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Phylogenetically Independent Associations between Autonomous Self-Fertilization and Plant Invasiveness

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ABSTRACT: Many plant species have been introduced from their native ranges to new continents, but few have become naturalized or, ultimately, invasive. It has been predicted that species that do not require the presence of compatible mates and the services of pollinators for reproduction will be favored in establishment after long-distance dispersal. We tested whether this hypothesis, generally referred to as Baker's law, holds for South African species of Iridaceae (iris family) that have been introduced in other regions for horticultural purposes. Fruit and seed production of flowers from which pollinators had been experimentally excluded was assessed for 10 pairs of species from nine different genera or subgenera. Each species pair comprised one naturalized and one nonnaturalized species, all of which are used in international horticulture. On average, species of Iridaceae that have become naturalized outside their native ranges showed a higher capacity for autonomous fruit and seed production than congeneric species that have not become naturalized. This was especially true for the naturalized species that are considered to be invasive weeds. These results provide strong evidence for the role of autonomous seed production in increasing potential invasiveness in plants.

Keywords: alien species, Baker's law, biological invasion, breeding system, pollination, self-compatibility.

Biological invasions are recognized as one of the greatest threats to both the ecological (Drake et al. 1989; Vitousek et al. 1997) and the economic (Pimentel et al. 2000) well-being of our planet. Of the many species that have been introduced from their native ranges to other continents, however, only a small subset have established naturalized populations, and even fewer species have spread and become invasive (Williamson and Fitter 1996*b*). Naturalized and nonnaturalized introduced species therefore offer unique study systems to assess which traits are associated with successful colonization and naturalization. Assessment of such traits contributes to understanding of the evolutionary ecology of colonization and provides valuable information required for the development of screening protocols of potential invasiveness of species considered for introduction into new regions (Pheloung et al. 1999; Daehler and Carino 2000). Information on such traits is still very restricted, however (Kolar and Lodge 2001; Pysek and Richardson 2007; van Kleunen and Richardson 2007).

Introduced plants can become naturalized and ultimately invasive (i.e., can spread) only if they manage to reproduce in the new range (Richardson et al. 2000). Self-compatibility, particularly in combination with self-pollination (i.e., autonomous self-fertilization), has been suggested as an important means of reproductive assurance in the case of mate and pollinator limitation following long-distance dispersal (Baker 1955, 1967). This hypothesis, generally referred to as Baker's law (Stebbins 1957), should apply not only to plants but to any organisms that have the capacity for unisexual or uniparental reproduction (Baker 1955). Even in the presence of some cross-pollination, autonomous self-fertilization may increase seed production and thereby propagule pressure, which has been suggested as an important factor in explaining invasions (e.g., Lockwood et al. 2005; Colautti et al. 2006). Baker's law may therefore help to explain why some species

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become naturalized and invasive while other introduced species do not (Baker 1974; Rambuda and Johnson 2004).

Despite the potential implications of Baker's law, little evidence exists either to support or to refute it (Price and Jain 1981; Barrett 1996). A generally observed high proportion of self-compatible species among invasive taxa (Brown and Marshall 1981; Williamson and Fitter 1996*a*; Rambuda and Johnson 2004) has, until recently, been the main evidence to suggest that Baker's law may hold for exotic plants. On the other hand, there are also examples of highly invasive species that are self-incompatible (Sun and Ritland 1998; Brennan et al. 2005; Lafuma and Maurice 2007) or dioecious (Cronk and Fuller 2001). However, in some of these species, leaky self-incompatibility or incomplete dioecy could contribute to colonization success (Pannell and Barrett 1998; Pannell and Dorken 2006).

A recent meta-analysis of life-history traits of 142 exotic weeds of the United States (Sutherland 2004) found that invasive species were less frequently self-compatible than noninvasive species, a finding that apparently refutes Baker's law. In contrast, another recent meta-analysis found that among 361 European species, those capable of autonomous seed production have a larger invaded range in the United States (van Kleunen and Johnson 2007*a*), which supports Baker's law. These two studies (Sutherland 2004; van Kleunen and Johnson 2007*a*) considered self-compatibility and capacity for autonomous seed production as binomial variables instead of as continuous ones and thus do not differentiate between species with low and high capacities for autonomous seed production. Furthermore, they compared successfully and unsuccessfully established plants (i.e., all plants were naturalized) instead of naturalized and nonnaturalized plants.

Invasiveness is biased with respect to taxonomy and phylogeny (Daehler 1998; Richardson and Rejmánek 2004), and it is thus important to control for this bias when testing for the association between species traits and naturalization or invasiveness (Pysek and Richardson 2007). Although the database study of van Kleunen and Johnson (2007*a*) corrected for phylogeny, there have been no previous experimental studies that have used phylogenetically independent comparisons to explicitly test the hypothesis that a capacity for autonomous seed production is associated with invasiveness. To address this shortcoming and thereby provide a rigorous test of Baker's hypothesis, we assessed levels of fruit and seed production after experimental exclusion of pollinators from plants in native populations of 10 congeneric species pairs (one naturalized elsewhere, the other not) of South African Iridaceae. Because species within genera are more closely related than species of different genera, the use of congeneric species pairs adequately controls for potential phylogenetic biases of naturalization and invasiveness (Felsenstein 1985). Since introduction itself is a major determinant of invasiveness in plants (van Kleunen et al. 2007), we used only species pairs in which both species are used in international horticulture (i.e., have actually been introduced elsewhere).

Material and Methods

Study System

Iridaceae were selected as a study system for several reasons: (1) the Iridaceae are a large, taxonomically well-studied family (e.g., Reeves et al. 2001) with more than half the species (>1,000) native to southern Africa (Goldblatt et al. 2003); (2) many species of Iridaceae from southern Africa (>300) are used in international horticulture (van Kleunen et al. 2007), indicating that they have been introduced outside of their native regions; (3) many (at least 67 species; Randall 2002; van Kleunen et al. 2007) have become naturalized in areas with similar climates, mainly Australia, New Zealand, and California (table 1; also see Thuiller et al. 2005); and (4) it is likely that more species of South African Iridaceae will be considered for international horticultural purposes in the future (Manning et al. 2002).

Ten species that have become naturalized elsewhere were selected from nine different genera and one subgenus. Each of the 10 naturalized species was paired with a congeneric partner species that has also been introduced into another region for horticultural purposes but has not become naturalized (table 1; van Kleunen et al. 2007). The genus *Moraea* was represented by two species pairs, one of which is from subgenus *Homeria*, which was until recently (Goldblatt 1998) treated as the separate genus *Homeria*. The naturalization status of each species was initially assessed from its presence or absence in *A Global Compendium of Weeds* (Randall 2002). However, because this compendium is not complete, and the naturalization status of some of the listed species is dubious (e.g., Richardson and Rejmánek 2004), the naturalization status of the species was also established by cross-checking their presence or absence in the Australian Plant Census database (http://chabg.gov.au/chah/apc/), the New Zealand Plant database (http://nzflora.landcareresearch.co.nz/), and the U.S. Department of Agriculture Plants database (http://plants.usda.gov/).

All 20 study species are native to the Cape Floral Region (Goldblatt and Manning 2000) and are perennial cormuous geophytes that might be capable of vegetative reproduction through the production of cormlets. Excavations of plants in the field indicated, however, that for most species there is only limited cormlet production (up to one cormlet per plant). Both *Chasmanthe* species pro-

Table 1: Congeneric pairs of naturalized and nonnaturalized study species

	No. populations	Pollinators	Country (state) of naturalization
Naturalized species:			
Babiana angustifolia	3	Bees	Australia (WA, Vic)
Chasmanthe floribunda[a]	3	Birds	Australia (WA, SA, NSW, Vic, Tas), New Zealand, USA (CA)
Ferraria crispa	3	Flies	Australia (WA, SA, NI, Vic)
Freesia leichtlinii[a]	1	Bees	Australia (WA, SA, Qld, NSW, Vic, Tas)
Gladiolus alatus	3	Bees	Australia (WA)
Hesperantha falcata	1	Bees, moths	Australia (WA, SA)
Moraea (Homeria) flaccida[a]	3	Bees	Australia (WA, SA, NSW, NI, Vic, Tas), New Zealand
Moraea fugax	2	Bees	Australia (WA, SA)
Romulea rosea[a]	2	Beetles	Australia (WA, SA, NSW, Vic, Tas), New Zealand, USA (CA)
Sparaxis bulbifera[a]	3	Bees, beetles	Australia (WA, SA, NSW, Vic, Tas), New Zealand
Nonnaturalized species:			
Babiana odorata	1	Bees	
Chasmanthe aethiopica	2	Birds	
Ferraria uncinata	3	Flies	
Freesia occidentalis	2	Bees	
Gladiolus meliusculus	2	Bees, beetles	
Hesperantha vaginata	2	Beetles	
Moraea (Homeria) elegans	2	Beetles	
Moraea villosa	2	Beetles	
Romulea sabulosa	2	Beetles	
Sparaxis elegans	2	Beetles, flies	

Note: CA = California, NI = Norfolk Island, NSW = New South Wales, Qld = Queensland, SA = South Australia, Tas = Tasmania, Vic = Victoria, WA = Western Australia.

[a] Species considered invasive (Weber 2003).

duced up to three cormlets per plant, and the naturalized *Gladiolus alatus* produced up to eight cormlets per plant, while its nonnaturalized congener, *Gladiolus meliusculus*, produced three to 40 cormlets per plant. All species have biotic pollen vectors, including birds, flies, beetles, and bees, and the naturalized and nonnaturalized species include the same spectrum of pollinators (table 1). Both *Chasmanthe* species produce red seeds that might be dispersed by birds, and both *Gladiolus* species produce winged seeds, indicating wind dispersal. The other species do not appear to have any specific dispersal syndromes. Overall, this indicates that the major life-history characteristics are similar for the naturalized and nonnaturalized species in our study.

Data Collection

Data were collected from breeding system experiments conducted on one to three natural populations of each of the 20 target species (table 1; 44 populations in total) during the 2006 spring flowering season. All populations were in the Western Cape province of South Africa and the area around Nieuwoudtville in the Northern Cape province (all part of the Cape Floral Region). We compared the capacity for autonomous fruit and seed production between the 10 naturalized and the 10 nonnaturalized species. The capacity for autonomous fruit and seed production in each population was assessed by experimentally excluding pollinators from the fully developed but as yet unopened flowers of 10 plants by covering them with nylon mesh bags. The number of flowers per plant ranged from one to 50, and this largely depended on the genus and species. Because of intrinsic variation among species in absolute seed production, and because of potential effects of plant age and local environment on the potential absolute seed production of plants, the capacity for autonomous fruit and seed production was assessed relative to the potential values of fruit and seed production of each species.

Because it was not feasible to count the number of nonfertilized ovules in fruits, and because plants may produce an excess of ovules, we assessed potential seed production of species by doing supplemental hand-pollinations of one to 10 open flowers on 10 plants per population. Pollen was collected from another plant that was at least 1 m away to increase the likelihood of cross-pollination. A total of three to five pollen donors were used per population. It was logistically impossible to do supplemental hand-pollination on all flowers that opened on a plant during the flowering season. As a consequence, the potential seed production may be overestimated (Knight et al. 2006). However, this applies equally to both the naturalized and nonnaturalized species and thus does not affect the comparison of autonomous seed production of these two groups. The nylon mesh bags were removed as soon as the plants had completed flowering in order to minimize any effect on plant growth. Fruit set was assessed as the proportion of flowers per plant that had produced fruits. The number of seeds per fruit was also counted.

Analyses

Because of the inherent variation in flower number among species and individuals and the unbalanced number of populations per species, we did the analyses on average species values. These average species values were calculated from the proportional fruit set and average seed production per fruit and per flower of individual plants. The main variable of interest for this study was the proportion of potential seed production achieved in the absence of pollinators. This was calculated by dividing the average number of seeds per flower of plants from which pollinators had been excluded by the average number of seeds per flower of plants that had received supplemental hand-pollination. To gain further insights into whether autonomous seed production was achieved through higher fruit set or a higher number of seeds per fruit, we additionally analyzed the average fruit set on plants from which pollinators had been excluded and the proportion of potential seed production per fruit observed without pollinators. The latter was calculated by dividing the average number of seeds per fruit on plants from which pollinators had been excluded by the average number of seeds per fruit on plants that had received supplemental hand-pollination. Because the data were not normally distributed and the variance was heterogeneous between the groups of naturalized and nonnaturalized species, the significance of differences in average fruit set and relative seed production between both groups was assessed using nonparametric Wilcoxon signed-ranks tests for paired data. Because we had explicit expectations for the differences in autonomous fruit and seed production between naturalized and nonnaturalized species, we used one-tailed significance tests (Sokal and Rohlf 1995).

