



Reproductive strategies of *Datura ferox*, an abundant invasive weed in agro-ecosystems from central Argentina

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ABSTRACT

Crop weeds develop in highly modified environments and are one of the most severe threats to agriculture worldwide, because their invasive nature determines competition for resources with crops and at the same time they can be hosts for pests and diseases. The information provided in this work is relevant both in scientific and technical terms, contributing to the design of effective strategies for the control of *Datura ferox* (Solanaceae). The aims of this work were to: (a) evaluate the reproductive strategies of *D. ferox* relative to fruit and seed production, (b) analyze the relationship between reproductive traits and persistence of these populations in agro-ecosystems of central Argentina, and (c) discuss different strategies to control crop weeds based on the knowledge of their reproductive ecology. *D. ferox* presented a great reproductive capacity that would not be constrained by limited pollen availability or pollinators in the populations studied. Flowers were pollinated by sphingids, coleopterans and *Apis mellifera*. The populations were self-compatible and autogamous; however, they exhibited higher fruiting percentages by natural pollination. Fruits produced by autogamy and geitonogamy had larger size and lower seed number and mass than those derived from natural pollination and xenogamy. *D. ferox* has combinations of traits (i.e., two flowering peaks, interactions with different pollinators, seed production after autogamy or xenogamy) that provide ecological advantages for establishment and survival processes in agro-ecosystems, hindering the species' control. Control strategies might be improved if *D. ferox* abundance would be reduced before flowering to avoid fruit and seed production. This management strategy should be consistent over several years because the soil seed bank would allow population recovery in subsequent years.

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Introduction

Crop weeds develop in highly modified environments and are one of the most severe threats to agriculture worldwide, because their invasive nature determines competition for resources with crops and at the same time they can be hosts for pests and diseases (Radosevich et al., 2007). The spread of these invasive plants can cause three types of economic impacts: loss of potential yield of the crop of interest, direct costs of weed control, and indirect costs of invasive species control that involve degradation of the soil, water and human health (Mack et al., 2000).

Understanding the reproductive processes of crop weeds is very important for implementing management practices that minimize

herbicide application. These costs are especially important in agriculture, because chemical control is the main technique currently used to combat crop weeds (Mack et al., 2000). In addition, these data are useful in designing effective strategies for reducing production costs and preserving agro-ecosystems (Radosevich et al., 2007). Ecological processes (e.g., animal–plant interactions related to pollination, predation, dispersion, herbivory) involved in seed production and dispersal, as well as the characteristics of the environment where the populations of a given weed develops, can affect gene flow within and among plants (Elle and Hare, 2002) and, therefore, determine the persistence of weed populations within crops.

Overall, there are complex interactions among weed plants, animals and the natural environment that may have direct effects on the functioning of the agro-ecosystem. Many interactions are species-specific, and therefore assessing the role of weed communities in the agro-ecosystem would benefit from further development of weed management at the field level (Petit et al., 2010). Weeds can respond to variations of biotic interactions and further ecological research is required to assess the biological regulation in the management of weeds.

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Pollination interactions and the prevailing compatibility system in a weed population are useful to estimate weed reproductive capacity and persistence in the agro-ecosystem (Radosevich et al., 2007), because the level of inbreeding or outbreeding can modify flower and fruit traits related to pollination (Nuñez-Farfán et al., 2007; Radosevich et al., 2007; but see Ebeling et al., 2012; Zhang et al., 2011), dispersal, seed incorporation to the soil seed bank and seedling recruitment (Brändel, 2004; Erfmeier and Bruelheide, 2004; Ferreras et al., 2008). The occurrence of high inbreeding rates may affect floral traits that may modify interactions with pollinators (Motten and Stone, 2000), tolerance to defoliation (Fornoni and Nuñez-Farfán, 2000) or may modify genetic diversity within and between populations. For example, in inbred populations the frequency of certain genotypes differentially affected by herbivorous insects may increase with respect to individuals originated by xenogamy (Nuñez-Farfán et al., 2007). If seed traits related to dispersal, persistence in the seed bank or germination are modified, reproductive capacity of a population and its possibilities of persistence in a certain region will be also modified (Radosevich et al., 2007).

