

# Modes of reproduction in three invasive milkweeds are consistent with Baker's Rule

Megan Ward · Steven D. Johnson ·  
Myron P. Zalucki

Received: 10 October 2010 / Accepted: 1 December 2011 / Published online: 14 December 2011  
© Springer Science+Business Media B.V. 2011

**Abstract** According to Baker's Rule, uniparental reproduction is associated with colonizing plants because it provides a means for population establishment following single long-distance dispersal events. There is, however, limited evidence for the applicability of Baker's Rule to invasive plants. We determined the breeding systems of three invasive milkweed species—*Asclepias curassavica*, *Gomphocarpus fruticosus* and *G. physocarpus*—in their invaded range in south-east Queensland, Australia. Although dependent on pollinators for reproduction, hand-pollinations revealed that all three species are self-compatible which is consistent with Baker's Rule and notable because milkweeds are generally self-incompatible. In progeny performance trials, seedlings from self-pollinations generally did not perform as well as those from cross-pollinations, but the differences were minor. Evidence for self-compatibility in *G. physocarpus* is a particularly noteworthy feature of this study, as this species has been reported to be self-

incompatible in its native range and may thus have evolved self-compatibility during the invasion process. Furthermore, potential for hybridization between the two *Gomphocarpus* species was observed. Hybridization may have assisted the invasion of these species through providing additional sources of pollen and/or broadening genetic variation. Our study adds to the growing evidence that breeding systems are significant for the process of plant invasion.

**Keywords** Asclepiadoideae · Baker's Rule · Breeding systems · Hybridization · Invasive plants · Progeny performance

## Introduction

It is well-recognized that biological invasions by plant species to areas outside their natural ranges can have detrimental ecological, agricultural and economic consequences (e.g. see Vitousek et al. 1997; Mack et al. 2000; Pimentel 2002). In Australia, the number of invasive plant species is enormous, with recent documentation of almost 3,000 exotic plant species that are “weedy” (Randall 2007). Accordingly, expenditure on control programs for invasive plants in Australia is substantial. The national expenditure on invasive plant control, together with the costs of agricultural loss, has been estimated as high as

---

M. Ward (✉) · M. P. Zalucki  
School of Biological Sciences, The University  
of Queensland, Brisbane, QLD 4072, Australia  
e-mail: megan.ward@uqconnect.edu.au

S. D. Johnson  
DST-NRF Centre for Invasion Biology, School  
of Biological and Conservation Sciences, University  
of KwaZulu-Natal, P. Bag X01, Scottsville,  
Pietermaritzburg 3209, South Africa

AU\$4.4 billion annually (Sinden et al. 2004). In order to effectively address the threat of invasive plant species, an understanding of the factors that control the process of invasion is essential.

Reproductive systems have the potential to greatly influence population dynamics of invasive plant species through their role in determining propagule supply in terms of both quality and quantity of seeds. It follows that knowledge of plant breeding system characteristics is crucial for understanding biological invasions. One hypothesis, which is referred to as Baker's Rule (or Baker's Law), proposes that plant species capable of uniparental reproduction are more likely to become successful colonists than species that are self-incompatible or dioecious, due to their ability to establish a population following a single long-distance dispersal event (Baker 1955, 1967, 1974; Stebbins 1957). Extending Baker's Rule to invasive plant species, it is reasonable to expect that uniparental reproduction will assist in alleviating mate shortages that introduced plant species in new habitats would typically experience when conspecific plants are scarce. Indeed, uniparental reproduction would be advantageous not only in the initial establishment of populations, but also in the establishment of additional populations along the leading edge of an invasion (Pannell and Barrett 1998).

Recognizing the lack of empirical evidence to support or refute the applicability of Baker's Rule to invasive plants, recent studies have investigated breeding systems of invasive plants in order to determine whether Baker's Rule holds true. As predicted, numerous invasive plant species have been found to possess self-compatible breeding systems, including a notable proportion that are capable of autonomous self-fertilization (Rambuda and Johnson 2004; Stout 2007; van Kleunen et al. 2007, 2008; Rodger et al. 2010; Hao et al. 2011). On the other hand, self-incompatible breeding systems have also been recorded in invasive plant species (e.g. Jesse et al. 2006; Liu et al. 2006; Hong et al. 2007; Lafuma and Maurice 2007). These apparently contradictory findings indicate the need for more research into the role of self-fertility in the process of biological invasions. Knowledge of the breeding systems of invasive plants in Australia is currently very poor, limited to a single case-study on one species by Simpson et al. (2005), thereby highlighting the need for further research on this topic in Australia.

Empirical tests of Baker's Rule have been applied to various ecological contexts in addition to invasive species, including breeding system characteristics of oceanic island flora, mating system variation across the distributions of species and variation in range sizes among species. With regards to island flora, the preponderance of self-compatible species is expected according to the predictions of Baker's Rule (e.g. see Barrett 1996). While some studies have confirmed a high representation of self-compatible species on islands (e.g. McMullen 1987; Barrett 1996; Bernardello et al. 2001), other studies have reported contrasting patterns such as a high incidence of dioecious species on islands (e.g. Sakai et al. 1995; Abe 2006). With regards to mating system variation across the distribution of a species, selfing populations should be more geographically peripheral than outcrossing populations according to the predictions of Baker's Rule (e.g. see Busch 2005). Evidence in support of this has been provided by studies that have documented selection for self-compatibility in isolated regions of the range of study species (e.g. Barrett et al. 1989; Moeller and Geber 2005). Similarly, Busch (2005) found populations at the centre of his study species' range to be self-incompatible while peripheral populations were self-compatible and have adaptations for self-fertilization; however, pollen limitation of seed set appeared to be relatively uniform across the geographical range such that selection for selfing is likely driven by other ecological factors that limit population size, plant density or pollen availability in peripheral populations. Also casting uncertainty on the functionality of adaptation for selfing in peripheral populations, Herlihy and Eckert (2005) documented that realised outcrossing rates did not differ in central and peripheral populations of their study species despite apparent adaptation for autogamy in peripheral populations. Randle et al. (2009) tested the extension of Baker's Rule that species with greater selfing ability can more readily expand their geographical range. By contrasting range size metrics between sister taxa that differed in selfing ability, Randle et al. (2009) demonstrated that species most proficient at selfing had significantly larger geographical ranges than those that were less proficient at selfing.

In addition to empirical tests, other studies have developed mathematical models to assess the validity of Baker's Rule. Pannell and Barrett (1998) modelled

the predictions of Baker's Rule in the context of a metapopulation under a variety of demographic and life-history conditions, and demonstrated that selection for selfing is greatest when the proportion of occupied sites is low, while selection for selfing becomes a relatively weak force as the proportion of occupied sites approaches its maximum. Similarly, a model developed by Dornier et al. (2008) showed that metapopulation viability is dependent on the selfing rate: although outcrossers were able form a viable metapopulation through high patch occupancy, only selfers were able to recover from very low density at the regional scale. A model developed by Cheptou and Massol (2009) casts doubt on whether adaptation favours both selfing and dispersal when both parameters are free to evolve in metapopulations that display spatio-temporal variability in pollen-limitation, thereby contradicting Baker's predictions that selfing should be selected during dispersal. However, it is to be noted that selection for selfing may not be entirely dependent on the pollination environment (Busch 2011); rather, selection for selfing may be more strongly determined by demographic conditions experienced during the bottleneck that is associated with a dispersal event (Dornier et al. 2008). Consequently, more than 50 years after its publication, Baker's Rule remains an unresolved question in ecology with seemingly no general consensus regarding its predictions (Busch 2011; Massol and Cheptou 2011).

Hybridization is another aspect of the reproductive biology of plant species that may influence the process of invasion. Hybridization of exotic plant species has been documented on numerous occasions (e.g. see Schierenbeck and Ellstrand 2009), and may involve cross-pollination with a species that is native to the ecosystem that has been invaded, or cross-pollination with another species that is also exotic. Hybridization can potentially have beneficial consequences for invasiveness if, for example, it increases the vigour of progeny, creates genotypes that are more reproductively successful, increases genetic variation that enables faster adaptation and/or increases the pollen supply in sparse populations (e.g. see Ellstrand and Schierenbeck 2006; Scofield and Schultz 2006; Ayres et al. 2008; Ridley and Ellstrand 2009; Meyerson et al. 2010). Alternatively, inter-species visits by pollinators may be wasteful of pollen and/or ovules if they do not lead to viable seeds or if they result in unfit offspring due to genetic incompatibilities.

Most studies of modes of reproduction in invasive plants have used seed-set data from breeding system experiments to test whether selfing may contribute to the invasion process (e.g. Rambuda and Johnson 2004; van Kleunen et al. 2007). However, there is now extensive data showing that selfed progeny, especially of woody taxa, often experience severe inbreeding depression and thus do not contribute to the demographic trajectory of populations for plant species in their native ranges (e.g. see Ramsey et al. 2006; Scofield and Schultz 2006). It is thus critical to monitor the fates of selfed progeny in relation to crossed progeny in order to ascertain whether selfing can contribute to the invasion process.

This study investigated the breeding systems, hybridisation potential and progeny performance of three milkweed species (Apocynaceae, Asclepiadoideae c.f. Endress and Bruyns 2000) that have become highly successful weed species in Australia, namely, *Asclepias curassavica* L., *Gomphocarpus fruticosus* (L.) W.T. Aiton and *Gomphocarpus physocarpus* E. Mey. The two *Gomphocarpus* species are native to southern Africa, while *A. curassavica* is thought to have originated from South America, Central America or the Antilles (Woodson 1954). A documentation of ability to self in the study species would provide evidence in support of Baker's Rule in invasive plants. Furthermore, given that genetically-controlled self-incompatibility is almost ubiquitous within milkweeds (Wyatt and Broyles 1990), a finding of self-compatibility in these species would be highly novel. While the breeding systems of these three species have not been studied in Australia, Wyatt and Broyles (1997) found self-compatibility in a Costa Rican population of *A. curassavica* and in *G. fruticosus* from an unknown source, whereas *G. physocarpus* was reported to be self-incompatible in its native South African range (Coombs et al. 2009). Additionally, there have been suggestions that hybridization has occurred between the two *Gomphocarpus* species both in their native southern African range (Weale 1873; Goyder and Nicholas 2001) and invaded range in Australia (Forster 1994).

## Methods

### Breeding system experiments

To investigate the breeding systems of the three study species, controlled hand-pollinations were performed

during the flowering period from August 2006 to March 2007. These experiments were conducted at a single large natural population for each of the species: the *A. curassavica* population was located in Brisbane (27°31'53.9"S 152°55'09.7"E), the *G. fruticosus* population was located in the Bunya Mountains (26°51'52.2"S 151°34'13.2"E) and the *G. physocarpus* population was located in Eagleby (27°42'31.2"S 153°13'48.4"E).

In preparation for hand-pollinations, three umbels on each of 50 plants per population were bagged at the bud stage with fine-mesh cloth netting in order to exclude visits by potential pollinators to the flowers. Bagged umbels were assigned to one of the following treatments: (1) cross-pollination with a pollinium from a donor plant located at a minimum distance of 10 m from the recipient plant, (2) self-pollination with a pollinium from a different flower on the same plant and (3) unmanipulated to test for autonomous self-pollination. All three treatments were performed on every experimental plant (i.e. one umbel per treatment per plant).

Bagged umbels were checked daily and flowers were hand-pollinated on the first day of opening, thereby ensuring consistency in stigmatic chamber receptivity at the time of pollinium deposition. Umbels were individually marked with coloured string according to the treatment received. Three flowers per umbel were pollinated, as it is very rare for more than three fruit to maturity on a single umbel (M. Ward, personal observation). Only one stigmatic chamber per flower was pollinated, as a single pollinium has been shown to contain sufficient pollen for full seed set in numerous milkweed species, including *A. curassavica* and *G. fruticosus* (Wyatt et al. 2000).

The hand-pollination technique was based on a method developed by Wyatt (1976). Firstly, a pollinarium was obtained from the donor flower by using a needle to hook the corpusculum and ease the pollinia from the anther sacs. The translator arms of the removed pollinarium were severed in order to separate the two pollinia. The stigmatic chamber of the recipient flower was then exposed by sliding the needle longitudinally between a pair of anther flaps and gently easing the needle sideways to splay apart the anther flaps. While the anther flaps naturally retained an opened position, the needle was used to insert a single pollinium into the stigmatic chamber with the convex (outer) surface of the pollinium

orientated towards the interior of the flower. Using the needle, the anther flaps were then pushed together into the original position covering the stigmatic chamber.

Following hand-pollinations, pollinator-exclusion bags were immediately replaced over umbels in order to prevent subsequent pollinator visits, and to prevent insect damage to the developing fruit. After a period of 5–8 weeks, when all hand-pollinated flowers had either developed fruit or abscised, the number of fruit per treatment was recorded, the number of filled seeds per fruit was counted, and mature seeds for use in the progeny performance experiments were collected. Several pollinator-exclusion bags were destroyed during the experiments, thereby reducing the total number of plants to 45 individuals for *A. curassavica* (i.e. 135 umbels), 44 individuals for *G. fruticosus* (i.e. 132 umbels) and 49 individuals for *G. physocarpus* (i.e. 147 umbels) from a potential of 50 individuals for each species.

#### Hybridisation experiments

To investigate the potential for hybridisation between the study species, controlled hand-pollination experiments were performed between species. This was done in the same populations and during the same flowering season as the breeding system hand-pollination experiments. Fresh flowers of the three species were transported daily between the populations and used as a source of pollinia for the hand-pollinations.

In preparation for hand-pollinations, two umbels were bagged on each of 25 additional plants in each of the three populations. Using the hand-pollination technique described above, reciprocal inter-species crosses were performed such that each umbel received pollinia from one of the two other species. As in the breeding system experiment, three flowers per umbel each received a single pollinium and were individually marked with coloured string according to the treatment received. Pollinator-exclusion bags were immediately replaced over umbels following hand-pollinations.

After a period of 5–8 weeks, when all hand-pollinated flowers had either developed fruit or abscised, the number of fruit per treatment was recorded, the number of filled seeds per fruit was counted, and mature seeds for use in the hybrid progeny performance experiment were collected. Several pollinator-exclusion bags were destroyed

during the experiments, thereby reducing the total number of plants that could be used to 23 individuals for *A. curassavica* (i.e. 69 umbels), 23 individuals for *G. fruticosus* (i.e. 69 umbels) and 22 individuals for *G. physocarpus* (i.e. 66 umbels) from a potential of 25 individuals for each species.

### Performance of progeny

A glasshouse experiment was performed in order to compare the performance of selfed and crossed progeny obtained from the breeding system hand-pollination experiment. For each species, 300 seeds per pollination treatment (i.e. selfed and crossed) were selected by randomly choosing 30 seeds per fruit from ten fruit, obtained from ten different plants per treatment. Additionally, in order to determine whether hybridization has implications for progeny performance, 100 seeds per hybrid treatment were selected by randomly choosing ten seeds per fruit from ten fruit, obtained from ten different plants per hybrid treatment.

Seeds were placed on moistened filter paper in Petri dishes, which were then sealed with Parafilm in order to minimize desiccation. Petri dishes were randomly positioned on a bench in a temperature-controlled glasshouse at 28°C daytime temperature and 23°C overnight temperature, under natural light conditions. Seeds were checked for germination every 24 h for a period of 30 days, and the number of days to germination was noted for each individual seed.

After germinated seeds had grown two leaves, 20 seedlings from each crossed and selfed fruit (i.e. 200 seedlings per treatment for each species) were randomly selected and were individually potted in 15 cm pots containing general-purpose potting mix. All hybrid seedlings were similarly potted. Potted plants were randomly positioned on benches in a standard glasshouse under natural temperature and light conditions, and were watered daily. As *A. curassavica* exhibited faster growth than the two *Gomphocarpus* species, plant height was measured 8 weeks after potting for *A. curassavica* (and *A. curassavica* maternal hybrids) and after 12 weeks for *G. fruticosus* and *G. physocarpus* (and *Gomphocarpus* spp. hybrids). Ten hybrid seedlings from each treatment were kept for a longer period in order to observe whether hybrid plants reach reproductive maturity.

### Data analysis

The results of the hand-pollination experiments were analysed in order to determine, firstly, whether there were significant differences in reproductive success between cross-pollinated, self-pollinated and unmanipulated flowers, and, secondly, whether there were significant differences in reproductive success between intraspecific and interspecific crosses. Similarly, the results of the progeny performance experiments were analysed in order to determine, firstly, whether there were significant differences in performance of progeny from cross- and self-pollinations, and, secondly, whether there were significant differences in performance of intraspecific and interspecific crosses. The three study species were analysed separately, and statistical analyses were designed so as to take parent plant effects into consideration (i.e. parent plant was included as a random effect where more than one data point per plant was used in certain analyses, or only one data point per plant was used in other analyses; see descriptions of individual analyses below for further details). All statistical analyses were performed using R version 2.11.1 (R Core Development Team 2009). For the generalised linear mixed-effects models (GLMM), the 'lme4' R library was used.

In order to examine differences in fruit-set between hand-pollination treatments, a GLMM was constructed to analyse proportions of pollinated flowers per inflorescence that successfully set fruit. In order to account for any potential parent plant effects, plant identity was used as a random effect in the GLMM. The model was constructed using a binomial error structure and a logit link function. To examine differences in seed-set between hand-pollination treatments, a GLMM was constructed to analyse number of seeds per fruit. In order to account for any potential parent plant effects, plant identity was used as a random effect in the GLMM. As the data were counts, the model was constructed using a Poisson error structure and a log link function.

To determine whether pollination treatment significantly impacted on germination success, a generalised linear model (GLM) with a binomial error structure and logit link function was used to analyse the proportions of seeds per fruit that germinated (i.e. a single data point per plant, as each fruit originated from a different plant). For the seeds that germinated, a GLMM with fruit identity (i.e. parent plant) as a

random effect was constructed in order to determine if pollination treatment had a significant effect on the time to germination. As these are time data where the variance increases disproportionately with the mean, gamma errors and an inverse link function were used in this GLMM. To determine if pollination treatment had a significant effect on survival of the potted seedlings, proportions of seedlings per fruit that survived the entire duration of the experiment were analysed using a GLM with a binomial error structure and logit link function (i.e. a single data point per plant, as each fruit originated from a different plant). For plant height data, a GLMM was constructed with fruit identity (i.e. parent plant) as a random effect in order to determine if pollination treatment had a significant effect on the growth of seedlings.

## Results

### Breeding system experiments

For all three study species, no significant differences in either the proportion of flowers that set fruit or the number of seeds produced per fruit were detected in the cross-pollinated as compared to the self-pollinated treatments (Table 1), indicating that they are genetically self-compatible. The proportion of flowers that produced fruit was slightly higher for cross-pollinations as compared to self-pollinations for *G. fruticosus* and *G. physocarpus*, whereas self-pollinations had a greater success than cross-pollinations for *A. curassavica* (Fig. 1). Numbers of seeds per fruit were slightly higher in the crossed-treatment as compared to the selfed-treatment for *G. physocarpus*, while numbers of seeds per fruit were slightly higher in the selfed-treatments as compared to the crossed-treatments for *A. curassavica* and *G. fruticosus* (Fig. 1). None of the unmanipulated flowers set fruit (Fig. 1), indicating that all three study species are incapable of autonomous self-pollination (Table 1).

### Hybridization experiments

Flowers of the two *Gomphocarpus* species did not set fruit when pollinated with *A. curassavica* pollinia, and *A. curassavica* flowers did not set fruit when pollinated with *G. fruticosus* pollinia (Fig. 2). However,

*A. curassavica* flowers did very rarely set fruit when pollinated with *G. physocarpus* pollinia, although numbers of seeds per fruit was significantly reduced in hybrid fruit as compared to crossed *A. curassavica* fruit (Fig. 2). Flowers of the two *Gomphocarpus* species readily set fruit after reciprocal hand-pollinations. For *G. fruticosus* flowers, significantly higher proportions of fruit-set and significantly greater numbers of seeds were recorded following hybrid pollinations as compared to intraspecific *G. fruticosus* crossed pollinations (Table 2; Fig. 2). For *G. physocarpus* flowers, levels of fruit-production were similar when using *G. fruticosus* pollinia or *G. physocarpus* pollinia, although significantly lower numbers of seeds were recorded for hybrid fruit as compared to fruits arising from intraspecific crosses (Table 2; Fig. 2).

### Performance of progeny

#### *Intraspecific progeny*

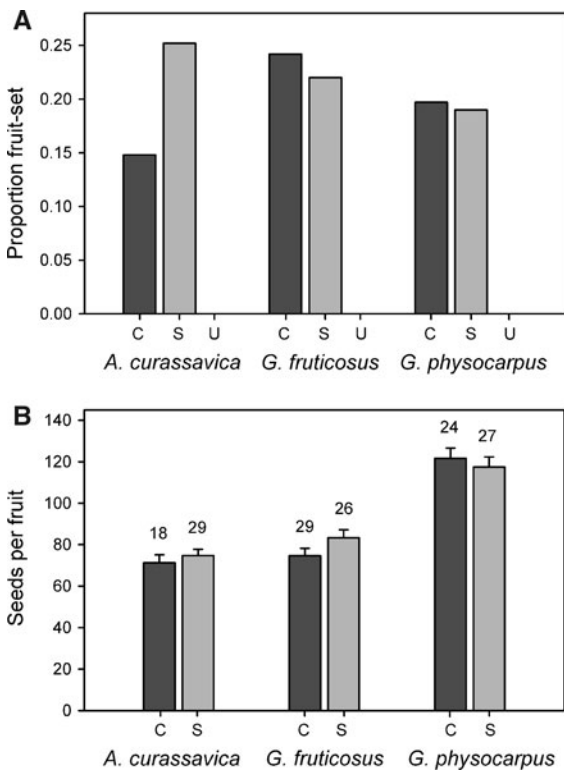
All crossed and selfed *A. curassavica* seeds germinated within the first eleven days of the experiment, with no significant difference between treatments in the time taken for seeds to germinate, showing that selfed progeny are able to perform as well as crossed progeny in this stage of the life cycle (Table 3; Fig. 3). Similarly, germination was high for all *G. fruticosus* seeds, with no significant differences in the proportion of seeds per fruit that germinated or the time taken for seeds to germinate (Table 3; Fig. 3). In contrast to these two species, self-pollination was observed to have distinct performance consequences for germination of *G. physocarpus* seeds: although seeds that germinated did not significantly differ in their time to germination, significantly fewer selfed seeds germinated per fruit than crossed seeds (Table 3; Fig. 3).