Results

When pollinators were excluded from plants, 16 (seven nonnaturalized and nine naturalized species) of the 20 species produced at least one fruit. Fruit set was higher in naturalized species (median = 0.109) than in the congeneric nonnaturalized species (median = 0.030) for eight out of 10 congeneric pairs (fig. 1*A*; $Z = -1.988$, $P = .024$). Of the six congeneric species pairs in which both species produced some fruits in the absence of pollinators, the number of seeds per fruit as a proportion of the number of seeds after pollen supplementation was higher in naturalized species (median = 0.407) than in the congeneric nonnaturalized species (median = 0.158) for five congeneric pairs, but this effect was not significant (fig. 1*B*; $Z = -1.153$, $P = .125$). Overall, in the absence of pollinators, a higher relative number of seeds was produced per flower in naturalized species (median = 0.068) than in congeneric nonnaturalized species (median = 0.006) for eight out of 10 congeneric pairs (fig. 1*C*; $Z = -1.784$, $P = .037$).

Discussion

Our results indicate that autonomous seed production is positively associated with South African species of Iridaceae that have become naturalized in other regions. Autonomous seed production increases the chance of establishment of naturalized populations when only a few individuals are introduced and when there are no suitable pollinators (Baker 1955). Even when suitable pollinators are present, they might only incidentally visit the initially small populations, as has been shown for rare native species (e.g., Ward and Johnson 2005). Autonomous seed production of horticultural plants is also likely to facilitate their propagation by gardeners and consequently to increase propagule pressure (Colautti et al. 2006). In other words, autonomous seed production thus might increase the possibility that a species will establish and maintain naturalized populations not only directly but also indirectly through increased opportunities for doing so.

An exception to the observed pattern was the nonnaturalized species *Hesperantha vaginata*, in which fruit and seed production in the absence of pollinators was higher than in its naturalized congener *Hesperantha falcata* (fig. 1). Together with the large variation in the degree of autonomous seed production among naturalized species, this emphasizes that the capacity for autonomous seed production is not the only factor that determines the establishment success of a species. Another reproductive trait that may be important for naturalization is the degree of vegetative reproduction (Baker 1974). Excavation of corms, however, revealed no signs of vegetative reproduction in either *Hesperantha* species. This implies that the unsuccessful naturalization of *H. vaginata* elsewhere, despite its relatively high capacity for autonomous seed production, is a consequence of traits other than reproduction or of extrinsic factors that codetermine naturalization success.

Previous studies of South African Iridaceae showed that their naturalization in other regions is associated also with low maximum altitude in the native range, the number of subtaxa per species, maximum plant height (van Kleunen et al. 2007), and rapid and profuse seedling emergence (van Kleunen and Johnson 2007*b*). Studies of other taxa, such as pine tree (*Pinus*) species, showed that invasiveness is associated with small seed size, a short generation time (Rejmánek and Richardson 1996), and a high relative growth rate (Grotkopp et al. 2002). Overall, however, few general predictors of naturalization and invasiveness have been identified (see review by Pysek and Richardson [2007]; van Kleunen and Richardson 2007). Therefore, continued research is required to identify other factors that are important for successful establishment of alien plant species.

In the absence of general agreement on how invasiveness should be quantified (Richardson et al. 2000; Colautti and MacIsaac 2004), we did not distinguish in our analyses between species that are considered naturalized only and those that are considered invasive. Significantly, however, the four species that contribute most strongly to the observed correlation between autonomous seed set and successful naturalization, *Chasmanthe floribunda*, *Romulea rosea*, *Sparaxis bulbifera*, and *Moraea flaccida* (fig. 1), all are listed as invasive weeds (Weber 2003). Restriction of the data set to the five genera of which the naturalized species are listed as invasive (table 1) does not affect the results, and the difference in relative number of seeds per flower between the nonnaturalized and naturalized species remains significant ($Z = -1.753$, $P = .040$), despite the reduction in statistical power.