In addition, the different agricultural practices (e.g., different tillage systems) can produce changes in composition and abundance of weed species present in the crop systems (Petit et al., 2010). In crops under conventional tillage, weeds are controlled mainly with machinery, whereas in crops under no-till, weeds present during and between crop cycles are treated almost exclusively with herbicides. The lack of soil removal in no-till system can modify weed seed distribution with respect to distribution under conventional tillage (Radosevich et al., 2007). Most soybean and maize crops produced in Argentina are planted under direct seeding at present, with weed control largely depending on herbicides (Tuesca et al., 2001). Both in soybean (Kapusta and Krauz, 1993) and maize (Ball and Miller, 1993), changes in weed populations with modification of tillage system (conventional versus no-till) have been observed. In general, annual weeds (such as *D. ferox*) occur in high densities with respect to perennial weeds under a no-till system (Radosevich et al., 2007; Tuesca et al., 2001).

The genus *Datura* (Solanaceae) comprises 10–12 species (Geeta and Gharaibeh, 2007). According to some authors (e.g., Bye, 1986), seven to nine species are native to the south of North America. By contrast, the three species that occur in South America could have been introduced there already in pre-Columbian times (Geeta and Gharaibeh, 2007). They are thought to be native in other parts of the world: *D. ferox* L. originating from China, *D. stramonium* L. from Eurasia, and *D. metel* L. from the south and west of Asia. However, other authors attribute the hypothetical Chinese origin of *D. ferox* to a mistake made in the first publication by Linné (Symon and Haegi, 1991) and suggest that all *Datura* species evolved and diversified in the New World (Symon, 1991). At present, *D. ferox* is distributed mainly in Argentina, Bolivia, the United States and South Africa. In Argentina, this species is commonly known as “chamico” (Hunziker, 2001) and it is distributed in a vast portion of the territory, always in fertile soil areas (Deloach et al., 1989).

Datura ferox occurs naturally in disturbed and recently opened spaces, such as cultivated fields, crop residues, and road edges (Ballaré et al., 1987, 1996). It is a common weed in summer crops (maize, potato, sunflower, sorghum, soybean, Cucurbitaceae), that may become invasive and form large populations. Seeds of *D. ferox* can be found among the grains of some of these crops, posing commercialization problems because they are poisonous. In Argentina, the species was declared an agricultural pest by the national government (government decree no. 6704/63), because it is one of the broadleaved species most damaging to soybean production in the pampas region. This occurs mainly because of its bioecological characteristics, especially its simultaneous emergence with the crop

and a production of seeds of high and long-lasting viability in the soil (Bianchi and Massiero, 1984; Tuesca et al., 2001).

The reproductive biology of this genus has received little attention. The reproductive biology of one of the species, *Datura stramonium* was studied in detail (Motten and Antonovics, 1992; Nuñez-Farfán et al., 1996). The behavior of pollinators on *D. meteloides* (syn. *D. wrightii*) and *D. stramonium* has also been analyzed (Grant and Grant, 1983). Studies on *D. ferox* have focused on factors and processes affecting seed germination (Soriano et al., 1964; Sánchez et al., 1981).

The aims of this work were to: (a) study the reproductive strategies of *D. ferox* in relation to fruit and seed production, taking into account interactions with pollinators, (b) analyze the relationship between reproductive traits and persistence of populations of this species in agro-ecosystems from central Argentina, and (c) discuss different strategies to control crop weeds based on the knowledge of their reproductive ecology.

Materials and methods

Study species

Datura ferox is an annual herb of about 50 cm in height and with alternate, irregularly serrated leaves. Stems have atypical secondary growth, which might be related to water accumulation (Liscovsky et al., 2001). Flowers are large, developing solitary in branch forks, with a tubular calyx and a white and infundibuliform corolla. The fruit is an ovoid, erect capsule covered with spines. Seeds are reniform, and are the means of plant propagation. Flowering occurs from late spring or early summer and fruits are observed up to mid or late autumn. Roots, stems, leaves, flowers, and seeds contain several alkaloids (Deloach et al., 1989; Steenkamp et al., 2004; Vitale et al., 1995). Hence, this species is considered toxic to livestock. In Argentina, few cases of cattle intoxicated with these plants have been recorded; indeed, animals do not usually ingest the leaves because they are unpalatable. By contrast, seed ingestion causes mortality in pigs and poultry and this happens when seeds are accidentally mixed with edible seeds, such as sorghum caryopses and sunflower achenes (Gallo, 1987).

Field studies were conducted in two *D. ferox* populations, Morteros and Colonia Isleta, San Justo department, Córdoba province, between January and April 1999. Herbarium specimens of the plants are deposited in CORD (Leonardo Galetto y Mariana Mimosa CORD 902, 903).

Breeding system

To study the breeding system, we performed controlled hand-pollinations in flowers bagged with fine mesh cloth bags before the start of anthesis at the two study sites. Six treatments were performed with each plant (6 flowers per plant): apomixis (by cutting anthers and stigmas in flower buds), autonomous self-pollination (flower buds were not manipulated during anthesis), hand self-pollination (flowers were hand-pollinated with pollen of the same flower), geitonogamy (flowers were hand-pollinated with pollen from flowers of the same individual), hand cross-pollination (flowers whose anthers were cut and hand-pollinated with pollen from another plant), and control (flowers that were not bagged and were exposed to pollinator visitation). Based on these data, we estimated fruit set as fruit/flower ratio for the different pollination treatments. See Table 1 to find the total number of flowers treated for each pollination treatment at each population.

In those treatments in which fruits were developed, fruits were collected before dehiscence, left to dry completely at room temperature in the laboratory, and the following variables were measured:

Table 1

Data on fruits and fructification in *Datura ferox* after natural and experimental pollination treatments. Data show the fruit set and traits of fruits and seeds obtained from natural and hand-pollinations performed in two weed populations. Values represent means \pm SD. Abbreviations: *n* = number of fruits measured; P1 = Morteros population; P2 = Colonia Isleta population; χ^2 = Chi-square test. Statistical analyses show the results of the two-way ANOVA performed (factors: T = pollination treatment, P = population). The letters A, B and a, b indicate the results of the Bonferroni a posteriori tests performed among pollination treatments and between populations, respectively.

Variable	P	Fruit mass (g)	Total mass of seeds per fruit (g)	Fruit length (mm)	Fruit width (mm)	No. of seeds per fruit	Fruit set (fl/fru)
Natural pollination	P1	3.49 \pm 1.02	2.45 \pm 0.78	34.09 \pm 5.04	22.00 \pm 2.63	175.5 \pm 5.81	0.53 (40/75)
<i>n</i> = 42	P2	3.03 \pm 1.02	1.79 \pm 0.79	35.25 \pm 3.50	23.37 \pm 2.79	197.6 \pm 55.03	0.63 (47/75)
Hand self-pollination	P1	4.1 \pm 0.82 a	2.95 \pm 0.63 a	35.40 \pm 1.93	24.36 \pm 1.79	201.0 \pm 58.07 a	0.32 (10/31)
<i>n</i> = 14	P2	2.00 \pm 0.46 b	1.27 \pm 0.44 b	36.5 \pm 4.10	19.31 \pm 0.68	96.0 \pm 23.31 b	0.82 (14/17)
Geitonogamy	P1	2.23 \pm 1.64	1.52 \pm 1.32	28.17 \pm 8.81	20.37 \pm 7.60	125.2 \pm 76.79	0.20 (3/15)
<i>n</i> = 8	P2	1.17 \pm 0.78	0.46 \pm 0.44	23.94 \pm 5.94	17.72 \pm 5.19	153.8 \pm 75.82	0.39 (5/13)
Hand cross-pollination	P1	2.99 \pm 0.93	2.16 \pm 0.74	32.18 \pm 3.62	21.28 \pm 3.35	149.3 \pm 46.06	0.26 (6/23)
<i>n</i> = 13	P2	3.04 \pm 1.06	2.22 \pm 0.92	37.34 \pm 3.98	21.73 \pm 3.01	192.0 \pm 70.39	0.59 (13/22)
Autonomous self-pollination	P1	3.17 \pm 0.85	2.25 \pm 0.66	32.30 \pm 3.28	22.19 \pm 2.43	154.1 \pm 36.56	0.20 (7/35)
<i>n</i> = 14	P2	2.84 \pm 1.03	1.91 \pm 0.95	34.72 \pm 3.68	22.2 \pm 2.88	157.2 \pm 47.89	0.32 (7/22)
Statistical analyses		T $F_{(4,89)} = 4.3$ <i>P</i> < 0.003 AABAA	T $F_{(4,89)} = 3.9$ <i>P</i> < 0.006 AABAA	T $F_{(4,89)} = 8.2$ <i>P</i> < 0.0001 AABAA	T $F_{(4,89)} = 1.6$ <i>P</i> = 0.20 ABBAB	T $F_{(4,89)} = 5.4$ <i>P</i> < 0.0006 ABBAB	P1 $\chi^2 = 190.3$ <i>P</i> < 0.001 P2 $\chi^2 = 86.2$ <i>P</i> < 0.001
		P $F_{(1,89)} = 13.0$ <i>P</i> < 0.001	P $F_{(1,89)} = 21.7$ <i>P</i> < 0.0001	P $F_{(1,89)} = 1.4$ <i>P</i> = 0.25	P $F_{(1,89)} = 0.4$ <i>P</i> = 0.55	P $F_{(1,89)} = 3.2$ <i>P</i> = 0.08	