For the potted seedlings grown from the germination trials, the proportions of seedlings per fruit that survived the duration of the experiment and the height of these seedlings were greater in crossed treatments than in selfed treatments for all three plant species (Figs. 4, 5). However, the difference in survival between the two treatments was not significant for *A. curassavica* or *G. physocarpus*, but was significant for *G. fruticosus* (Table 4). Conversely, selfed seedlings were significantly shorter than crossed seedlings

**Table 1** Results of statistical comparisons of fruit-set and numbers of seeds per fruit for treatments in the breeding system experiments (see Fig. 1)

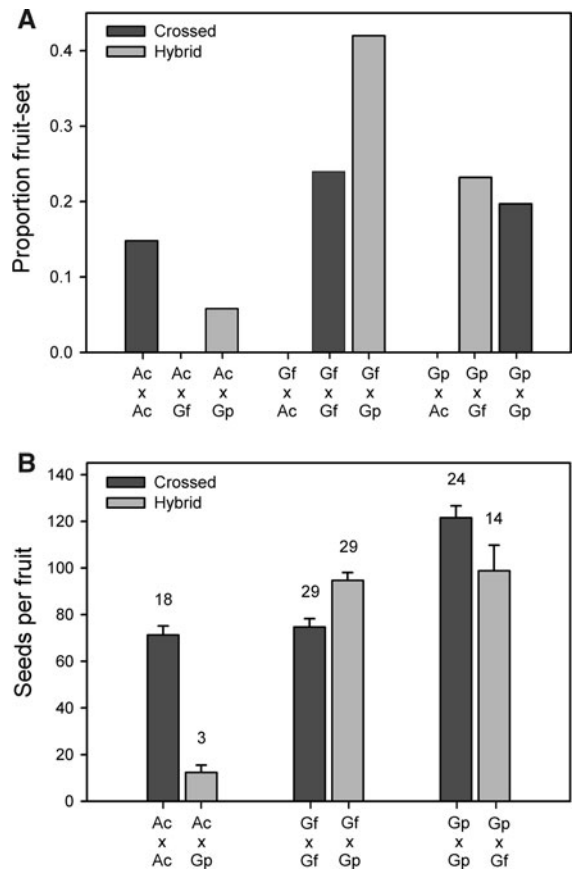
| Species                      | Proportion fruit-set |     |        |        | Seeds per fruit |    |        |        |
|------------------------------|----------------------|-----|--------|--------|-----------------|----|--------|--------|
|                              | Z                    | df  | P      | rD     | Z               | df | P      | rD     |
| <i>A. curassavica</i>        |                      |     |        |        |                 |    |        |        |
| Crossed versus selfed        | 2.558                | 132 | <0.014 | 43.647 | 0.501           | 32 | <0.625 | 13.075 |
| Crossed versus unmanipulated | -5.572               | 132 | <0.001 |        | -               | -  | -      | -      |
| <i>G. fruticosus</i>         |                      |     |        |        |                 |    |        |        |
| Crossed versus selfed        | -0.434               | 129 | <0.667 | 63.843 | 1.586           | 28 | <0.125 | 17.715 |
| Crossed versus unmanipulated | -5.851               | 129 | <0.001 |        | -               | -  | -      | -      |
| <i>G. physocarpus</i>        |                      |     |        |        |                 |    |        |        |
| Crossed versus selfed        | -0.172               | 144 | <0.864 | 41.176 | 0.293           | 34 | <0.772 | 10.680 |
| Crossed versus unmanipulated | -7.100               | 144 | <0.001 |        | -               | -  | -      | -      |

Where rD is the residual deviance of the model



**Fig. 1** Proportion fruit-set (a) and number of seeds per fruit (mean + SE, b) in the breeding system experiments for the three study species. Treatments are cross-pollinated (C), self-pollinated (S) and unmanipulated (U). Numbers above bars are sample sizes

for *A. curassavica* and *G. physocarpus*, while plant height did not differ significantly between selfed and crossed *G. fruticosus* seedlings (Table 4).



**Fig. 2** Proportion fruit-set (a) and number of seeds per fruit (mean + SE, b) in the hybridisation experiments for the three study species. Treatments are reciprocal hand-pollinations between *A. curassavica* (Ac), *G. fruticosus* (Gf) and *G. physocarpus* (Gp) written as maternal species × paternal species. Numbers above bars are sample sizes

**Table 2** Results of statistical comparison of fruit-set and numbers of seeds per fruit for treatments in the hybridisation experiments (see Fig. 2)

| Treatment                                     | Proportion fruit-set |    |        |        | Seeds per fruit |    |        |        |
|---|----------------------|----|--------|--------|-----------------|----|--------|--------|
|   | Z                    | df | P      | rD     | Z               | df | P      | rD     |
| <i>A. curassavica</i> × <i>A. curassavica</i> |                      |    |        |        |                 |    |        |        |
| <i>A. curassavica</i> × <i>G. fruticosus</i>  | -7.022               | 64 | <0.001 | 43.647 | -               | -  | -      | -      |
| <i>A. curassavica</i> × <i>G. physocarpus</i> | -7.022               | 64 | <0.001 |        | 10.530          | 20 | <0.001 | 7.241  |
| <i>G. fruticosus</i> × <i>G. fruticosus</i>   |                      |    |        |        |                 |    |        |        |
| <i>G. fruticosus</i> × <i>G. physocarpus</i>  | 2.674                | 63 | 0.007  | 18.355 | 8.228           | 57 | <0.001 | 25.940 |
| <i>G. fruticosus</i> × <i>A. curassavica</i>  | 0.011                | 63 | <0.001 |        | -               | -  | -      | -      |
| <i>G. physocarpus</i> × <i>G. physocarpus</i> |                      |    |        |        |                 |    |        |        |
| <i>G. physocarpus</i> × <i>G. fruticosus</i>  | -0.441               | 67 | 0.660  | 56.999 | 6.340           | 37 | <0.001 | 6.697  |
| <i>G. physocarpus</i> × <i>A. curassavica</i> | -0.011               | 67 | <0.001 |        | -               | -  | -      | -      |

Where rD is the residual deviance of the model; treatments are written as maternal species × paternal species

**Table 3** Results of statistical comparisons between crossed, selfed and hybrid treatments of the progeny performance experiments for germination (see Fig. 3)

| Species                            | Proportion germinated |    |        |        | Time to germination |    |        |       |
|------------------------------------|-----------------------|----|--------|--------|---------------------|----|--------|-------|
|                                    | Z                     | df | P      | rD     | Z                   | df | P      | rD    |
| <i>A. curassavica</i>              |                       |    |        |        |                     |    |        |       |
| Crossed versus selfed              | 0.003                 | 21 | <0.998 | 10.777 | -0.793              | 21 | <0.438 | 0.221 |
| Crossed versus hybrid <sup>a</sup> | -4.294                | 21 | <0.001 |        | 3.058               | 21 | <0.011 |       |
| <i>G. fruticosus</i>               |                       |    |        |        |                     |    |        |       |
| Crossed versus selfed              | -1.666                | 28 | <0.096 | 7.767  | 0.361               | 28 | <0.722 | 3.383 |
| Crossed versus hybrid <sup>b</sup> | -2.572                | 28 | <0.101 |        | -0.024              | 28 | <0.981 |       |
| <i>G. physocarpus</i>              |                       |    |        |        |                     |    |        |       |
| Crossed versus selfed              | -6.238                | 28 | <0.001 | 9.360  | -1.304              | 28 | <0.210 | 1.672 |
| Crossed versus hybrid <sup>c</sup> | 4.957                 | 28 | <0.001 |        | 4.083               | 28 | <0.001 |       |

