
Effects of Self-Compatibility on the Distribution Range of Invasive European Plants in North America

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Abstract: *Many plant species have been introduced to new continents, but only a small subset of these have become invasive. It has been predicted that self-compatible species, particularly those that do not need the services of pollinators, are more likely to establish and spread after long-distance dispersal. We tested whether this hypothesis, commonly called Baker's law, applies to 361 species that have invaded the United States from Europe. Species capable of autonomous seed production occurred in significantly more states than species requiring a pollen vector. Moreover, of the species that are not capable of autonomous seed production, self-compatible species occurred in significantly more states than those that are not self-compatible. The positive effect of autonomous seed production on the range of invasion was larger for abiotically pollinated species than for biotically pollinated species and for monocarpic species than for polycarpic species. These results support Baker's law, and we recommend that screening protocols for predicting invasiveness of species considered for introduction should include assessment of their breeding system.*

Keywords: alien plants, biological invasion, breeding system, nonindigenous plants, phylogenetically independent contrast, plant life span, pollen vector, vegetative reproduction

Efectos de la Autocompatibilidad sobre el Rango de Distribución de Plantas Europeas Invasoras en Norte América

Resumen: *Muchas especies de plantas han sido introducidas a nuevos continentes, pero solo un pequeño subconjunto se ha convertido en invasoras. Se ha pronosticado que es muy probable que especies autocompatibles, particularmente las que no requieren los servicios de polinizadores, se establezcan y dispersen. Probamos si esta hipótesis, comúnmente denominada ley de Baker, aplica a 361 especies que han invadido los Estados Unidos desde Europa. Las especies capaces de la producción autónoma de semillas estuvieron presentes en significativamente más estados que las especies que requieren un vector de polen. Más aun, de las especies que no son capaces de la producción autónoma de semillas, las especies autocompatibles ocurrieron en significativamente más estados que aquellas que no son autocompatibles. El efecto positivo de la producción autónoma de semillas en el rango de invasión fue mayor en especies polinizadas abióticamente que en especies polinizadas bióticamente y en especies monocárpicas que en especies policárpicas. Estos resultados soportan la ley de Baker, y recomendamos que los protocolos de monitoreo para la estimación de la capacidad invasiva de especies consideradas para su introducción incluyan la evaluación de su sistema de reproducción.*

Palabras Clave: contraste filogenéticamente independiente, invasión biológica, longevidad de plantas, plantas exóticas, plantas no nativas, reproducción vegetativa, sistema de reproducción, vector de polen

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Introduction

Biological invasions are recognized as one of the greatest threats to the ecological (Drake et al. 1989; Vitousek et al. 1996) and economic (Pimentel et al. 2000) well-being of our planet. Of the many species that have been introduced from their native range to new continents, only a small subset has become invasive (e.g., Groves 1991). To prevent new introductions of potentially invasive species, predictors of invasiveness are needed. Unfortunately, too little is known about determinants of invasiveness for this ideal to be realized (Kolar & Lodge 2001).

Introduced plants can become invasive only if they manage to reproduce in the new range, where they may suffer from mate and pollinator limitation. Five decades ago, Baker (1955, 1967) suggested that the means of reproductive assurance after long-distance dispersal was self-compatibility in the case of mate limitation and autonomous seed production and vegetative reproduction in the case of pollinator limitation. This hypothesis was later called Baker's law (Stebbins 1957). Nevertheless, the promotion of Baker's hypothesis to a law may have been premature because evidence in support of the hypothesis is largely anecdotal or confined to single-species studies (Barrett 1996; but see Price & Jain 1981 for an exception). Nevertheless, it is commonly mentioned as a potential explanation for why some species become invasive and others do not (Baker 1974; Rambuda & Johnson 2004).

A high proportion of self-compatible species within the group of invasive species (Williamson & Fitter 1996; Rambuda & Johnson 2004) suggests that Baker's law may hold for invasive plants. On the other hand, several recent studies report that evidence for the role of pollination and breeding systems determining invasiveness of plants is equivocal (Rejmánek 1996; Richardson et al. 2000a; Memmot & Waser 2002). So far, however, hardly any study (but see Sutherland 2004) has explicitly tested the hypothesis that self-compatibility and autonomous seed production contribute to the invasion process.