mass, length and width of fruit, number of seeds, and total mass of seeds per fruit. On the other hand, these variables were also measured for fruits originated by natural pollination in marked flowers in the two populations and at three different times during the flowering period, to evaluate possible differences in reproductive traits.

Flower visitors

Field data on flower visitors were obtained by direct observation of the plants studied at both study sites. Walking surveys were conducted along 50-m long transects at a constant pace for 30 min at sunset and in the early morning hours, for 15 days regularly distributed throughout the flowering period. Each flower visitor, its behavior and the frequency of visits to each plant were recorded, and individuals were captured and photographed for further identification.

Flowering phenodynamics

Flowering phenodynamics was characterized in the population from Colonia Isleta (*n* = 96 individuals). Flowering individuals were recorded every 10 days throughout the flowering period, by estimating the population dynamics for this phenological stage based on the relative percentages of flowering and non-flowering plants.

Statistical analysis

Statistical analysis was performed using the methods described by Sokal and Rohlf (1995). To analyze fruit traits between populations and pollination treatments, a two-way ANOVA (“population” and “type of pollination”) was performed. Distributions were evaluated considering data independence (Runs test), variance homogeneity (Levene test) and their normality (Kolmogorov–Smirnov: goodness of fit test). Data of the variables “fruit width” and “number of seeds per fruit” were transformed to comply with the assumptions. A Bonferroni a posteriori test was performed for those variables that showed significant differences among treatments. The Chi-square test was used to compare fruit set among pollination treatments. Likewise, a correlation analysis was made for some fruit variables, using the Pearson coefficient to define possible predictors of the number of seeds per fruit that can be easily and rapidly measured in the field.

To analyze the traits of fruits obtained from natural pollination between populations and different moments during flowering

period, a two-way ANOVA (“population” and “flowering period”) was performed using SPSS (1999). Distributions were analyzed to evaluate the assumptions. For those variables that showed significant differences among treatments, the a posteriori Bonferroni test was used.

Results

Breeding system

Data on fruit set and traits of fruits and seeds obtained from the different pollination treatments are presented in Table 1. The results of controlled hand-pollinations indicate that *D. ferox* is a self-compatible and self-pollinating species. Fruit sets were significantly different among treatments and between the studied populations. One of the populations (Colonia Isleta) always showed higher fruit sets than the other population (Morteros), regardless of the pollination treatment. In general, high fruit set by natural pollination and low percentages by hand-pollination with pollen of the same individual (i.e., autonomous and hand self-pollination and geitonogamy; Table 1) were observed. However, in one of the populations (Colonia Isleta) very high values of fruit set by hand self-pollination were found, as well as great differences in fruiting between populations after hand cross-pollination (Table 1). Flowers treated to evaluate the occurrence of apomixis did not produce any fruit.