Where rD is the residual deviance of the model; <sup>a</sup> hybrid is *A. curassavica* × *G. physocarpus*, <sup>b</sup> hybrid is *G. fruticosus* × *G. physocarpus* and <sup>c</sup> hybrid is *G. physocarpus* × *G. fruticosus*

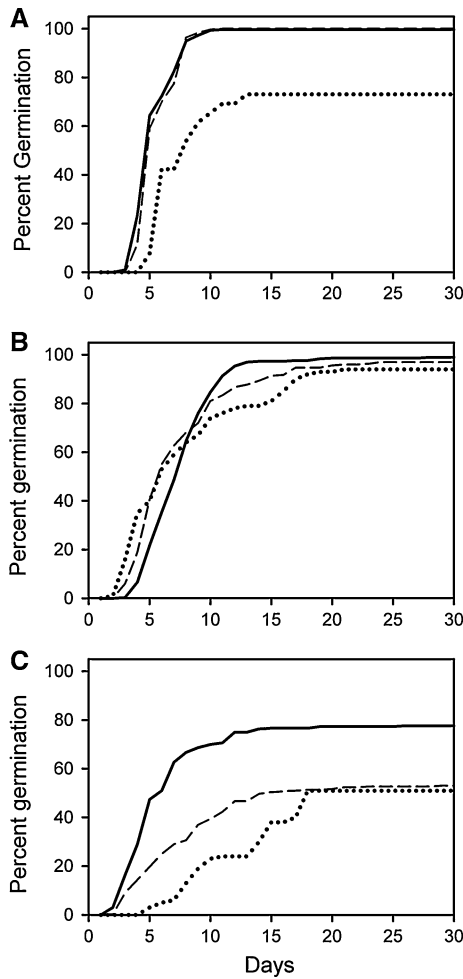
### Hybrid progeny

Significantly lower performance was displayed by *A. curassavica* × *G. physocarpus* hybrid progeny as compared to intraspecific *A. curassavica* crossed progeny in three of the four components of the progeny performance experiment (Tables 3, 4). Specifically, germination time was significantly slower (Table 3; Fig. 3), the proportion of seedlings per fruit that survived was significantly lower (Table 4; Fig. 4) and seedlings were significantly shorter (Table 4; Fig. 5). Although the proportion of seeds per fruit that germinated was also lower for hybrid seeds as

compared to intraspecific *A. curassavica* crossed seeds (Fig. 3), the difference was not significant (Table 3). The *A. curassavica* × *G. physocarpus* hybrid seedlings produced flowers of seemingly normal morphology, but hand-pollinations with *A. curassavica* pollinia were unsuccessful in producing fruit, therefore suggesting that *A. curassavica* × *G. physocarpus* hybrids are sterile.

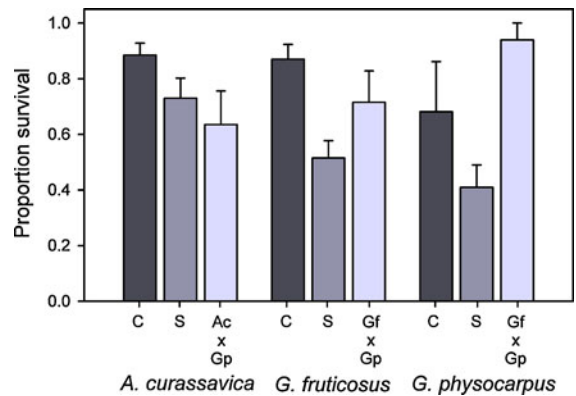
A slightly lower proportion of seeds per fruit germinated for *G. fruticosus* × *G. physocarpus* hybrid progeny as compared to intraspecific *G. fruticosus* crossed progeny (Fig. 3), but the difference was not significant (Table 3). The *G. fruticosus* × *G. physocarpus* hybrid



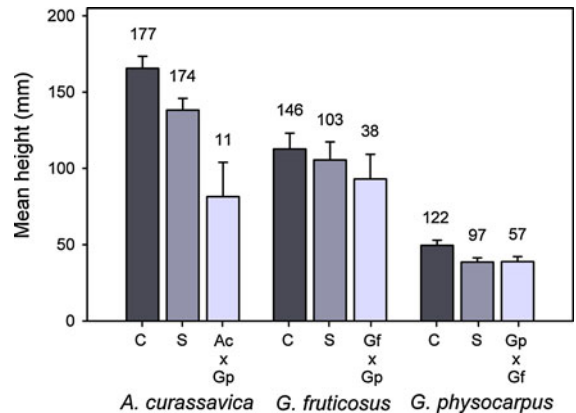


**Fig. 3** Germination of seeds in progeny fitness trials for *A. curassavica* (a), *G. fruticosus* (b) and *G. physocarpus* (c). Treatments are cross-pollinated (solid line), self-pollinated (dashed line) and hybrid-pollinated (dotted line). Hybrid pollinations are *A. curassavica* × *G. physocarpus* (a), *G. fruticosus* × *G. physocarpus* (b) and *G. physocarpus* × *G. fruticosus* (c)

seeds germinated at a rate similar to intraspecific *G. fruticosus* crossed seeds (Table 3; Fig. 3), and the *G. fruticosus* × *G. physocarpus* hybrid seedlings grew to similar heights as intraspecific *G. fruticosus* crossed seedlings (Table 4; Fig. 5). However, the proportion of seedlings per fruit that survived the duration of the experiment was significantly lower for *G. fruticosus* × *G. physocarpus* hybrid seedlings as compared to intraspecific *G. fruticosus* crossed seedlings (Table 4; Fig. 4). *Gomphocarpus fruticosus* × *G. physocarpus* hybrid seedlings reached reproductive maturity, and



**Fig. 4** Proportion of seedlings that survived (mean per fruit + SE) in progeny fitness trials for the three study species. Treatments are cross-pollinated (C), self-pollinated (S) and hybrid-pollinated where Ac is *A. curassavica*, Gf is *G. fruticosus* and Gp is *G. physocarpus*



**Fig. 5** Height of seedlings (mean + SE) in progeny fitness trials for the three study species. Treatments are cross-pollinated (C), self-pollinated (S) and hybrid-pollinated where Ac is *A. curassavica*, Gf is *G. fruticosus* and Gp is *G. physocarpus*. Numbers above bars are sample sizes

produced fruit containing viable seeds when hand-pollinated with *G. fruticosus* pollinia.

