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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.

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: