al. 2008; Lambdon et al. 2008; van Kleunen et al. 2008) suggest that the ability for autonomous seed set might contribute to invasion success, we cannot exclude the possibility that other species traits that are frequently associated with autonomous seed set are the real determinants of invasiveness. For example, self-fertilization is frequently associated with an annual life-cycle (e.g. Lloyd and Schoen 1992; Barrett et al. 1996). Because annual species are frequently prevalent among invasive species, particularly as ruderals in areas disturbed by humans (e.g. Mulligan and Findlay 1970; Pyšek et al. 1995), it is well possible that other characteristics associated with annual species are the ultimate determinants of invasiveness. In our study, there were nine annual species, and all were capable of autonomous seed set. On the other hand, two of the three perennial species were self-incompatible. Nevertheless, among the nine invasive annual species in our study, the size of the invaded range in China was positively associated with the degree of autonomous seed set (Fig. 2), although this was not significant ($r = 0.603$, $P = 0.086$). Similarly, van Kleunen and Johnson (2007) showed that among monocarpic species (mostly annual and biennial species) in their data set of European species, the ones capable of autonomous seed set had larger invaded ranges in North America than the ones not capable of autonomous seed set. Therefore, we conclude that the association of autonomous seed set with invasion success is, at least partly, independent of the life-cycle of the species.

Current spread of the invasive species of Asteraceae in China might not only be affected by species characteristics such as the breeding system and life-cycle, but also by the time since introduction. Accurate data for the year of introduction are not available for most of the species in our study, but we have some information on the time of first record in China (Appendix S2—Electronic supplementary material). As one might expect, species that were recorded before 1,900 occurred in more provinces

(mean \pm SE: 27.6 ± 2.2 , $n = 8$) than species that were recorded after 1,900 (9.9 ± 1.6 , $n = 23$; t -test: $t = 6.55$, $df = 15.2$, $P < 0.001$). Consequently, the association between the breeding system and spread in China is not significant if one includes time of first record in the statistical models (results not shown). However, because invasive, widespread species are more likely to be collected than less widespread species, time of first record might simply reflect invasiveness of the species rather than time of introduction (Bucharova and van Kleunen 2009). If the time of first record would correctly reflect the time of introduction, our results would indicate that self-compatible species and species with autonomous seed production were introduced earlier than self-incompatible species and species without autonomous seed production. Because there are no specific reasons to expect such a biased introduction, we think that this is a less likely explanation of our results than that self-compatibility and autonomous seed production contribute to invasiveness of alien plant species.

Implications for risk assessment

For prevention and management of plant invasions, identification of invasive species based on functional traits is an indispensable cornerstone of designing protocols for risk-assessment of species considered for introduction (Groves et al. 2001). Based on theoretical considerations, such as the ones behind Baker's Law (Baker 1955), many weed-risk assessment protocols like the Australian Weed Risk Assessment (Pheloung et al. 1999) include already the breeding system of plants. However, the empirical basis for considering breeding systems for risk-assessment was still relatively weak. Our study and other recent studies (Rambuda and Johnson 2004; van Kleunen and Johnson 2007; Küster et al. 2008; Lambdon et al. 2008; van Kleunen et al. 2008) provide empirical support for the inclusion of the breeding system as one of the key elements in risk assessment protocols for plant invasiveness.

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