The *G. physocarpus* × *G. fruticosus* hybrid seeds displayed weakened germination abilities as compared to intraspecific *G. physocarpus* crossed seeds. Specifically, significantly fewer hybrid seeds per fruit germinated, and time to germination was significantly slower (Table 3; Fig. 3). Furthermore, the *G. physocarpus* × *G. fruticosus* hybrids seedlings were significantly shorter than the intraspecific *G. physocarpus* crossed seedlings (Table 3; Fig. 5). However, the *G. physocarpus* × *G. fruticosus* hybrids seedlings

**Table 4** Results of statistical comparisons between crossed, selfed and hybrid treatments of the progeny performance experiments for seedling survival and height (see Fig. 4, 5)

| Species                            | Proportion survived |    |        |       | Seedling height |    |        |       |
|------------------------------------|---------------------|----|--------|-------|-----------------|----|--------|-------|
|                                    | Z                   | df | P      | rD    | t               | df | P      | rD    |
| <i>A. curassavica</i>              |                     |    |        |       |                 |    |        |       |
| Crossed versus selfed              | -0.457              | 21 | <0.647 | 5.301 | -1.983          | 21 | <0.062 | 2.353 |
| Crossed versus hybrid <sup>1</sup> | -3.242              | 21 | <0.001 |       | -2.610          | 21 | <0.024 |       |
| <i>G. fruticosus</i>               |                     |    |        |       |                 |    |        |       |
| Crossed versus selfed              | -4.387              | 28 | <0.001 | 4.858 | -0.121          | 28 | <0.903 | 8.096 |
| Crossed versus hybrid <sup>2</sup> | -5.242              | 28 | <0.001 |       | -0.699          | 28 | <0.493 |       |
| <i>G. physocarpus</i>              |                     |    |        |       |                 |    |        |       |
| Crossed versus selfed              | 1.331               | 28 | <0.183 | 5.360 | -2.41           | 28 | <0.028 | 1.777 |
| Crossed versus hybrid <sup>3</sup> | -3.196              | 28 | <0.001 |       | 1.152           | 28 | <0.260 |       |

Where rD is the residual deviance of the model; hybrid<sup>1</sup> is *A. curassavica* × *G. physocarpus*, hybrid<sup>2</sup> is *G. fruticosus* × *G. physocarpus* and hybrid<sup>3</sup> is *G. physocarpus* × *G. fruticosus*

displayed significantly superior survival as compared to intraspecific *G. physocarpus* crossed seedlings (Table 4; Fig. 4). *Gomphocarpus physocarpus* × *G. fruticosus* hybrid seedlings reached reproductive maturity, and hand-pollinations with *G. physocarpus* pollinia produced fruit containing viable seeds.

## Discussion

In conformance with Baker's prediction about the breeding system characteristics of colonizing species, our results show that all three study species have the capacity to produce fruit through uniparental reproduction (Table 1; Fig. 1). However, none of the species were able to set seed through autonomous selfing, and therefore all three study species rely on the services of pollinators for reproduction.

Studies of milkweeds in their native ranges suggest that geitonogamy accounts for a high percentage of pollination events, although this does not contribute to seed production in most milkweeds because of their genetic self-incompatibility (e.g. Pleasants 1991; Finer and Morgan 2003; Ivey et al. 2003). Indeed, only one other milkweed species has been found to have a completely self-compatible breeding system, namely *A. incarnata* (Swamp Milkweed). In studies of this species, Kephart (1981) documented nearly equivalent success rates of fruit-set in crossed treatments as compared to selfed treatments in a hand-pollination experiment, whereas Ivey et al. (1999)

found cross-pollinations to be more successful than self-pollinations in hand-pollination experiments as well as in open-pollinated progeny arrays.

Most previous studies of Baker's Rule in invasive plants have relied on seed production experiments to determine a species' ability to produce progeny through selfing (e.g. Rambuda and Johnson 2004; Rodger et al. 2010; Hao et al. 2011). However, it is well known that self-fertilization involves a complex trade-off between the advantage of circumventing partner limitation when populations are small and a potential disadvantage in terms of the lower fitness of selfed progeny (e.g. see Charlesworth and Charlesworth 1987; Husband and Schemske 1996; Johnston 1998). Our study addressed this issue by including measures of the performance of selfed and crossed progeny in a glasshouse experiment. These data showed that inbreeding depression in selfed progeny, measured in terms of seed germination, seedling survivorship and seedling growth, was relatively weak (Tables 3, 4; Figs. 3, 4, 5). However, studies have shown that greenhouse experiments may overestimate the performance of selfed progeny relative to experiments conducted under harsher field conditions (Ramsey and Vaughton 1998; Hayes et al. 2005).

Although our study demonstrates the potential for self-pollination to contribute to the demography of populations, the actual rates of selfing in these three milkweed species remain unknown. Factors that would affect selfing rates include the complex floral morphology of the study species, including

post-removal pollinarium reconfiguration which may restrict insertions of self-pollinia (Harder and Johnson 2008), and the duration and number of flowers visited during foraging bouts by pollinators (Harder and Barrett 1995). Further, if self-pollination is occurring, it is not known whether these species depend on uniparental reproduction only during the initial colonization phase of population establishment and favour outcrossing when populations are established, or whether uniparental reproduction is common in large populations. We are currently using molecular techniques to reveal the realized mating systems of the study species, and thus the role of uniparental reproduction in various stages of plant invasions. Only one study has examined the contribution of self-fertilization to reproduction in different sized populations of an invasive plant: van Kleunen et al. (2007) found low outcrossing rates across a wide range of population sizes for *Datura stramonium* in South Africa, indicating that self-fertilization may be important for all stages of plant invasions and not only in establishing founder populations.

Although selfing and outcrossing breeding systems have both been documented in invasive plants, a recent study by van Kleunen and Johnson (2007) demonstrated that selfing species tend to display superior levels of invasiveness. In their meta-analysis of the reproductive characteristics and the range of invasion of European plants naturalised in the United States, self-incompatible species were found to have significantly smaller ranges than species that are self-compatible, and of the self-compatible species, those dependent on pollinator vectors had significantly smaller ranges than those species capable of autonomy. In a similar study of Asteraceae that are invasive in China, Hao et al. (2011) documented that percentages of self-compatible species and autogamous species were significantly larger than percentages of Asteraceae species with these breeding systems as represented in a global dataset, and that self-compatible species were more geographically widespread than self-incompatible species. Furthermore, in a study of Iridaceae that controlled for phylogenetic effects, ability to self-fertilize emerged as a highly significant predictor of naturalization of species outside their native range (van Kleunen et al. 2008). These results indicate that a plant's breeding system is an important determinant of its potential invasiveness,

thereby providing firm support for the applicability of Baker's Rule to plant invasions.

It has been proposed that incorporation of breeding system characteristics into attribute profiles should enhance the ability to predict invasiveness (Rambuda and Johnson 2004; van Kleunen and Johnson 2007; Hao et al. 2011). However, a question to consider is whether species may evolve self-fertility after introduction to a new range. Intriguingly, *G. physocarpus*, which we found in this study to be self-compatible, was recently reported to be self-incompatible in its native range (Coombs et al. 2009). Indeed, the inbreeding depression observed in *G. physocarpus* in our study is consistent with a history of outcrossing. This apparent case of an evolutionary shift in the breeding system during the invasion process requires further verification. In particular, the possibility that invasive Australian populations were derived from self-compatible populations should be tested by examining the breeding system of *G. physocarpus* over a wider geographic area in South Africa, as this would shed light on whether populations in the native range vary in their levels of self-incompatibility, as has been reported for other milkweed species (e.g. *A. incarnata*, see Lipow and Wyatt 2000).

The notion that self-incompatibility may breakdown during the invasion process has previously been hypothesized by Hiscock (2000), who found pseudo-self-compatibility to be operational in the invasive species *Senecio squalidus* (Oxford Ragwort) in Britain and proposed that flexibility in the breeding system may be crucial to the successful colonization by this species. However, when Brennan et al. (2005) investigated the extent and inheritance of pseudo-self-compatibility in *S. squalidus* across the invaded British range, it was found that self-incompatibility was strongly expressed across the entire range. The potential for variation in the strength of self-incompatibility has also been tested in *Campanula rapunculoides* that is naturalized in the United States: studies have documented that self-incompatibility becomes less strong as the flowers of this species age, thereby increasing the likelihood of reproductive assurance after most opportunities for outcrossing have occurred (Stephenson et al. 2000; Vogler and Stephenson 2001). Furthermore, Davis (2005) found that seed production under forced self-pollination was doubled in invasive *Spartina alterniflora* as compared to native *S. alterniflora*, thereby suggesting the

potential for greater self-compatibility in invasive populations of this species.

