

PREPRINT

Author-formatted, not peer-reviewed document posted on 28/06/2022

DOI: <https://doi.org/10.3897/arphapreprints.e89390>

The reproductive traits that contribute to the invasive success of Mediterranean onionweed (*Asphodelus fistulosus*)

Sandino Guerrero-Eloisa,  Maria Mandujano,  Pedro Luis Valverde,  Jordan Golubov

The reproductive traits that contribute to the invasive success of Mediterranean onionweed (*Asphodelus fistulosus*)

Oscar Sandino Guerrero-Eloisa^{1,2}, Jordan Golubov^{1*}, María C. Mandujano³ and Pedro Luis Valverde⁴

¹ Universidad Autónoma Metropolitana – Xochimilco, Departamento de El Hombre y su Ambiente, C.P. 04960, Ciudad de México, México; osge44@gmail.com

² Doctorado en Ciencias Biológicas y de la Salud. Universidad Autónoma Metropolitana. C.P. 04960, Ciudad de México, México

³ Instituto de Ecología, Universidad Nacional Autónoma de México, UNAM, Ciudad Universitaria, 70275, Ciudad de México, México; mcmandujano@gmail.com

⁴ Universidad Autónoma Metropolitana – Iztapalapa, Departamento de Biología, C.P. 09430, Ciudad de México, México; plvp@xanum.uam.mx

*Corresponding author: gfjordan@correo.xoc.uam.mx

Background and aims - Understanding the traits that lead to the invasion potential of alien invasive species (AIS) provides insight for their management. The reproductive traits of AIS help us to understand the mechanisms that allow for their invasive potential, and colonization into new ranges. *Asphodelus fistulosus* is a native Mediterranean species commonly found invading Australia, South-East Asia and North America.

Materials and methods - Two populations in the Chihuahuan Desert of *A. fistulosus* were followed for reproductive phenology. Floral visitors and their behavior were described, and we assessed the breeding system through floral morphological characters and the mating system in controlled pollination experiments.

Key results - Reproductive phenology shows a continuous reproduction throughout the year. Floral morphology suggests a facultative autogamous breeding system, but the mating system is mixed with autonomous selfing. Flowers longevity was one day, with anthesis lasting 11 h. Floral visitors of *A. fistulosus* consisted of a variety of taxa including species of Coleoptera, Hymenoptera and Lepidoptera, the exotic *Apis mellifera* being the most frequent visitor.

Conclusions - The reproductive traits of *A. fistulosus* in the invaded range provide the biological potential for further invasion. The continuous production of reproductive structures attracts many pollinators, and the autonomous self- pollination implies that a single plant has the potential to develop new populations, posing the control of this AIS as a global challenge.

Keywords: breeding and mating system; floral visitors; alien invasive species; phenology

INTRODUCTION

Current severe environmental threats are brought about by changes in land use, climate change and alien invasive species (AIS; Dirzo & Raven 2003), that have been identified as one of the leading causes of species extinctions worldwide (Pimentel et al. 2000; McNeely 2001; Pejchar, & Mooney 2009). Several hypotheses have been put forward to explain the success of biological invasions (Essl et al. 2015) such that for successful invasive plant species, a subgroup of these hypotheses is linked to identifying traits that allow these species to establish new populations in their invaded range such as the ability for sexual and asexual reproduction (Moravcová et al. 2015), multiple phenological strategies (Wolkovic et al. 2011) and even high germination rates (Gioria & Pyšek 2009), among others. These traits, many of which were partially described by Baker (Baker 1965) in his treatment of the perfect weed, usually confer an advantage that favor population growth over native species (Doody et al. 2009) and provide a working hypothesis expected to be found in AIS. The identification of traits that confer invasive potential (Van Kleunen et al. 2013) is also an important component of risk assessment protocols (Pheloung et al. 1999) and a means of characterizing weedy species (Baker 1965; Sutherland 2004), although results do not always support the predictions.

