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## The Rare *Asclepias texana* and its Widespread Sister Species, *A. perennis*, are Self-incompatible and Interfertile

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**ABSTRACT.** Like most other species of *Asclepias*, *A. texana* and *A. perennis* are entirely self-incompatible. They therefore differ from *A. incarnata* and *A. curassavica*, which are also members of the supposedly primitive series *Incarnatae*, but which are self-compatible. Interspecific crosses of *A. texana* and *A. perennis* showed that the two taxa are freely and reciprocally interfertile, with fruit-set levels (26.5%) as high as for intraspecific cross-pollinations. Crosses that used *A. texana* as the female parent had significantly fewer seeds per fruit (19.8) than did those in which *A. perennis* served as the female parent (42.8), suggesting some form of unilateral interspecific incongruity. In contrast, interspecific crosses between *A. perennis* and *A. curassavica* (also *Incarnatae*) were totally unsuccessful, as were interspecific crosses of *A. incarnata* with both *A. perennis* and *A. texana*.  $F_1$  interspecific hybrids of *A. perennis*  $\times$  *A. texana* were male-sterile. The occurrence of both self-incompatible (*A. perennis*, *A. texana*, and *A. verticillata*) and self-compatible (*A. curassavica* and *A. incarnata*) species in Woodson's series *Incarnatae* may reflect problems in the taxonomic delimitation of subgroups within *Asclepias*. We believe, however, that self-compatibility has probably arisen independently numerous times within the genus.

*Asclepias texana* Heller is a narrowly-distributed milkweed that is rare within its geographical range in western Texas and adjacent Mexico (Edwards and Wyatt 1994). Woodson (1954) suggested that it is the progenitor of *A. perennis* Walter, a species that is widespread in floodplain forests of the southeastern United States (Edwards and Wyatt 1994). The two species differ in two striking characters, both of which are apparently related to the unusual water-dispersal syndrome of *A. perennis*: its fruits are pendulous at maturity, rather than erect, and its seeds lack comose hairs, having instead an expanded corky margin (Edwards et al. 1994). Surprisingly, isozyme studies revealed that these two taxa are quite distinct genetically, with genetic identities between populations averaging only 0.79 (Edwards and Wyatt 1994), which agrees exactly with the mean for pairs of congeneric species reported by Crawford (1983).

Wyatt and Broyles (1994) have recently summarized what is known about the breeding systems of milkweeds. They concluded that species of *Asclepias* are either (1) largely or entirely self-incompatible or (2) largely or entirely self-compatible. Among the first group are *A. verticillata* L. (Kephart 1981), *A. exaltata* L. (Broyles and Wyatt 1993), and *A. subulata* Decaisne (Wyatt et al. 1996). Also among these largely self-incompatible species are *A. syriaca* (Kephart 1981; Kahn and Morse 1991; Morse 1994)

and *A. tuberosa* L. (Wyatt 1976), both of which, however, do show plant- and population-level variation for low levels (< 5%) of fruit-set from self-pollinations. Self-compatible species include *A. incarnata* L. (Fischer 1941; Kephart 1981), *A. curassavica* L., and *A. fruticosa* L. (Wyatt and Broyles 1997).

Based on cytological and anatomical studies, it appears that species of *Asclepias* possess an unusual late-acting form of self-incompatibility (Wyatt and Broyles 1994). The incompatibility reaction occurs in the ovary (Sparrow and Pearson 1948; Kephart 1981; Seavey and Bawa 1986; Kahn and Morse 1991; Broyles and Wyatt 1993; Sage and Williams 1993; Wyatt et al. 1996). This system is wasteful, since self-pollen can preempt or outcompete outcross-pollen for ovules (Broyles and Wyatt 1993). It is therefore intriguing that it exists in the otherwise morphologically advanced genus *Asclepias*. This form of ovarian self-incompatibility appears to be widespread in the Apocynaceae/Asclepiadaceae clade (Lipow and Wyatt 1998) and has been retained even in those subgenera and series of *Asclepias* that Woodson (1954) considered "advanced."