Hybridization is unusual among milkweeds (Wyatt and Broyles 1994). The virtual inability of *A. curassavica* to produce fruit and seeds following pollination with *G. physocarpus* pollinia, and the inability of the *Gomphocarpus* species to produce fruit with *A. curassavica* pollinia indicate that these species are not inter-fertile. Furthermore, observations of potential pollinators in Australia indicate that *A. curassavica* is predominantly pollinated by Lepidoptera while the two *Gomphocarpus* species are predominantly pollinated by Hymenoptera (M. Ward, personal observation), and therefore opportunities for these species to hybridize in the field would be limited. In contrast to this, the two *Gomphocarpus* species appear to be inter-fertile and produce offspring with reasonable performance levels. Observations that the two *Gomphocarpus* species overlap in pollinator assemblages (M. Ward, personal observation) indicate that the opportunity exists for these species to hybridize in the field. Likely hybrids have also been reported in the native range of these species (Weale 1873; Goyder and Nicholas 2001). Interfertility between these two species means that there can be additional sources of pollen for fertilization when conspecific plants are limiting, thereby potentially contributing to the invasion process of these species. Additionally, the invasion process may have been assisted by interfertility through the potential for broadening of the genetic variation in each species as a result of introgressive hybridization (Rieseberg et al. 2000, 2007). However, we do not yet know the extent to which hybrids are successful in terms of pollinator attraction, nor the extent of introgressive gene flow.

In conclusion, the results of our study add to the growing evidence that self-fertility is a significant contributor to the process of biological invasion. However, there are a number of challenges that have to be solved before the link between self-fertility and plant invasiveness can be established beyond a reasonable doubt. Statistical comparison of modes of reproduction in invasive and non-invasive introduced species allows robust testing of Baker's Rule (van Kleunen and Johnson 2007; van Kleunen et al. 2008; Harmon-Threatt et al. 2009), but application of this approach is generally hampered by the paucity of data on the frequency of plant species that have been introduced without becoming invasive. Furthermore,

the role of selfing in the invasion process remains enigmatic. Does selfing alleviate pollinator limitation and/or partner limitation, and does its importance change with the various stages from naturalization to invasion? The ability to accurately predict species invasiveness is one of the long-term goals of invasion biology, and will not be accomplished by a single study, but is likely to benefit greatly from further case studies examining modes of reproduction in invasive species.

**Acknowledgments** The authors thank Y. Buckley, A. House, J. Rodger, J. Zalucki and anonymous reviewers for comments on previous drafts of the manuscript. Funding for this research was provided by CSIRO Sustainable Ecosystems and the DST-NRF Centre for Invasion Biology.

## References

- Abe T (2006) Threatened pollination systems in native flora of the Ogasawara (Bonin) Islands. *Ann Bot* 98:317–334
- Ayres DA, Zaremba K, Sloop CM, Strong DR (2008) Sexual reproduction of cordgrass hybrids (*Spartina foliosa* × *alterniflora*) invading tidal marshes in San Francisco Bay. *Divers Distrib* 14:187–195
- Baker HG (1955) Self compatibility and establishment after long distance dispersal. *Evolution* 9:347–349
- Baker HG (1967) Support for Baker's Law—as a rule. *Evolution* 21:853–856
- Baker HG (1974) The evolution of weeds. *Ann Rev Ecol Syst* 7:1–24
- Barrett SCH (1996) The reproductive biology and genetics of island plants. *Philos Trans R Soc Lond B Biol Sci* 351:725–733
- Barrett SCH, Morgan MT, Husband BC (1989) The dissolution of a complex genetic polymorphism: the evolution of self-fertilisation in tristylous *Echornia paniculata* (Pontederiaceae). *Evolution* 43:1398–1416
- Bernardello G, Anderson GJ, Stuessy TF, Crawford DJ (2001) A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Bot Rev* 67:255–308
- Brennan AC, Harris SA, Hiscock SJ (2005) Modes and rates of selfing and associated inbreeding depression in the self-incompatible plant *Senecio squalidus* (Asteraceae): a successful colonizing species in the British Isles. *New Phytol* 168:475–486
- Busch JW (2005) The evolution of self-compatibility in geographically peripheral populations of *Leavenworthia alabamica* (Brassicaceae). *Am J Bot* 92:1503–1512
- Busch JW (2011) Demography, pollination, and Baker's Law. *Evolution* 65:1511–1513
- Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Ann Rev Ecol Syst* 18:237–268