The variation in mating and breeding systems of invasive plant species is broad (Barret 2002). Reproductive systems can change after colonization (Ferrero et al. 2020) and Baker's Law emphasizes a preference of self-compatible over self-incompatible species (Baker 1965; Williamson & Fitter 1996; Barret 2011). However successful invasive plant species have a wide variety of mating systems, from self-compatibility (Jacquemart et al. 2015; Redmond & Stout 2018), self-incompatibility (Sutherland 2004; Friedman & Barrett 2018) and even mixed mating systems (Souza et al. 2016). There is also the argument that AIS benefit from non-specialized pollination systems under the assumption that new habitats pose pollinator limitations that can be avoided (Stout et al. 2002) with generalized pollinators found in the invaded range (D'Antonio et al. 2000; Stotu & Tiedeken 2017) or in the absence of pollinators, favor species with autonomous self- pollination (Pannell et al. 2015). Even though most plants including AIS are pollinated by animals (Ollerton et al. 2011), self-compatibility and autonomous pollination reduces the dependence on biotic interactions (Van Kleunen, & Johnson 2005; Van Kleunen et al. 2008) favoring invasion success. The loose interactions with native pollinators can even decrease fitness (Knight et al. 2005; Burns et al. 2013) or may generate new interactions with native pollinators causing a shift in preference and a competition for floral visitors that negatively impact native plant species (Chittka & Schürkens 2001; Mitchell et al. 2009).

Seed output in AIS is thought to be high (Díaz-Segura et al. 2020), and even though AIS invasions benefit from asexual reproduction as clonal spread (Guerra-García et al 2015) there are successful AIS that rely entirely on sexual reproduction (Forman & Kesseli 2003). The overall behavior of reproductive traits in terms of seasonality is correlated with overall fitness linked to environmental signals, for example, phenology is a key component of plant reproduction (Cleland et al. 2007), it provides relevant information to understand the

impacts of AIS in invaded ecosystems (Vilà et al. 2011) and hypotheses that help explain their success (Wolkovich et al. 2013; Wolkovich & Cleland 2014; Gioria & Pyšek 2017). The variation in phenological phases can increase or decrease niche overlap with native plants species or increase fitness when cued with the prevailing environmental conditions at the site of introduction (Alexander & Levine 2011).

The purpose of this study was threefold (1) describe the flowering phenology of *Asphodelus fistulosus* at two invaded sites in the Chihuahuan Desert, (2) identify floral visitors and how these change over floral anthesis and (3) describe the breeding system using morphological floral characters and define the mating system through field-controlled pollination experiments to assess how these traits can favor the invasion potential of *A. fistulosus* in Mexico.

MATERIAL AND METHODS

Study area

Field work was carried out at two sites in the Southern Chihuahuan Desert. Site QRO was located close to Cadereyta de Montes, Queretaro, Mexico (-99°42'53" W; 23°44'16" N), and the second site SLP was located in Guadalcázar, San Luis Potosí, Mexico (100°26'13" W; 22°38'18" N). The linear distance between sites was 224 km. This study was performed from September 2018 to July 2019.

Study species

Asphodelus fistulosus L. (Xanthorrhoeaceae) is a native herb from the South of Europe, found in the Mediterranean basin and considered invasive in Southeastern USA, Australia, India and New Zealand (Boatwright, 2012). Introductions have been intentional for ornamental purposes (Bailey & Bailey 1976; Russel 2008), but can easily escape from cultivation (USDA, 2016) and establish populations in disturbed, over-grazed habitats (Victoria State Department 2016) with impacted vegetation cover (Martínez-Cruz & Téllez-Valdés 2004). In Australia, *A. fistulosus* forms dense populations in arid and semi-arid environments and disturbed areas (Parsons et al. 2001; Cullen 2012). The first reports of *A. fistulosus* in Mexico locate their presence in northern arid environments (Conzatti 1946; Villaseñor & Espinosa-García 2004), and since then, the species has considerably increased its geographical distribution, now found in 15 out of 32 states in Mexico (Guerrero-Eloisa 2017).

Phenology

Three phenophases (floral buds, flowers and fruits) were recorded on individuals of *A. fistulosus*. At each site 1 × 1 m plots ($N = 17$ plots in QRO and $N = 10$ plots in SLP) were set up in 2018 and individuals of *A. fistulosus* were tagged, mapped and the frequency of their phenological phase recorded every two months from September 2018 to July 2019.