Self-compatibility probably evolved independently in several different lineages of *Asclepias*. It occurs in Woodson's (1954) "most primitive" and "natural" series, the *Incarnatae* (*A. incarnata*, *A. curassavica*), and series *Fruticosae* (*A. fruticosa*), which is only distantly related to the *Incarnatae* and

often treated in the segregate Old World genus *Gomphocarpus* (e.g., Forster 1994). Woodson (1954) placed *A. texana* and *A. perennis* in the *Incarinatae*. The first goal of our research was to determine if these species, like *A. incarnata* and *A. curassavica*, are self-compatible. Our second goal was to determine if these species are interfertile. Woodson's (1954) emphasis of their extremely similar vegetative and floral morphology would suggest that these sister species might be interfertile. On the other hand, the relatively strong genetic divergence shown using isozyme markers (Edwards and Wyatt 1994) would argue against the possibility of interspecific hybridization.

#### MATERIALS AND METHODS

Apparently viable seeds were selected from collections of pods from populations of *A. texana* and *A. perennis*. Dehiscid seeds of *A. texana* were collected in December of 1992 from the Boot Spring Trail in Big Bend National Park in Brewster County, Texas. Follicles of *A. perennis* were collected in South Carolina between August and October of 1991 from the Congaree Swamp National Monument in Richland County and the Savannah River Site in Barnwell County. Voucher specimens are deposited in the University of Georgia Herbarium (GA). Seeds were germinated to produce 10 plants of *A. texana*, of which 9 were used for hand-pollinations. Seeds of *A. perennis* were germinated to produce 25 plants, of which 10 were used for hand-pollinations. The greenhouse-grown plants were approximately 18-months-old when we began to perform hand-pollinations in May-June 1993. The plants grew vigorously and provided many more umbels for pollination than were actually used. We doubt that fruit production was ever resource-limited.

Hand-pollinations were extremely difficult to perform because of the small size of the flowers. We used straight dissecting needles and/or small insect pins. Pollinaria were removed by carefully hooking the corpusculum and easing the pollinia from the anther sacs. We then delicately splayed apart the anther flaps of the recipient flowers to expose the stigmatic chamber. A pollinium was gently nudged into the chamber with its convex surface innermost. Following insertion, we carefully pushed the anther flaps back into their original orientation (cf. Wyatt 1976; Sage et al. 1990). We pollinated only one stigmatic chamber per flower. Typically, we chose two umbels per plant, randomly assigning one to be self-pollinated and the

second to be cross-pollinated. Three flowers per umbel were pollinated, each of which received one of two treatments: (1) self-pollination, using a pollinium from another flower on the same plant; or (2) cross-pollination, using a pollinium from another plant. On each day that pollinations were performed, we tried to select recently-opened umbels whose flowers had only small volumes of freshly-secreted nectar. Pollinated flowers were marked uniquely using consecutively numbered jewelry tags. As fruits began to develop, they were enclosed in bridal veil bags, so that all seeds could be retained for counting. Fruits were harvested at maturity, and seeds were counted.

Interspecific crosses were performed using methods identical to those described above. The 102 crosses included 51 each with *A. texana* and *A. perennis* as maternal parents. For purposes of comparison, we also performed reciprocal interspecific crosses between *A. perennis* and two other members of series *Incarinatae* (sensu Woodson 1954), *A. curassavica* and *A. incarnata*. The plants of *A. curassavica* were approximately 2-years-old at the time of the crosses and were grown from seeds collected in Costa Rica in 1991 (Wyatt and Broyles 1997). The plants of *A. incarnata* were grown from seeds collected in Clarke County, Virginia, in 1993.

#### RESULTS

For *A. texana*, 23 of 102 cross-pollinations produced a fruit (Table 1). This high success rate contrasts sharply with that for self-pollinations, for which none of the 102 resulted in fruit-set. Cross-pollinated fruits contained about 35 seeds on average. This represents about 75% of the reproductive potential of *A. texana*, which averages  $48.8 \pm 10.6$  (mean  $\pm$  standard deviation, based on a sample of 10 flowers) ovules per ovary (Broyles and Wyatt, unpubl. data). Plants that were most successful as fruit producers tended to be less successful as pollen donors. Of the 9 plants actually used in the crosses, 8 produced at least one fruit and 7 sired at least one fruit on another plant.