We assessed autonomous self-fertilization of species in their native ranges because of our aim to identify predictors of invasiveness that can be assessed before a species is actually introduced. Our results suggest that breeding systems that are present before the introduction of species determine their own naturalization success. Similar studies on species from other families and other geographical regions should show how general this pattern is. It is also conceivable that breeding systems undergo further evolution in the invasive range of species. Amsellem et al. (2001), for example, found that *Rubus alceifolius* switched from self-incompatibility to apomixis, probably as a consequence of hybridization, during its invasion of Madagascar and La Réunion. On the other hand, two other recent studies showed that self-incompatibility of *Senecio*

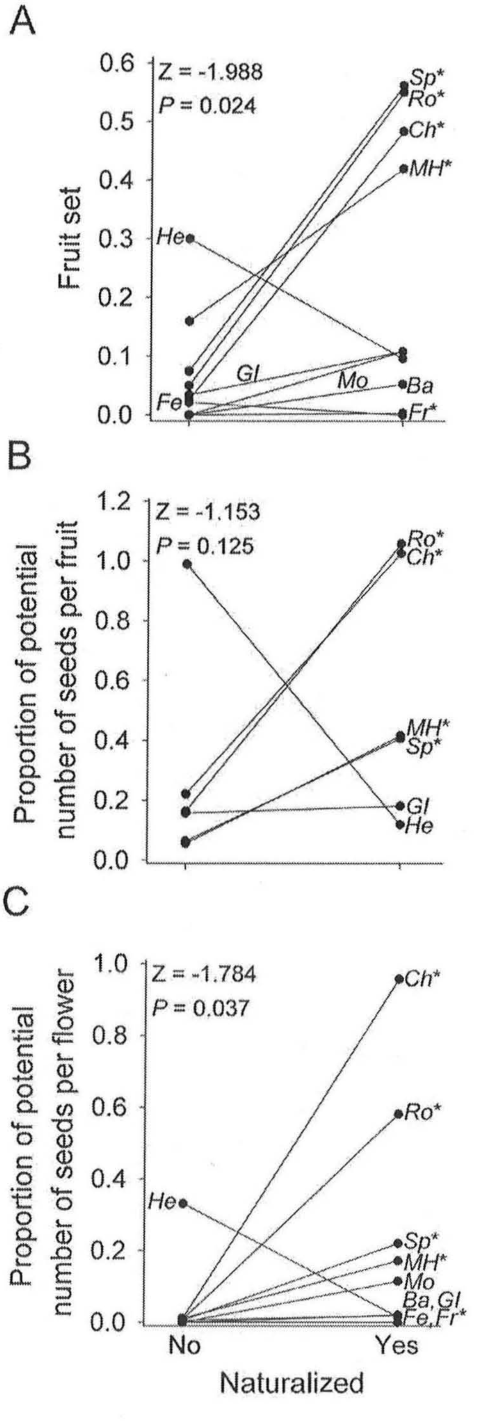

Figure 1: Naturalization within congeneric pairs of South African Iridaceae that have been introduced elsewhere for horticultural purposes is positively associated with the capacity for autonomous reproduction. *A*, Fruit set after exclusion of pollinators. *B*, Number of seeds per fruit when pollinators have been excluded relative to the number of seeds per fruit after pollen supplementation. *C*, Number of seeds per flower when pollinators have been excluded relative to the number of seeds per flower after pollen supplementation. *Ba* = *Babiana*, *Ch* = *Chasmanthe*, *Fe* = *Ferraria*, *Fr* = *Freesia*, *Gl* = *Gladiolus*, *He* = *Hesperantha*, *MH* = *Moraea* (*Homeria*), *Mo* = *Moraea*, *Ro* = *Romulea*, *Sp* = *Sparaxis*. An asterisk indicates that the naturalized species in these congeneric pairs is considered invasive (Weber 2003).

squalidus (Brennan et al. 2005) and *Senecio inaequidens* (Lafuma and Maurice 2007) has not broken down during their invasion of the British Isles and continental Europe, respectively. More studies are required to determine the extent to which breeding systems of plants evolve in regions of introduction (Barrett 1996).

Conclusions

Screening protocols for predicting potential invasiveness of species that are being considered for introduction outside their native ranges require knowledge of species traits that are known to determine invasiveness (Pheloung et al. 1999; Daehler and Carino 2000). Although evidence for the existence of general predictors of invasiveness is still limited (Kolar and Lodge 2001; Pysek and Richardson 2007), our results point to an important role for autonomous seed production in plant invasions. On the basis of this empirical support for Baker's law, we recommend that protocols for screening potentially invasive plant species include assessment of breeding systems.

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