The number of plots was based on abundance of *A. fistulosus* individuals at each site, sample size started at QRO = 1015 and SLP = 999 individuals and diminished over the study period to QRO = 791 and SLP = 856 individuals. Phenophases were analyzed with circular statistics using a Rayleigh test and a Watson-Williams U^2 test was used to detect significant differences in phenophases between sites. All circular statistics by phenophases were run with Oriana 4.0 (Kovach 2011).

Meteorological data was obtained (average temperature and average precipitation) online (www.wunderground.com) from the nearest weather station. We correlated these environmental variables with the phenology observed in QRO.

Floral visitors

Observations of floral visitors were carried out in February 2019 at QRO and March 2019 in SLP. At each site, five flowers of 15 individual of *A. fistulosus* in each of three plots were monitored for visitor activities. Each plot was monitored by one observer during anthesis (225 flowers in QRO, five observers, 15 flowers in three plots and 180 flowers in SLP, four observers, 15 flowers in three plots). Forty-five-minute observation periods were made at each site from 0700 to 1800 h with 15-minute breaks for each hour of observation. The identity (species or morphospecies) of the visitor, activity (catalogued as pollen or nectar collection) and period of observation were recorded for each visit (Dafni, 1992). Visitors were captured for identification in ethyl acetate lethal chambers for identification (Márquez 2005). The Shannon diversity index (H') were calculated for both sites and evaluated the diversity between sites with a Hutcheson t test.

Anthesis was followed in QRO (February 2019) and SLP (March 2019) in which three plots having *A. fistulosus* were selected and in these, 15 flowers of three different individuals were followed. Corolla aperture was measured with a digital caliper (0.05 mm) in 15-minute intervals from 0700 to 1800 h when flowers closed completely. Stigmas were considered receptive when surfaces developed moisture while anther dehiscence was detected with the presence of pollen. Circular statistics were used to describe floral behavior where the mean angle (μ) represents mean time of aperture and the vector (r) the concentration of frequency around the mean through a Rayleigh test (Batschelet 1981; Morellato et al. 2010).

Accumulated nectar production was obtained from 30 flowers using microcapillary tubes (1 μ l) on flowers bagged before anthesis (0900 h) and evaluated at 1800 h, The total nectar production and concentration of sugars was estimated with a field refractometer (Atago mod. N-1 α).

Mating and breeding system

The mating system was determined through controlled pollination experiments in the QRO population during February 2020. The same experiment was established at SLP but was

soon vandalized. One flower of each of 50 individuals was assigned to one of the following seven treatments: (1) control, flowers were tagged and exposed to natural pollination; (2) supplementary pollen to evaluate pollinator limitation, additional pollen from other individuals was deposited on exposed flowers; (3) artificial self-pollination, flowers were bagged with bridal cloth before anthesis, manually pollinated with self-pollen and rebagged; (4) autonomous self-pollination, flowers were bagged with bridal cloth before anthesis without further manipulation; (5) artificial cross pollination, flowers were bagged with bridal cloth before anthesis, emasculated at the onset of anthesis, pollinated manually with pollen from other individuals and rebagged; (6) natural cross pollination (cross pollination control), flowers were bagged before anthesis not emasculated at the onset of anthesis, pollinated manually with pollen from other individuals; (7) geitonogamy, flowers of the same plant were bagged and manually pollinated with pollen from flowers of the same individual. An agamospermy treatment was attempted, but self-pollen contamination precluded further evaluation. Fruit set was recorded three weeks after the onset of the pollination treatments. Results of the pollination experiments were analyzed through GLM with a binomial error distribution in JMP® version 16.0.0 (JMP, 2021).

Floral morphological traits were taken to determine the breeding system. An out-crossing index (OCI) and pollen/ovule ratios (P/O; Cruden 1977) were estimated using (a) corolla aperture (mm), (b) presence of dichogamy (temporal separation of sexual functions) and (c) hercogamy (spatial separation of sexual functions). Five flowers of 65 individuals were collected and stored in FAA. A digital caliper (0.05 mm) was used to measure the following: corolla aperture (mm) (CA), minimum anther-stigma distance (mm) (ASD) and flower length (mm) (FL). To estimate the number of pollen grains per flower (GP), sixty-five anthers were collected before pollen release, stored in 5 ml Eppendorf tubes with alcohol. Tubes were homogenized with a vortex before an aliquot (10 µl) was sampled, and pollen grains counted. Data was then extrapolated to volume and number of stamens per flower (six stamens) (Cruden 1977). The number of ovules per flower were obtained dissecting the ovarian chamber and counting the ovules present in each of the 65 flowers.