For *A. perennis*, 15 of 141 cross-pollinations produced a fruit, but none of the 141 self-pollinations was successful (Table 1). Cross-pollinated fruits averaged about 46 seeds, which represents full fruit-set from the  $43.8 \pm 6.20$  ovules per ovary (Broyles and Wyatt, unpubl. data, based on a sample of 10 flowers). There was a weak tendency for plants with high female success to be less successful as males. Of the 10 plants used in the crosses, 7

TABLE 1. Results of hand-pollinations of *Asclepias texana* and *A. perennis*. For each type of pollination, the number of flowers pollinated, the number of fruits set, and the percentage fruit-set are shown. For each successful type of pollination, the mean number of filled seeds per fruit is given, along with the associated standard deviation and range. Fruits marked by an asterisk were unusually small and contained no viable seeds.

| Type                        | Flowers | Fruits | Fruit-set | Seeds/Fruit         |
|-----------------------------|---------|--------|-----------|---------------------|
| Intraspecific               |         |        |           |                     |
| <i>A. texana</i>            |         |        |           |                     |
| self-pollination            | 102     | 0      | 0         | —                   |
| cross-pollination           | 102     | 23     | 22.5%     | 34.5 ± 6.86 (23–45) |
| <i>A. perennis</i>          |         |        |           |                     |
| self-pollination            | 141     | 0      | 0         | —                   |
| cross-pollination           | 141     | 15     | 10.6%     | 45.9 ± 4.91 (38–53) |
| Interspecific               |         |        |           |                     |
| <i>A. texana</i> (♀)        |         |        |           |                     |
| x <i>A. perennis</i> (♂)    | 51      | 14     | 27.5%     | 19.8 ± 5.85 (10–29) |
| <i>A. perennis</i> (♀)      |         |        |           |                     |
| x <i>A. texana</i> (♂)      | 51      | 13     | 25.5%     | 42.8 ± 5.89 (33–52) |
| <i>A. perennis</i> (♀)      |         |        |           |                     |
| x <i>A. curassavica</i> (♂) | 96      | 0      | 0         | —                   |
| <i>A. curassavica</i> (♀)   |         |        |           |                     |
| x <i>A. perennis</i> (♂)    | 102     | 0      | 0         | —                   |
| <i>A. perennis</i> (♀)      |         |        |           |                     |
| x <i>A. incarnata</i> (♂)   | 138     | 1*     | 0.7%      | 0                   |
| <i>A. incarnata</i> (♀)     |         |        |           |                     |
| x <i>A. perennis</i> (♂)    | 162     | 0      | 0         | —                   |
| <i>A. texana</i> (♀)        |         |        |           |                     |
| x <i>A. incarnata</i> (♂)   | 159     | 2*     | 1.3%      | 0                   |
| <i>A. incarnata</i> (♀)     |         |        |           |                     |
| x <i>A. texana</i> (♂)      | 105     | 0      | 0         | —                   |

produced at least one fruit, but only 5 sired at least one fruit on another plant.

Interspecific crosses between *A. perennis* and *A. texana* resulted in fruit-set as high as that seen for intraspecific crosses (Table 1). Of 102 total hybridizations, 27 resulted in fruit-set. These interspecific crosses were perfectly reciprocal, with equal success regardless of whether *A. texana* or *A. perennis* was used as the female parent. There were dramatic differences, however, in terms of numbers of seeds per fruit. Fruits produced on *A. perennis* yielded nearly full fruit-set: about 43 seeds per pod (of the potential 44 ovules per ovary), comparable to the 46 seeds per pod from intraspecific crosses. With *A. texana* as the female parent, however, there was drastically lower seed-set than expected. The 20 seeds per fruit represent less than half of the potential 49 (ovules per ovary) and are significantly fewer than the 35 seeds per pod obtained from intraspecific crosses ( $t = 9.67$ ;  $P < 0.001$ ). To confirm that the plants resulting from these crosses were indeed  $F_1$  interspecific hybrids, we used two diagnostic isozyme markers (*Pgi-2* and *Tpi-2*) previously discovered using horizontal starch-gel electrophoresis (Edwards and Wyatt 1994). Five randomly selected seeds from each cross were germinated, and leaf tissue extracts were electrophoresed. In every case, the

plants displayed heterozygous combinations of the diagnostic alleles of the parents, confirming their status as  $F_1$  interspecific hybrids.