Significant differences were observed among pollination treatments for all the fruit and seed variables analyzed, except for fruit width (Table 1). The hand-pollination treatment with pollen from flowers of the same individual (geitonogamy) produced fruits of smaller size (mass and length) and smaller seed mass than the remaining treatments, which yielded comparable results (Table 1). Significant differences were also detected in the number of seeds per fruit between natural pollination and outbreeding treatments (higher average numbers per fruit) and the remaining treatments (Table 1). The comparison of results between populations shows that fruit mass, seed mass per fruit and number of seeds per fruit were higher in one of the populations (Morteros) upon self-pollination (Table 1) than in the other population. By contrast, there were no differences in fruit size (fruit width and length, number of seeds per fruit; Table 1) between populations.

Table 2 shows the traits of fruits produced by natural pollination throughout the season. Significant differences in fruit mass and width and total number of seeds per fruit were detected

Table 2
Variability of fruit traits in *Datura ferox* throughout the flowering season. Data show the traits of fruits and seeds of this weed obtained from natural pollination at different times during the flowering period. For each variable, values represent means \pm SD for the total number of fruits compared between periods, since no significant differences between populations were detected for these variables. Statistical analyses show the results of the two-way ANOVA performed (Factors: Pe = flowering period, P = population). The letters a and b indicate the results of the Bonferroni a posteriori tests performed among flowering periods.

Flowering periods	Fruit mass (g)	Total mass of seeds per fruit (g)	Fruit length (mm)	Fruit width (mm)	No. of seeds per fruit
1 (19/1)	2.74 \pm 0.69 a	1.78 \pm 0.61	35.77 \pm 2.62	21.01 \pm 1.75 a	138.4 \pm 23.9 a
2 (4/2)	3.31 \pm 1.05 b	2.17 \pm 0.79	34.67 \pm 5.49	22.57 \pm 3.26 ab	193.4 \pm 59.3 ab
3 (19/2)	3.72 \pm 1.13 b	2.41 \pm 1.01	33.56 \pm 4.39	24.46 \pm 2.02 b	227.9 \pm 26.5 b
Statistical analyses	Pe $F_{[2,41]} = 3.6$ $P < 0.04$ P $F_{[1,21]} = 0.006$ $P < 0.94$	Pe $F_{[2,41]} = 2.1$ $P = 0.14$ P $F_{[1,21]} = 3.11$ $P < 0.09$	Pe $F_{[2,41]} = 0.9$ $P = 0.41$ P $F_{[1,21]} = 1.8$ $P = 0.19$	Pe $F_{[2,41]} = 7.8$ $P < 0.002$ P $F_{[1,21]} = 1.7$ $P = 0.19$	Pe $F_{[2,41]} = 7.2$ $P < 0.0004$ P $F_{[1,21]} = 0.20$ $P = 0.66$

among the three times of their assessment during flowering period (Table 2). The trend indicates that, as the flowering period progresses, larger fruits and fruits with a higher number of seeds are produced (Table 2). No significant differences between populations were detected for any of those variables (Tables 1 and 2).

Positive and statistically significant correlations ($P < 0.01$) were found between fruit size (fruit length, width and mass) and seeds produced (number of seeds per fruit: $r = 0.32$; $r = 0.83$; $r = 0.83$, respectively; or with seed mass per fruit: $r = 0.43$; $r = 0.70$; $r = 0.96$, respectively).

Flower visitors

The most frequent flower visitor was *Diabrotica speciosa* (Coleoptera), which accounted for 51% of the visits (413 of 811 visits recorded). This species displays large populations with many individuals on the same plant, shifting among flowers of a single plant or to flowers of other individuals. Several individuals were observed on the same flower (up to six individuals per flower) searching for pollen. *Apis mellifera* (Hymenoptera) was also recorded on the flowers very frequently (25% of all the recorded visits), especially on the hottest days. These bees were seen inside the corolla, moving to the base of the flower where the nectary is located, and taking nectar. The hind legs were full of *Datura* pollen in most bees observed.

Hawkmoths of the family Sphingidae (*Xylophanes tersa* and *Manduca sexta*) were observed during the late afternoon hours (sunset) and earliest evening hours (24% of all the visits recorded). These sphingids have rapid movements between plants, taking nectar from flowers. These lepidopterans also use *D. ferox* as oviposition site, depositing their eggs on young leaves which are further consumed by the larvae. In addition, several species of the families Pentatomidae (Hemiptera) and Acrididae (Orthoptera) use these plants as mating and oviposition sites. Noticeably, *Phthia picta* (Hymenoptera, family Coreidae) was the only insect that was seen feeding on the fruit.