RESULTS

Phenology

Reproductive phenophases at the two studied populations in the Chihuahuan desert (QRO and SLP) were studied throughout the 10-month study period (Fig 1), with peaks in QRO during late autumn and peaks at SLP concentrated during spring. [QRO, floral buds ($Z = 14$, $r = 0.25$, $p < 0.0001$), flowers ($Z = 164.96$, $r = 0.15$, $p < 0.0001$), fruits ($Z = 133.47$, $r = 0.47$, $p < 0.0001$); [SLP, floral buds ($Z = 50.16$, $r = 0.38$, $p < 0.0001$), flowers ($Z = 25.5$, $r = 0.35$, $p < 0.0001$), fruits ($Z = 131.21$, $r = 0.47$, $p < 0.0001$)] (Figure 1). The pattern on the periods of floral buds ($F = 162.131$, $p < 0.001$), flowers ($F = 299.098$, $p < 0.001$) and fruits ($F = 1443.044$, $p < 0.001$) did not match between sites. Results of phenology on *A. fistulosus* suggest that the floral buds, flowers, and fruits are influenced with at least one

environmental variable in QRO site. Floral buds shown a positive correlation with precipitation ($r = 0.97$, $p < 0.001$), flowers were positively correlated with temperature ($r = 0.69$, $p < 0.001$) and fruits were correlated with precipitation ($r = 0.30$, $p < 0.001$) and temperature ($r = 0.38$, $p < 0.001$).

Floral visitors and flowering time

During the 10 observation periods at each site, 13 species were identified visiting flowers in QRO belonging to the Hymenoptera (six spp), Coleoptera (one sp) and Lepidoptera (six spp) and eight species were registered in SLP of the Formicidae (one sp), Hymenoptera (three spp) and Lepidoptera (four spp; Table 1). The diversity calculated for floral visitors was $H' = 0.923$ (QRO) and $H' = 0.330$ (SLP), a Hutcheson t test showed ($t_{768} = 18.45$, $p < 0.0001$) that QRO site was significantly more diverse than SLP. The exotic bee *A. mellifera* was the only common species at both sites. The genus *Lasioglossum* was also found at both sites, but we were unable to identify the specimen to the level of species.

The activities (collecting nectar or pollen) were divided into the Lepidoptera that exclusively collected nectar (using their proboscis) while the Hymenoptera collected both nectar and pollen (bees fill pollen-bags with pollen) (Table 1). At both sites, visitors were mostly active at midday but the exotic bee *A. mellifera* was active throughout the 10 h observation period (Figure 2A, 2B). Flowering was of approximately 11 h (0700 - 1800), concentrated at midday for both sites (QRO $Z = 32.58$, $r = 0.38$, $p < 0.0001$, SLP $Z = 26.89$, $r = 0.33$, $p < 0.0001$) with maximum corolla aperture (QRO mean = 16.77 mm, \pm SE = 0.847; SLP mean = 15.80 mm, \pm SE = 0.736), stigma receptivity (identifies by a change in coloration) and pollen release coinciding with the peak of visitor activities (1000 - 1200 h) (Figure 3A, 3B).

The average production of nectar was 0.15 μl ($\pm \text{SE} = 2.778$) per day, this volume is small, and it was not possible to measure the concentration of sugars in the nectar with the refractometer. When the measurement of the nectar was carried out, the presence of springtails (Subclass Collembola) was observed, possibly taking the nectar present in the ovary.

Mating and breeding system

Asphodelus fistulosus produced fruits without pollinators, had the capacity for autonomous pollination and is self-compatible. Pollination experiments showed high fruit set with no differences between treatments ($\chi^2 = 9.17$; $df = 6$; $p = 0.164$) which indicates a mixed mating system. Floral morphometric data (Table 2) as well as the timing of floral phenophases suggest a facultative autogamous breeding system according to Cruden's index.