Given the high success of interspecific crosses between *A. texana* and *A. perennis*, it is notable that none of the 198 interspecific hybridizations between *A. perennis* and *A. curassavica* successfully set fruit (Table 1). This was true regardless of which species was used as the female parent. There was also a complete failure to produce any viable seeds from interspecific hybridizations involving *A. incarnata* and either *A. perennis* or *A. texana*. Only three follicles appeared to mature, but these were unusually small and contained only aborted seeds. Initially, a few fruits produced on *A. incarnata* appeared to be the result of successful interspecific crosses. When the progeny were examined using genetic markers, however, these plants proved to be spontaneous self-pollinations (cf. Wyatt and Broyles 1997) of *A. incarnata*, lacking any of the diagnostic alleles of the other species.

#### DISCUSSION

Our hand-pollinations clearly show that both *A. texana* and *A. perennis* are genetically self-incompatible. None of more than 100 self-pollinations,

performed on 9–10 plants of each species, successfully matured a fruit. Fruit-set from cross-pollinations, performed simultaneously on the same set of plants, was reasonably high for milkweeds (11–23%). Thus, *A. texana* and *A. perennis* join most other species of *Asclepias* investigated to date, which have proved to be largely or entirely self-incompatible (Wyatt and Broyles 1994). This result, however, is somewhat unexpected, as two other species of the 16 that Woodson (1954) placed in his series *Incarnatae* are reported to be self-compatible (*A. incarnata*: Fischer 1941, Kephart 1981; *A. curassavica*: Wyatt and Broyles 1997). To the extent that Woodson's (1954) classification reflects true phylogenetic relationships, it would appear that self-compatibility has arisen independently in multiple lineages of *Asclepias*, since Wyatt and Broyles (1997) have shown that *A. fruticosa* (series *Fruticosae*) also is self-compatible. This should not be surprising, as similar patterns of mating system evolution exist in many genera of flowering plants (Stebbins 1970). Moreover, the third species of series *Incarnatae* that has been studied, *A. verticillata*, is reported to be entirely self-incompatible (Kephart 1981).

It is not known why overall levels of fruit-set in milkweeds are low, even from compatible cross-pollinations, compared to other groups of angiosperms (Wyatt and Broyles 1994). Hand-pollinations typically increase fruit-set well above field levels, to about 15–20% (e.g., Wyatt 1976, 1981; Queller 1985; Wyatt et al. 1996). Thus, the overall 22.5% success rate we observed for *A. texana* fits this pattern, but the 10.6% observed for *A. perennis* is a bit low. Our success rate with *A. perennis* was low at first and increased over time. It is possible that our initial attempts to manipulate these extremely small flowers were clumsy and caused some trauma and that our technique improved with experience. We were careful to perform crosses only on recently opened flowers and to restrict our activities to the early morning hours, to avoid potential problems with overly-concentrated nectar (cf. Wyatt et al. 1996).

Unfortunately, we do not have hard data regarding natural levels of fruit-set in *A. texana*, but fruit-set in natural populations of *A. perennis* are around 1% (A. L. Edwards, unpubl. data). Casual observations suggest that, as in most other milkweeds, hand-pollination probably increased fruit-set by an order of magnitude over field levels. Unlike the self-compatible *A. incarnata*, in which levels of fruit-set are often quite high (C. T. Ivey and R. Wyatt,

pers. obs.), fruit-set in these self-incompatible species may be partially limited by the level of compatible pollination. This may pose special difficulties for the rare *A. texana*, which typically occurs in relatively small, isolated populations.