Although outcrossing, when possible, might be beneficial for the evolution of invasive plants (Baker 1974), the capacity for autonomous seed production, which does not necessarily preclude outcrossing, is likely to be important during several stages of the invasion process. This is contrary to the common misconception, corrected by Pannell and Barrett (1998), that Baker's law applies only to the initial colonization of a landmass. First, autonomous seed production is likely to enable introduced plants to become naturalized (i.e., to reproduce consistently and sustain populations over many life-cycles without direct intervention by humans) (Richardson et al. 2000b). Second, autonomous seed production is likely to enable further spread of the naturalized plants by increasing propagule pressure and thus to become invasive (i.e., to produce reproductive offspring at considerable distances from parent plants) (Richardson et al. 2000b). The contribution

of autonomous seed production to naturalization will be difficult to assess for nonnaturalized species because it is generally not known whether they have been introduced. The contribution of autonomous seed production to invasiveness, nevertheless, can be assessed by comparing invasive and noninvasive naturalized species.

Unfortunately, owing to inconsistent use of terminology in the field of invasion biology, it has been hard to measure actual invasiveness of a species. A promising approach that has been successfully applied recently, and which is consistent with the concept that invasiveness involves range expansion (Richardson et al. 2000a; Colautti & MacIsaac 2004), is to quantify invasiveness as size of the range of invasion in which a species is considered noxious (e.g., Mitchell & Power 2003) or, more neutrally, present (e.g., Muth & Pigliucci 2006).

The contribution of self-compatibility and autonomous seed production to the range of invasion is likely to depend on several other characteristics of the species. The importance of pollinator limitation in reducing seed production is most likely to apply to species that require biotic instead of abiotic pollen vectors (Carlquist 1974; Ehrendorfer 1979). Reproductive assurance through self-compatibility and autonomous seed production are likely to be less essential for polycarpic species that can wait for suitable mates and pollinators than for monocarpic species that have only one reproductive opportunity (Cox 1989; Lloyd & Schoen 1992; Bond 1994). The same applies to species that have a means of vegetative reproduction. Furthermore, invasiveness is often linked to taxonomic group or phylogeny (Daehler 1998; Pyšek 1998; Richardson & Rejmánek 2004), which implies that analyses testing for predictors of invasiveness should correct for phylogenetic affinity. This can be done by accounting for the variation explained by families and genera within families or by using phylogenetically independent contrasts (Felsenstein 1985).

To test whether Baker's law applies to invasive plants and whether it depends on a species' life cycle, capacity for vegetative reproduction, and need for a biotic pollen vector, we compiled and analyzed a large data set on the range of invasion and reproductive characteristics of 361 European seed plants naturalized in the United States.

Methods

Data Collection

We focused on seed plants naturalized to the United States from Europe because for these plants there are comprehensive data on both their distribution in the introduced range and their reproductive traits. We used the U.S. Department of Agriculture (USDA) Plants Database (freely accessible at <http://plants.usda.gov>) to compile a list of alien species naturalized in the United States. For each of these species, we checked whether they were listed in the

BiolFlor Database on the German flora (accessible for registered users from <http://www.ufz.de/biolflor/index.jsp>; Klotz et al. 2002) either as native plants or archaeophytes (i.e., species that had become naturalized in central Europe from the surrounding areas prior to the discovery of the Americas).

From the BiolFlor Database, we extracted data on self-compatibility, autonomous self-pollination, autonomous apomixis, vegetative reproduction, and life cycle (monocarpic, polycarpic). Species were categorized as having the capacity for autonomous seed production if they had autonomous apomixis or were self-compatible and had the capacity for autonomous self-pollination. Capacity for autonomous self-pollination in plants generally does not exclude outcrossing through the actions of pollen vectors. Thus, all species, regardless of their capacity for autonomous self-pollination, were assigned to either the biotic or abiotic pollen-vector trait category, unless they were strictly self-pollinating. Although some species in the BiolFlor Database have been assigned to trait categories based on available information from other species of the same genus or family, we only included data that had been assessed at the species level. The final data set (available from M.v.K.) included 361 species representing 225 genera and 61 families.

As a measure of size of the range of invasion, we compiled the number of U.S. states in which each of the species occurs from the distribution maps in the USDA Plants Database (see also Muth & Pigliucci 2006). The number of U.S. states is a crude estimate of invasiveness because it does not consider the species distribution within the states and the size of the states. Nevertheless, our measure of range of invasion corresponds well with other measures of invasiveness. Species that are listed as noxious in the United States (freely accessible at http://invader.dbs.umt.edu/Noxious_Weeds/) are present in more states than the species that are not considered noxious (medians are 40 and 15, respectively; Mann-Whitney $U = 5110.50$, $Z = -6.584$, $p < 0.001$). Moreover, species that are listed as natural-area invaders (freely accessible at <http://www.nps.gov/plants/alien/list/all.htm>) are also present in more states than the species that are not listed as such (medians are 38 and 11, respectively, Mann-Whitney $U = 6261.00$, $Z = -9.774$, $p < 0.001$). Therefore, we were confident that our estimate of range of invasion was sufficiently accurate for our purpose.

Analyses

We tested for differences in the number of occupied U.S. states between autonomous and nonautonomous seed-producing species and between self-compatible and self-incompatible species with a nonparametric Mann-Whitney test. Because this test does not correct for phylogeny, we used the CAIC software (Purvis & Rambaut 1995) on the phylogeny of German plants (compiled

by Durka [2002]; available in the BiolFlor database) to test also for such differences with phylogenetically independent contrasts. We did not have information on the branch lengths of this phylogeny and therefore assigned equal lengths to them (i.e., we implicitly assumed a punctual form of evolution). Because the independent variables (autonomous seed production and self-compatibility) were binomial, we used the brunch algorithm in CAIC (Purvis & Rambaut 1995). Significance of the deviation of the average contrast from zero was tested with a t test. Because it is not possible to test for interactions between autonomous seed production and other noncontinuous traits (pollen vector, life cycle, and capacity for vegetative reproduction) within the framework of phylogenetically independent contrasts, we also used the general linear mixed model (GLMM) restricted maximum likelihood (REML) method with the binomial distribution and the logit link function (Mitchell & Power 2003), implemented in the statistical software Genstat 9.0. In these analyses, testing for effects of autonomous seed production and self-compatibility on size of the range of invasion, we controlled for effects of taxonomy by including family, genus nested within family, and their interactions with autonomous seed production and self-compatibility as random factors. In these analyses we considered species trait categories to be fixed. When we tested for effects of pollen vector, life cycle, vegetative reproduction, and their interactions with autonomous seed production, we also included family and genus but not their interactions with the other factors because the models did not converge. All χ^2 statistics are type III Wald tests unless stated otherwise.

Results

Overall, species capable of autonomous seed production had a larger range of invasion than species that are not capable of autonomous seed production (Fig. 1a; Mann-Whitney $U = 12891.00$, $Z = -2.916$, $p = 0.004$). This effect remained significant when using phylogenetically independent contrasts ($t_{87} = 2.70$, $p = 0.008$) and when using GLMM to control for taxonomy and its interactions ($\chi^2 = 7.92$, $p = 0.005$). The GLMM analysis also showed that size of the range of invasion did not differ significantly among families (variance component \pm SE = 0.276 ± 0.246 ; $Z = 1.12$, one-tailed $p = 0.131$) or among genera within families (variance component \pm SE = 0.781 ± 0.695 ; $Z = 1.12$, one-tailed $p = 0.131$). The effect of autonomous seed production on size of the range of invasion did not differ significantly among families (variance component \pm SE = 0.029 ± 0.198 ; $Z = 0.15$, one-tailed $p = 0.442$) but differed among genera within families (variance component \pm SE = 2.739 ± 0.713 ; $Z = 3.84$, one-tailed $p < 0.001$). Furthermore, the differences in size of the range of invasion between species with and