The P/O ratio was high (QRO = 384:1 and SLP = 378:1) and consistent with the out-crossing index (OCI) estimation for facultative autogamous species. When comparing autonomous pollination treatments (autonomous self- pollination, artificial self- pollination and geitonogamy) vs cross pollination treatments (supplementary pollen, natural cross pollination and artificial cross pollination), we found a small but significant difference ($\chi^2 = 9.17$; $df = 6$; $p = 0.028$) in fruit set which means that even though *A. fistulosus* is basically capable of both self and cross pollination, autonomous pollination does have a slight advantage over cross pollination (Table 3).

DISCUSSION

Reproductive traits in AIS are considered important components in their invasion potential (Baker 1974). Phenological events provide information on the success of AIS (Baker 1974) which can be expressed as: phenotypic plasticity whereby the potential to change phenophases in response to different habitats, anticipated or delayed flowering, and extended or continuous phenophases (Wolkovich & Cleland 2011, Wolkovich et al. 1013; Wolkovich & Cleland 2014). AIS have been shown to extend flowering periods that confer advantages over native plant species (Pyšek et al. 2008; Pyšek & Richardson 2008), with examples across the taxonomic spectrum such as in *Bidens frondosa* (Yan et al. 2017), *Leonotis nepetifolia* (Díaz-Segura et al. 2020), *Coreopsis lanceolata* (Zeng et al. 2021) and *A. fistulosus* (this study). When using *A. fistulosus* citizen science data for Mexico that compiled data for 578 observations (O.S. G-E. Pers. Obs.), reproductive phenophases could be seen year-round with two flowering peaks during March and September, consistent with what was found in this study. A second component in the success of AIS that is reflected in phenological events is plastic response. At our study sites in the Chihuahuan Desert, *A. fistulosus* reproduction peaked during two different seasons (autumn in QRO and spring in SLP) while data from USA suggests flowering peaks in summer (DiTomaso et al. 2013)

and during spring in South Africa (August-October; Boatwright 2012). In the Mediterranean native range of *A. fistulosus*, flowering occurs between December to June (Boatwright 2012), while congeners report of flowering in March-May for *A. albus* (Obeso 1992) and June to September for *A. aestivus* in Spain and May to April in Portugal (Lifante 1996). There is evidence then that phenologically, *A. fistulosus* and potentially the congeners obey two strategies: extended flowering periods as well as the potential to easily change phenophases depending on the local conditions.

As a possible consequence to extended flowering periods, there is also an enhanced attraction of flower visitors (Ojija et al. 2019). The extended flowerings periods of *A. fistulosus* and the interaction with climatic variables suggest a response to different habitats that provides an advantage over native species (Pyšek et al. 2008, this study). The floral resources generated by a single individual of *A. fistulosus* can be significant, producing 30-60 flowers per plant (O.S.G-E. Pers. Obs.). The abundance of floral resources has been shown to divert native pollinator species from visiting native flora (Powell et al. 2011; Yan et al. 2017) and even increases visitor frequency in congeneric sympatric species (Zeng et al. 2021). Generalist pollination systems are thought to favor invasive potential of AIS (Baker 1974) such that attraction is not confined to a specific group of visitors (Stout et al. 2006). Within the genus *Asphodelus*, a diverse assemblage of species visits the flowers in its native range, *A. mellifera* being common but can also include *Xylocopa*, *Bombus*, *Anthidium*, *Chelostoma* and *Megachile* (Obeso 1992; Lifante 1996; Ruiz 2003). In Mexico (Ruiz 2003, this study), *A. mellifera* was the most common visitor, also described by Ruiz (2003), that would mean a first step in invasive species favoring the success of another AIS (invasion meltdown, Simberloff & Holle 1999) but there were also new associations with three insect orders (Hymenoptera, Lepidoptera and Coleoptera). The presence of *A. mellifera* impacts pollination systems in invaded ranges because of their negative effect on native plants and positive effects on invasives (Morales et al. 2017). Secondly, *A. mellifera* is not usually an efficient pollinator in native plants (Santos et al. 2012) and is resilient to disturbance (Winfree et al. 2009). In the native range of *A. fistulosus*, *Agapanthia asphodeli* (Coleoptera) acts as a floral visitor while *Trichochrous* sp. (Coleoptera) was found in QRO. If we consider the extended flowering period, generalist pollination systems, new associations with native visitors, and positive feedbacks with exotic floral visitors, the potential success of *A. fistulosus* as an AIS are certainly favored. These interactions not only benefit the exotic but may cause competition with native plant species for floral visitors (Stout & Tiedeken 2017). Of the native pollinator species found on *A. fistulosus* in this study, *Lasioglossum* sp. (native to America) and *Trichochrous* sp. have been reported as frequent visitors of the Cactaceae in the same area (Briseño-Sánchez et al. 2020). For the butterflies, even though the main activity on *A. fistulosus* was the collection of nectar, it is known that they can be an important pollinator for plant species (Zhang et al. 2011; Geerts & Adedjoja 2021).