Flowering phenodynamics

The flowering period of *D. ferox* lasted approximately 10 weeks, from mid January to the first days of April. The start of flowering (January 19) was defined as the moment when 6% of individuals had flowers. Flowering peak occurred at mid February (February 19), when all the individuals had flowers. A few days later (February 29), only 10% of the individuals had flowers. Then, a second flowering peak occurred at mid March, with flowering ending in early April.

Discussion

The results of this work show that *D. ferox* has combinations of reproductive traits that would be advantageous for the species'

persistence in modified environments, such as agro-ecosystems. This species presents a great capacity to produce seeds in unpredictable environments, showing an expanded flowering and two peaks within the season. If pollinators and weeds are abundant, natural-pollination is favored and greater numbers of larger seeds are produced. If such conditions are not met, this weed can also self-fertilize and produce a high number of viable seeds. All these reproductive traits and the ecological circumstances of its growing sites contribute to the difficulty in controlling this weed.

Taking into account some floral traits, such as the occurrence of flower opening at sunset, the deep tubular white corolla or the presence of nectar at the base of the corolla tube, and based on the theory of floral syndromes, it could be speculated that the principal pollinators of *D. ferox* would be nocturnal Lepidoptera. However, field observations showed that, besides sphingids also the melliferous bee and coleopterans can be considered pollinators because they are capable of transferring pollen within and between flowers during their visits. The flower visitors observed in *D. ferox* agree in part with those reported for *D. stramonium*, in which sphingids were detected at night and bees during the day (Nuñez-Farfán et al., 1996, and references therein). Considering the great flight capacity of sphingids and their feeding behavior (Amorim et al., 2013), these animals can promote mainly the transfer of exogamous and/or geitonogamous pollen, whereas the melliferous bee and the coleopterans transport mostly geitonogamous or autogamous pollen.

The increasing expansion of the melliferous bee to natural ecosystems in the Americas has produced some disturbance of native pollinator–plant relationships (Aizen and Feinsinger, 1994). In several cases the production of seeds of plants visited by *A. mellifera* was distinctly greater than of those pollinated by other insects, especially when the plant species were invasive or exotic (Aizen and Feinsinger, 1994). In central Argentina the interaction of *A. mellifera* with invasive exotics has been frequently observed (e.g., Aizen and Feinsinger, 1994; Ferreras et al., 2008; Torres and Galetto, 2008). Therefore, it would be of great interest to study the interaction between *D. ferox* and *A. mellifera* in greater detail, since it might represent a case of invasive mutualism.

Self-pollination is frequent and successful in several herbaceous angiosperm species of modified environments (Morales and Galetto, 2003). For *D. ferox*, self-pollination of flowers is expected to be a strategy for increasing seed set when the chances of insect-mediated pollination are reduced. Thus, the occurrence of self-fertilization appears related to poor and unpredictable pollination environments, such as disturbed habitats like the agro-ecosystems where *D. ferox* grows. In addition, if the opportunities for outcrossing are not equal between populations, different amounts of the various reproductive strategies (autogamy, geitonogamy or xenogamy) may lead to and explain the differences found in fruit set and fruit and seed traits between the populations studied. Nevertheless, self-pollination before the

opportunity of cross-pollination is generally regarded less advantageous than self-pollination after opportunities for cross-pollination are no longer possible, because the former strategy can lead to lower seed set or seeds of lower quality, as it seems to be the case also with flowering and seed set of *D. ferox*. Moreover, high self-pollination rates within a population can cause that no pollen of enough quality or quantity arrives at the stigmas (Morales and Galetto, 2003).

Datura ferox can have two flowering peaks and the resulting fruits contain numerous seeds, independently of the type of pollinator and of the pollen origin. In consequence, *D. ferox* has a high reproductive capacity (58% natural fruiting) which apparently was not strongly limited by the quality of the pollen deposited in the stigmas or by the abundance of pollinators in the populations studied. Seed number per fruit is an important component of reproductive success, particularly in annual plants. Number of seeds in self-pollinated *D. ferox* flowers is significantly lower than in naturally or artificially cross-pollinated ones. This is similar to the situation in *D. stramonium*, where studies on the breeding system also reported smaller seed numbers for self-pollination treatments (Nuñez-Farfán et al., 1996).