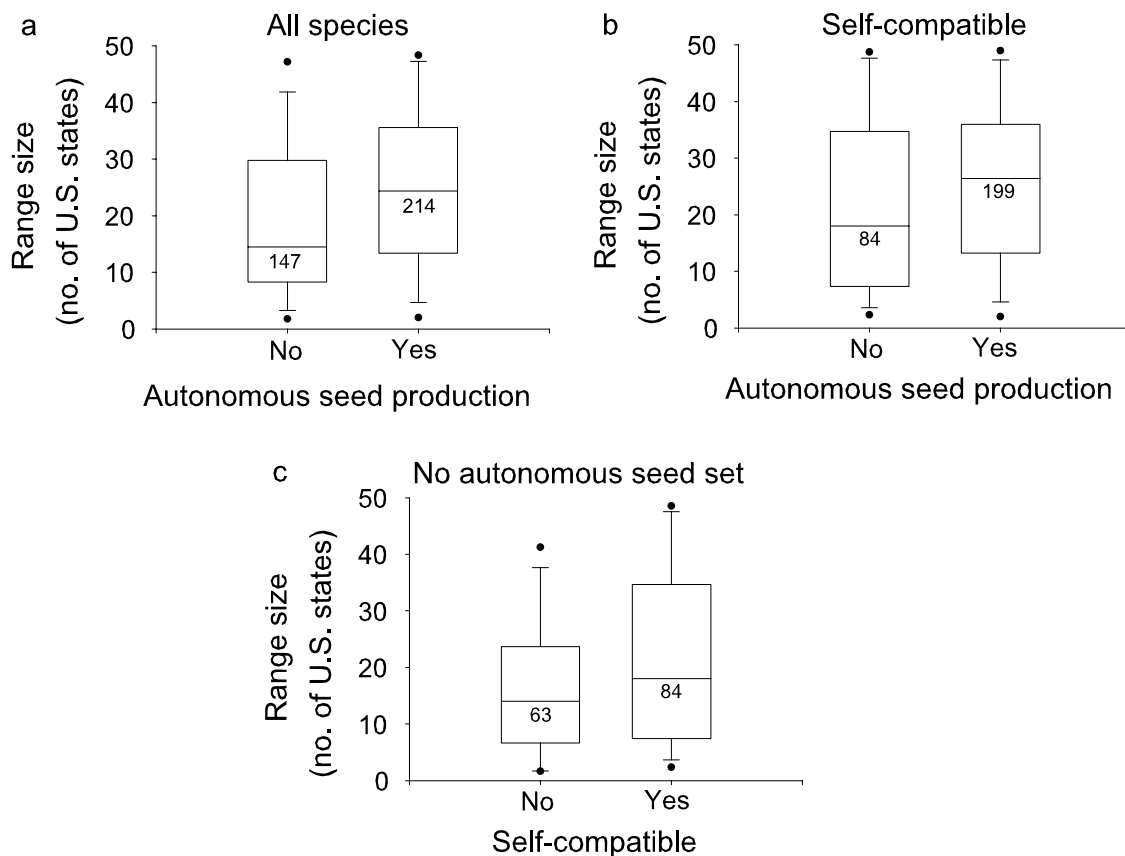


Figure 1. Range of invasion of European plants in North America as associated with capacity for autonomous seed production and self-compatibility: (a) range size of all species with and without the capacity for autonomous seed production, (b) range size of self-compatible species with and without the capacity for autonomous seed production, and (c) range size of self-compatible and self-incompatible species without the capacity for autonomous seed production (i.e., species without the capacity for autonomous self-pollination and autonomous apomixis). Figures are based on fitted values from general linear mixed model REML analyses accounting for taxonomy. The boundaries of the box around the median indicate the 75th and 25th percentiles. The whiskers indicate the 90th and 10th percentiles, and the dots above and below each box indicate the 95th and 5th percentiles, respectively. Numbers below the medians indicate the number of species.

without autonomous seed production remained significant when controlling for pollen vector (biotic, abiotic), life cycle (monocarpic, polycarpic), and the capacity for vegetative reproduction ($\chi^2 = 46.82$, $p < 0.001$ in Table 1).

These results could indicate that after introduction to a new region, autonomous seed production alleviates a lack of suitable mates, suitable pollen vectors, or both. To test these possibilities, we analyzed the subset of 283 self-compatible species. The self-compatible species capable of autonomous seed production (i.e., self-pollination) had on average a larger range of invasion (Fig. 1b). This difference, nevertheless, was not significant with a Mann-Whitney test (Mann-Whitney $U = 7265.00$, $Z = -1.739$, $p = 0.082$), phylogenetically independent contrasts ($t_{61} = 1.78$, $p = 0.080$), or GLMM ($\chi^2 = 1.36$, $p = 0.243$). When we analyzed the subset of 147 species without ca-

capacity for autonomous seed production (i.e., the species that require a pollen vector), the self-compatible species had a larger range of invasion than the self-incompatible ones (Fig. 1c). Although this effect was not significant in the analysis without phylogenetic correction (Mann-Whitney $U = 2201.50$, $Z = -1.742$, $p = 0.082$), it was significant for phylogenetically independent contrasts ($t_{39} = 2.09$, $p = 0.043$) and when correcting for taxonomy in GLMM ($\chi^2 = 4.47$, $p = 0.034$).