Our finding that *A. texana* and *A. perennis* are fully and reciprocally interfertile supports Woodson's (1954) view that these taxa are closely related sister species within his series *Incarnatae*. This is so despite isozyme data that show a mean genetic identity between the two of only 0.79. It is possible that milkweed species are unusually strongly differentiated genetically, as the genetic identities between *A. exaltata* of series *Exaltatae* and *A. texana* (0.39) and between *A. exaltata* and *A. perennis* (0.63) are also remarkably low for congeneric species (Edwards and Wyatt 1994), which typically average 0.79 (Crawford 1983).

Given that these taxa are freely interfertile when hand-pollinated in the greenhouse, we might naturally ask what reproductive barriers prevent them from hybridizing in nature. Woodson's (1954) original emphasis on the "lock-and-key" fit between the size and shape of the pollinium and the stigmatic chamber into which it must be inserted was apparently misplaced (Kephart and Heiser 1980; Kephart 1981; Kephart et al. 1988). Certainly, in the case of *A. texana* and *A. perennis*, whose floral morphology Woodson (1954) described as "indistinguishable," mechanical isolation plays no role. The present-day distributions of the two species are allopatric, with even their nearest populations being separated by more than 300 km (Edwards and Wyatt 1994). Thus, geographical isolation is one barrier to natural hybridization. The occurrence of *A. texana* in upland sites on the Edwards Plateau of central Texas and at higher elevations in the mountains of western Texas and adjacent Mexico contrasts with restriction of *A. perennis* to floodplain forests in the Southeast and enforces ecological isolation. In our experience growing these plants in a greenhouse, *A. texana* is unable to survive in waterlogged soils, where *A. perennis* thrives. Little is known about the pollinators of these species, but it is likely that they both have a "generalist" pollination strategy, as is typical of most milkweeds (Wyatt and Broyles 1994). Many species of Lepidoptera, Hymenoptera, and Diptera have been observed on the flowers of *A. perennis* in South Carolina (A. L. Edwards, pers. obs.).

The complete interfertility between *A. texana* and *A. perennis* in greenhouse crosses stands in stark contrast to the complete lack of success of crosses

between *A. perennis* and another member of series *Incarnatae*, *A. curassavica*. Both *A. perennis* and *A. texana* were also unable to cross with *A. incarnata*. Our results therefore appear to support Woodson's (1954) hypothesis of a close relationship between *A. texana* and *A. perennis*. On the other hand, they may also indicate that Woodson's (1954) placement of all these species within a single series is artificial. In this case, *A. curassavica*, a widespread weed of the tropics whose place of origin is uncertain (Wyatt and Broyles 1997), may be misplaced. It is also possible that further studies will reveal that *A. perennis* and *A. texana* should not be placed close to *A. incarnata*. Although Woodson (1954) considered the *Incarnatae* to be his most "natural" series, he was "surprised and rather disappointed" that his own attempts to cross species of *Incarnatae* in seven interspecific combinations were all unsuccessful. Moreover, nearly all of the known interspecific hybrids in *Asclepias* have involved plants that Woodson (1954) separated into divergent series (e.g., Kephart et al. 1988; Wyatt and Hunt 1991; Wyatt and Broyles 1992). Given the tendency of asclepiad taxonomists to emphasize single characters (e.g., pollinal apparatus, gynoeical structures, or coronal appendages) that may be extremely malleable to local selection in relation to pollination, it is highly likely that disparate elements have been combined in some cases (cf. Liede 1994).

Another unexpected observation from our crosses is the extremely low number of seeds per fruit obtained from interspecific hybridizations with *A. texana* as the female parent. Fewer than half of the expected number were observed, suggesting that there may be some asymmetric incongruity between the genomes of the two species that is expressed at the level of individual seeds. Like all other North American species of *Asclepias*, *A. perennis* and *A. texana* are diploids, with  $n = 11$  (Woodson 1954). We have also noted that all of the  $F_1$  interspecific hybrids, which germinated and grew vigorously to flowering age, are male-sterile. We are presently gathering more evidence regarding this phenomenon. Further studies of the  $F_1$ s and of backcrosses to both *A. texana* and *A. perennis* are in progress. In any event, complete male-sterility of  $F_1$  interspecific hybrids would prevent the production of  $F_2$ s and act as an additional strong physiological barrier to natural hybridization between these two species.

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