The weedy *Datura* species have a reasonable plasticity in producing seeds through different pollination means, depending on the particular conditions between years or sites. Nevertheless, empirical evidence (Nuñez-Farfán et al., 1996; this work) indicates that the possibility for xenogamy will be an advantage maintaining the genetic variability within a population in a given environment. In addition to maintenance of genetic heterogeneity on the long term by outcrossing possibilities – which can be of high importance keeping the population fitness high in disturbed environments, in situations of insufficient pollinator availability self-pollination and autogamy can be favorable as well, ensuring continuity between the population cohorts in such environments (Bond, 1994).

The capacity to produce seeds when pollinators or individuals of the same species are scarce has been proposed as the main advantage of self-pollination (Eckert and Schaefer, 1998 and references therein). This capacity is an attribute of a reasonable amount of weed species, conducive in highly modified environments or when climatic conditions do restrict pollen dispersal between different individuals (for instance, due to permanent rainfall, drought, extreme cold that can restrict strongly the activities of pollinators). It is advantageous also when new populations are established from isolated individuals, when the recessive homozygotic stage is environmentally more suitable, or when two closely related taxa, which produce sterile hybrids, occur in the same habitat without the presence of specific pollinators (e.g., Abbott et al., 2009; Daehler, 1998; Eckert and Schaefer, 1998; Lloyd, 1980; Wells, 1979).

Plants with traits that allow them to overcome or alleviate pollinator limitation, like *D. ferox*, can have a greater capacity to invade new environments outside their natural distribution area than species that lacking those traits (Abbott et al., 2009). According to Baker's law (Baker, 1955) self-compatible plants will be more successful than self-incompatible plants in long-distance colonization, because already one single propagule can establish a viable population. Indeed, self-compatible species are often more invasive than self-incompatible ones (Hao et al., 2011; van Kleunen and Johnson, 2007). Also under this aspect *D. ferox* must be ranked among the highly aggressive weeds.

Variations in the percentage of fruit production over a reproductive season can be related to diverse factors (environment, nutrition, competition, herbivory, etc.) that restrict the reproductive capacity of an individual (Stephenson, 1992). The “ecological windows” hypothesis (Sutherland, 1986) emphasizes the occurrence of temporal and spatial variations of resources needed for fruit maturation. For example, some studies documented a decrease in the number of fruits, seeds per fruit and/or mean seed

mass per fruit occurring at the end of the reproductive season (Stephenson, 1992). This latter pattern was not found in *D. ferox*, because fruits increased in size (width, mass and total seed set) with progress of the reproductive season. This might be attributed to the increase of rainfalls toward the end of summer, which might have increased the water availability for the plants. Also the application of fertilizers to the crops might have been favorable for better fruit and seed quality also of the weed species. Disentangling these interactions will require further studies.

Better knowledge about the ecological interactions between crop and weed species could improve weed management practices, so that weeds would be suppressed without environmental impacts in such highly productive agro-ecosystems (Petit et al., 2010). Although not all plants surrounding crops produce damages, species that become invasive, such as *D. ferox*, must be kept under strict control in order to avoid damage to the crop. Under non-tillage systems population density of *D. ferox* can decline (Buhler, 1995), probably because its germination is favored by soil disturbance (Tuesca et al., 2001). Information about the circumstances of pollination and seed set may contribute to control strategies for this weed. Since due to different reproductive strategies and the availability of different pollinators predictions of seed production of particular populations are difficult, weed control seems to be most effective if executed prior to the flowering peaks (mainly the second one). By this way seed production by both, autogamy and xenogamy, will become reduced and, in consequence, less seeds will be incorporated into the soil seed bank. If this is done for several consecutive growing seasons, a distinctly lower number of seeds produced will lead to less *D. ferox* individuals in the fields in subsequent cycles, so that, with time, the population might become substantially reduced in the mid-term, if not even completely eradicated locally.

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