On average, alien species requiring biotic pollen vectors had a larger range of invasion than abiotically pollinated species (Fig. 2a; Table 1). Nevertheless, the species with abiotic pollen vectors and a capacity for autonomous seed production had the largest range of invasion (Fig. 2a). This reflects the significant interaction of pollen vector and capacity for autonomous seed production (Table 1), which indicated that size of the range

Table 1. Results of general linear mixed model REML testing for the fixed effects of the capacity for autonomous seed production, other potentially important life-history traits, and their interactions on size of the range of invasion of European plants in North America.*

Effect	Wald statistic	P
Pollen vector	38.17	<0.001
Life cycle	18.52	<0.001
Capacity for vegetative reproduction	2.40	0.121
Capacity for autonomous seed production	46.82	<0.001
Pollen vector*capacity for autonomous seed production	38.28	<0.001
Life cycle*capacity for autonomous seed production	23.87	<0.001
Capacity for vegetative reproduction*capacity for autonomous seed production	0.01	0.906

*Significance levels of the type III Wald statistics were assessed from a χ^2 -distribution with 1 df. The random model of the analysis included family and genus.

of invasion for alien species that use biotic pollen vectors was not as strongly associated with capacity for autonomous seed production as was the case for species that use abiotic pollen vectors (Fig. 2a; Table 1).

Monocarpic species had a significantly larger range of invasion than polycarpic species (Fig. 2b; Table 1). Moreover, the apparent positive effect of autonomous seed production on the size of the range invasion was significantly larger for monocarpic species than for polycarpic ones (Fig. 2b; Table 1). On average, nonvegetatively reproducing plants had a larger range of invasion than vegetatively reproducing plants (Fig. 2c), but this effect was not significant (Table 1). Furthermore, size of the range of invasion was more strongly associated with autonomous seed production for nonvegetatively reproducing plants than it was for vegetatively reproducing plants (Fig. 2c), but this interaction was also not significant (Table 1).

Discussion

The results of our study support the hypothesis that the range of invasion of self-compatible species is larger than the range of invasion of species that are self-incompatible. These results thus provide strong support for Baker's law and its applicability to biological invasions. Our results suggest that a lack of suitable mates rather than a lack of suitable pollinators is the main barrier for establishment of introduced plants in a new region. This insight was derived from two main findings. First, among species that depend on pollen vectors, the range of invasion was larger for the self-compatible species (Fig. 1c). Second, among

self-compatible species, the range of invasion was not significantly larger for those capable of autonomous seed production (Fig. 1b). These results support the findings of other studies that show that alien plants are generally and frequently visited by potential pollinators (Memmot & Waser 2002; van Kleunen & Johnson 2005).

Some families and genera are overrepresented among invasive species (Daehler 1998; Pyšek 1998; Richardson & Rejmánek 2004). In our study the variance in size of the range of invasion explained by families and genera within families was not significant, but the effect of the capacity for autonomous seed production differed among genera within families. Thus, analyses of the association between life-history traits and invasiveness should contain a correction for the phylogenetic affinity of species. In our study differences in size of the range of invasion between species with capacity for autonomous seed production and species without this capacity remained significant in analyses with phylogenetically independent contrasts and when controlling for variation explained by families and genera within families (Table 1). For analyses of species that depend on pollen vectors, correction for phylogeny and taxonomy increased the significance of differences between self-compatible and self-incompatible species in the size of their range of invasion. This shows that it is important to correct for phylogenetic affinity.

In contrast to our study a recent meta-analysis of life-history traits of U.S. weeds (Sutherland 2004) indicates that invasive exotic weeds are less frequently self-compatible than noninvasive exotic weeds. There are several potential causes for this apparent discrepancy between these results and ours. First, in contrast to our study, Sutherland's (2004) comparison of noninvasive and invasive exotic plants was restricted to species that are considered weeds by different authorities. Second, although Sutherland (2004) does not provide a definition of *invasive*, it appears that only plants that invade natural areas were considered invasive. Third, in contrast to us, Sutherland (2004) treated invasiveness as a categorical factor instead of a continuous variable. Fourth, Sutherland (2004) did not correct for taxonomy and other life-history traits that may be confounded with self-compatibility. This means Sutherland (2004) addressed a different question—whether self-compatibility contributes to the invasion of natural areas by weedy species—and did not consider size of the range of invasion and taxonomy.