- Cheptou P, Massol F (2009) Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *Am Nat* 174:46–55
- Coombs G, Peter CI, Johnson SD (2009) A test for Allee effects in the self-incompatible wasp-pollinated milkweed *Gomphocarpus physocarpus*. *Austral Ecol* 34:688–697
- Davis HG (2005) r-Selected traits in an invasive population. *Evol Ecol* 19:255–274
- Dornier A, Munoz F, Cheptou PO (2008) Allee effect and self-fertilization in hermaphrodites: reproductive assurance in a structured metapopulation. *Evolution* 62:2558–2569
- Ellstrand NC, Schierenbeck KA (2006) Hybridization as a stimulus for the evolution of invasiveness in plants? *Euphytica* 148:35–46
- Endress ME, Bruyns PV (2000) A revised classification of the Apocynaceae s.l. *Bot Rev* 66:1–56
- Finer MS, Morgan MT (2003) Effects of natural rates of geitonogamy on fruit set in *Asclepias speciosa* (Apocynaceae): evidence favoring the plant's dilemma. *Am J Bot* 90:1746–1750
- Forster PI (1994) Diurnal insects associated with the flowers of *Gomphocarpus physocarpus* E. Mey. (Asclepiadaceae), an introduced weed in Australia. *Biotropica* 26:214–217
- Goyder DJ, Nicholas A (2001) A revision of *Gomphocarpus* R. Br. (Apocynaceae: Asclepiadeae). *Kew Bull* 56:769–836
- Hao JH, Quang S, Chrobok T, van Kleunen M, Liu QQ (2011) A test of Baker's Law: breeding systems of invasive species of Asteraceae in China. *Biol Invasions* 13:571–580
- Harder LD, Barrett SCH (1995) Mating costs of large floral displays in hermaphrodite plants. *Nature* 373:512–515
- Harder LD, Johnson SD (2008) Function and evolution of aggregated pollen in angiosperms. *Int J Plant Sci* 169:59–78
- Harmon-Threatt AN, Burns JH, Shemyakina LA, Knight TM (2009) Breeding system and pollination ecology of introduced plants compared to the native relatives. *Am J Bot* 96:1544–1550
- Hayes CN, Winsor JA, Stephenson AG (2005) Environmental variation influences the magnitude of inbreeding depression in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae). *J Evol Biol* 18:147–155
- Herlihy CR, Eckert CG (2005) Evolution of self-fertilisation at geographical range margins? A comparison of demographical, floral, and mating system variables in central versus peripheral populations of *Aquilegia canadensis* (Ranunculaceae). *Am J Bot* 92:744–751
- Hiscock SJ (2000) Self-incompatibility in *Senecio squalidus* L. (Asteraceae). *Ann Bot* 85:181–190
- Hong L, Shen H, Ye WH, Cao HL, Wang ZM (2007) Self-incompatibility in *Mikania micrantha* in South China. *Weed Res* 47:280–283
- Husband BC, Schemske DW (1996) Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* 50:54–70
- Ivey CT, Lipow SR, Wyatt R (1999) Mating systems and interfertility of swamp milkweed (*Asclepias incarnata* ssp. *incarnata* and ssp. *pulchra*). *Heredity* 82:25–35
- Ivey CT, Martinez P, Wyatt R (2003) Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). *Am J Bot* 90:214–225
- Jesse LC, Moloney KA, Obrycki JJ (2006) Insect pollinators of the invasive plant, *Rosa multiflora* (Rosaceae), in Iowa, USA. *Weed Biol Manag* 6:235–240
- Johnston MO (1998) Evolution of intermediate selfing rates in plants: pollination ecology versus deleterious mutations. *Genetica* 102(103):267–278
- Kephart SR (1981) Breeding systems in *Asclepias incarnata* L., *Asclepias syriaca* L., and *Asclepias verticillata* L. *Am J Bot* 68:226–232
- Lafuma L, Maurice S (2007) Increase in mate availability without loss of self-incompatibility in the invasive species *Senecio inaequidens* (Asteraceae). *Oikos* 116:201–208
- Lipow SR, Wyatt R (2000) Towards an understanding of the mixed breeding system of swamp milkweed (*Asclepias incarnata*). *J Torrey Bot Soc* 127:193–199
- Liu H, Pemberton RW, Stiling P (2006) Native and introduced pollinators promote a self-incompatible invasive woody vine (*Paederia foetida* L.) in Florida. *J Torrey Bot Soc* 133:304–311
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Massol F, Cheptou P (2011) When should we expect the evolutionary association of self-fertilization and dispersal? *Evolution* 65:1217–1220
- McMullen CK (1987) Breeding systems of selected Galápagos Islands angiosperms. *Am J Bot* 74:1694–1705
- Meyerson LA, Viola DV, Brown RN (2010) Hybridization of invasive *Phragmites australis* with a native subspecies in North America. *Biol Invasions* 12:103–111
- Moeller DA, Geber MA (2005) Ecological context of the evolution of self-pollination in *Clarkia xantiana*: population size, plant communities, and reproductive assurance. *Evolution* 59:786–799
- Pannell JR, Barrett SCH (1998) Baker's law revisited: reproductive assurance in a metapopulation. *Evolution* 52:657–668
- Pimentel D (2002) *Biological Invasions: economic and environmental costs of alien plant, animal and microbe species*. CRC Press, Boca Raton
- Pleasants JM (1991) Evidence for short-distance dispersal of pollinia in *Asclepias syriaca* L. *Funct Ecol* 5:75–82
- R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Rambuda TD, Johnson SD (2004) Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? *Divers Distrib* 10:409–416
- Ramsey M, Vaughton G (1998) Effect of environment on the magnitude of inbreeding depression in seed germination in a partially self-fertile perennial herb (*Blandfordia grandiflora*, Liliaceae). *Int J Plant Sci* 159:98–104
- Ramsey M, Vaughton G, Peakall R (2006) Inbreeding avoidance and the evolution of gender dimorphism in *Wurmbea biglandulosa* (Colchicaceae). *Evolution* 60:529–537
- Randall RP (2007) *The introduced flora of Australia and its weed status*. CRC for Australian Weed Management, Glen Osmond
- Randle AM, Snyder JB, Kalisz S (2009) Can differences in autonomous selfing ability explain differences in range size

- among sister-taxa pairs of *Collinsia* (Plantaginaceae)? An extension of Baker's Law. *New Phytol* 183:618–629
- Ridley CE, Ellstrand NC (2009) Evolution of enhanced reproduction in the hybrid-derived invasive, California wild radish (*Raphanus sativus*). *Biol Invasions* 11:2251–2264
- Rieseberg LH, Baird SJE, Gardner KA (2000) Hybridization, introgression, and linkage evolution. *Plant Mol Biol* 42:205–224
- Rieseberg LH, Kim S, Randell RA, Whitney KD, Gross BL, Lexer C, Clay K (2007) Hybridization and the colonization of novel habitats by annual sunflowers. *Genetica* 129:149–165
- Rodger JG, Van Kleunen M, Johnson SD (2010) Does specialised pollination impede plant invasions. *Int J Plant Sci* 171:382–391
- Sakai AK, Wagner WL, Ferguson DM, Herbst DR (1995) Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology* 76:2530–2543
- Schierenbeck KA, Ellstrand NC (2009) Hybridization and the evolution of invasiveness in plants and other organisms. *Biol Invasions* 11:1093–1105
- Scofield DG, Schultz ST (2006) Mitosis, stature and evolution of plant mating systems: low- $\Phi$  and high- $\Phi$  plants. *Proc R Soc B* 273:275–282
- Simpson SR, Gross CL, Silberbauer LX (2005) Broom and honeybees in Australia: an alien liaison. *Plant Biol* 7:541–548
- Sinden J, Jones R, Hester S, Odom D, Kalisch C, James R, Cacho O (2004) The economic impact of weeds in Australia. CRC for Australian Weed Management, Adelaide
- Stebbins GL (1957) Self fertilization and population variability in the higher plants. *Am Nat* 91:337–354
- Stephenson AG, Good SV, Vogler DW (2000) Interrelationships among inbreeding depression, plasticity in the self-incompatibility system, and the breeding system of *Campanula rapunculoides* L. (Campanulaceae). *Ann Bot* 85:211–219
- Stout JC (2007) Reproductive biology of the invasive exotic shrub, *Rhododendron ponticum* L. (Ericaceae). *Bot J Linn Soc* 155:373–381
- van Kleunen M, Johnson SD (2007) Effects of self-compatibility on the distribution range of invasive European plants in North America. *Conserv Biol* 21:1537–1544
- van Kleunen M, Fischer M, Johnson SD (2007) Reproductive assurance through self-fertilization does not vary with population size in the alien invasive plant *Datura stramonium*. *Oikos* 116:1400–1412
- van Kleunen M, Manning JC, Pasqualetto V, Johnson SD (2008) Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *Am Nat* 171:195–201
- Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *N Z J Ecol* 21:1–16
- Vogler DW, Stephenson AG (2001) The potential for mixed mating in a self-incompatible plant. *Int J Plant Sci* 162:801–805
- Weale JPM (1873) Observations on the mode in which certain species of Asclepiadeae are fertilised. *J Linn Soc Bot* 13:48–58
- Woodson RE (1954) The North American species of *Asclepias* L. *Ann Mo Bot Gard* 41:1–211
- Wyatt R (1976) Pollination and fruit-set in *Asclepias*: a reappraisal. *Am J Bot* 63:845–851
- Wyatt R, Broyles SB (1990) Reproductive biology of milkweeds (*Asclepias*): recent advances. In: Kawano S (ed) *Biological approaches and evolutionary trends in plants*. Academic Press, London, pp 255–272
- Wyatt R, Broyles SB (1994) Ecology and evolution of reproduction in milkweeds. *Ann Rev Ecol Syst* 25:423–441
- Wyatt R, Broyles SB (1997) The weedy tropical milkweeds *Asclepias curassavica* and *A. fruticosa* are self-compatible. *Biotropica* 29:232–234
- Wyatt R, Broyles SB, Lipow SR (2000) Pollen-ovule ratios in milkweeds (Asclepiadaceae): an exception that probes the rule. *Syst Bot* 25:171–180