If lack of suitable pollinators poses a major limitation for establishment of plants, species that use abiotic pollen vectors, such as wind and water, would be expected to be more successful at establishment than species that rely on biotic vectors (Carlquist 1974; Ehrendorfer 1979). Although the largest range of invasion was found for abiotically pollinated species with autonomous seed production, alien species requiring biotic pollen vectors had, on average, a larger range of invasion than abiotically

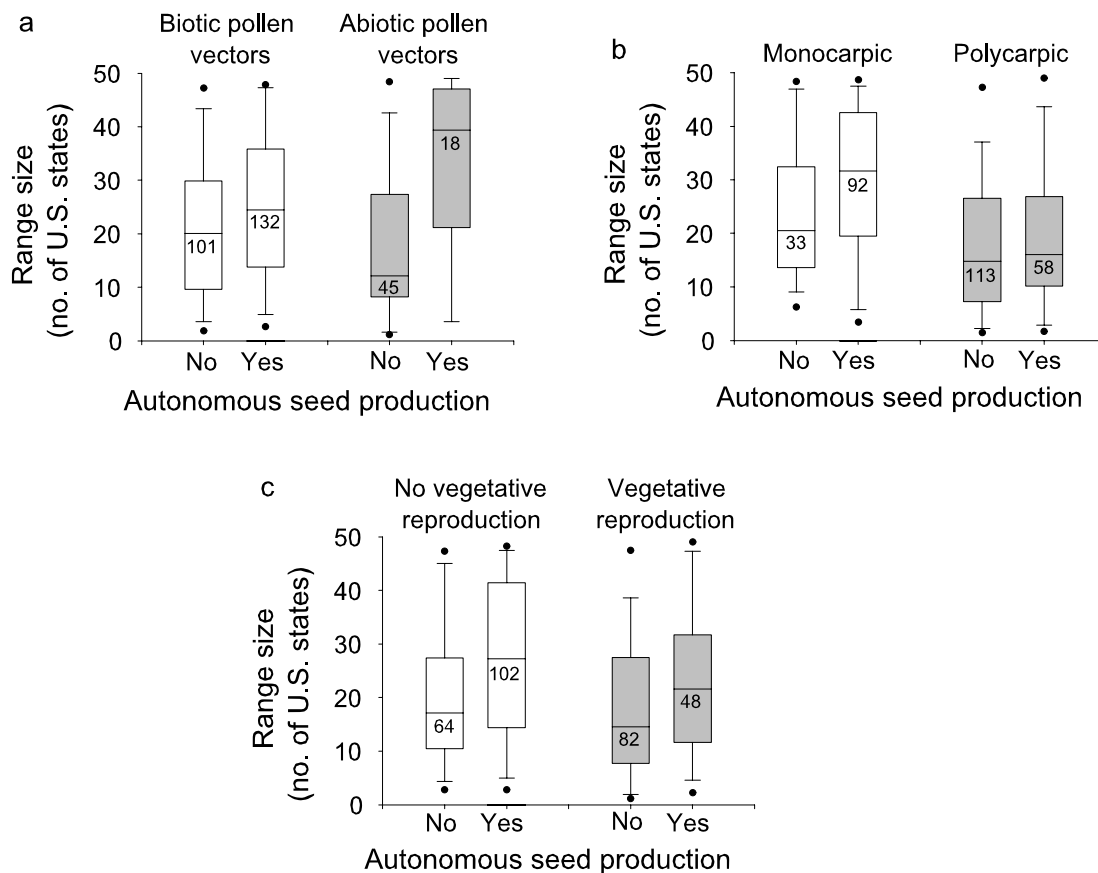


Figure 2. The positive effect of autonomous seed production on size of the range of invasion in relation to other plant life-history traits: (a) species with biotic pollen vectors only and species that can use abiotic pollen vectors, (b) monocarpic and polycarpic species, and (c) species without and with vegetative reproduction. Figures are based on fitted values from a generalized linear mixed model REML analysis (Table 1) accounting for taxonomy and the other life-history traits. See Fig. 1's caption for explanation of the box and whisker plots.

pollinated species (Fig 2a). This is in agreement with the results of other recent studies that indicate that pollen limitation in wind-pollinated plants may be larger than expected (Koenig & Ashley 2003). In addition, size of the range of invasion in alien species that use biotic pollen vectors was not as strongly associated with capacity for autonomous seed production as was the case for species that use abiotic pollen vectors. These results provide further evidence that invasiveness generally is not limited by the availability of suitable pollinators.

It is generally thought that long-lived plants with multiple flowering episodes depend less on reproductive assurance supplied by self-compatibility and autonomous seed production, particularly during population establishment, because they can wait for partners (Cox 1989; Lloyd & Schoen 1992; Bond 1994). Indeed, the positive effect of autonomous seed production on the size of the range of invasion was significantly larger for monocarpic plants than for polycarpic ones. Overall, nevertheless, monocarpic plants had a significantly larger range of invasion than polycarpic plants after controlling for capacity

for autonomous seed production. This probably occurred because alien plants have a high likelihood of establishing in disturbed sites where a ruderal strategy associated with an annual life cycle is favored (Grime 1979).

Vegetative reproduction may be an alternative for reproductive assurance through autonomous seed production (Baker 1955). Thus, it would be predicted that autonomous seed production is less important for vegetatively reproducing plants than for species that rely entirely on seeds for reproduction. Although the size of the range of invasion was more strongly associated with autonomous seed production in nonvegetatively reproducing plants than in vegetatively reproducing plants, this interaction was not significant. Overall, nonvegetatively reproducing plants tended to be more invasive than vegetatively reproducing plants, but this effect was also not significant. In a meta-analysis on introduced woody species in the United States, Reichard and Hayden (1997) found that the invasive species are more frequently capable of vegetative reproduction. The meta-analysis on weeds in the United States by Sutherland (2004),

nevertheless, did not reveal a difference in vegetative reproduction between invasive and noninvasive exotic weeds.

The reason the main effect of vegetative reproduction and its interaction with autonomous seed production were not significant in our analysis is probably that vegetative reproduction was confounded with polycarpy. Indeed, when we fitted vegetative reproduction before life cycle and the interaction of vegetative with autonomous seed production before the interaction of life cycle with autonomous seed production in a sequential GLMM, they were both significant ($\chi^2 = 62.98$, $p < 0.001$, and $\chi^2 = 16.05$, $p < 0.001$, respectively). Overall, nevertheless, these results suggest that in contrast to autonomous seed production, vegetative reproduction does not necessarily increase size of the range of invasion. The reason for this is probably that dispersal of vegetative offspring is generally more spatially restricted than dispersal of seeds. Consequently, vegetative reproduction may contribute to invasiveness by increasing the growth rate of local populations but generally not result in spread and establishment of new populations.

Our data set of 361 species native to Europe comprised both species that are considered native to Germany (259 species) and species considered archaeophytes in Germany (102 species). In a criticism of the study by Prinzing et al. (2002), Pyšek et al. (2004) argue that these groups should not be lumped because archaeophytes have ecologically distinct features and originate mainly from Mediterranean and western Asian regions. We think that in our study it is legitimate to lump both groups because they are part of the same source area (Europe) from which these species were introduced into North America. Our results, nevertheless, did not change when we included "native versus archaeophytes" as a factor in the analyses (results not shown). Furthermore, excluding archaeophytes from the analyses, as recommended by Pyšek et al. (2004), made the difference in size of the range of invasion between species with and without autonomous seed production even more pronounced.

Conclusions

The control of invasive organisms is expensive, labor intensive, and often meets with little success (e.g., Myers et al. 2000). Therefore, it is important to prevent new introductions of potentially invasive species. Protocols for screening species under consideration for introduction outside their native range require knowledge about traits that determine invasiveness (e.g., Pheloung et al. 1999; Daehler & Carino 2000), but the search for traits associated with invasiveness has met with little success (Kolar & Lodge 2001; but see Rejmánek & Richardson 1996). Our results point to a strong role of breeding system in plant invasions and show that the magnitude of its effects

depends on other life-history traits. Nevertheless, a considerable amount of the variance in the size of the range of invasion remains unexplained. Therefore, future studies should include additional life-history traits, environmental parameters, and introduction history. The ability to accurately predict species invasiveness is one of the ultimate long-term goals of invasion biology and will not be accomplished by a single study. Nevertheless, our results show that self-compatibility and autonomous seed production increased the size of range of invasion of most European species in North America. Therefore we recommend that the breeding system of a species be assessed before it is introduced outside its native range.

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