Not only is the length of the flowering period relevant for AIS success but also floral longevity, because these determine on one hand the seasonality in the reproduction periods and on the other the availability of resources at any given time (Janzen 1971). This can be

understood as two opposing strategies, short lived (< 1 d) floral resources that are spread over a long period of time or long-lived floral resources (> 1 d) over a shorter time period usually associated to generalist pollination syndromes (Yan et al. 2016). There are few studies that have addressed floral longevity in AIS (single flower), with evidence in species with anthesis that can last several days as 4 - 5 d in *Bidens frondosa* (Yan et al. 2016), 5 - 6 d in *Coreopsis lanceolata* (Zeng et al. 2021), 4 d in *Stapelia gigantea* and 6 - 11 d in *Kalanchoe daigremontina* (Herrera & Nassar 2009) and others that are short lived usually one day such as *Leonotis nepetifolia* (Díaz-Segura et al. 2020) or less than 24 h (Alegro et al. 2010, this study). Flowers provide nectar as a reward to insect visitors, that is especially relevant in generalist pollination syndromes that benefits invasive species as visitors (Lach 2008, Zhang et al. 2011, this study). Short lived floral resources that are spread over a long time period can favor recurrent visitors, which maximize the amount and activity of the floral visitors and promotes outcrossing due to the number of receptive flowers in a short time period (Janzen 1971). Even though outcrossing is unnecessary for *A. fistulosus*, it generates genetic recombination and can potentially increase seed set in some species (Díaz-Segura et al. 2020).

The role played by mating and breeding systems spurred Baker's law in which selfing species would be better colonizers (Baker 19767). The evidence supporting this hypothesis seems to be quite widespread among AIS (Baker 19767). Furthermore, mixed mating systems guarantee offspring in new habitats whereby autonomous self- pollination generates progeny and dispersal without the need of another individual (Cruden 1977), the reproductive success in *A. fistulosus* is a consequence of outcrossing and selfing system, a trait that leads to higher genetic variability and long-term survival (Cruden, 1977).

However, extreme cases of selfing may hinder future growth (Van Kleunen, & Johnson 2007) through inbreeding (Novak 2005; Sakai et al. 2001) but flower visitors can favor outcrossing, generating more vigorous recombinant seeds. Evidence of this is contradictory, some AIS species are highly successful through entirely clonal reproduction (Corredor-Prado et al. 20015; Guerra-García et al. 2015) while others have even higher genetic variation than the native populations (Wang et al. 2016; Lucardi et al. 2020; Smith et al. 2020). Furthermore, many AIS possess self-incompatibility (17 species in South Africa; Rambuda & Johnson 2004) among others *Mikania micrantha* (Hong et al. 2007) and *Ambrosia artemisiifolia* (Friedman & Barrett 2008). Self-compatibility would favor continuous seed production, population maintenance and some degree of dispersal (Herrera & Nassar 2009; Zhang et al. 2011; Zeng et al. 2021). The continuous periods of floral buds, flowers and fruits in *A. fistulosus* and the presence a mixed system could potentially lead to further invasion in arid environments (Janzen 1971; Díaz-Segura et al 2020).

In addition to the number of reproductive traits found in *A. fistulosus* that very likely favor invasive success, the establishment of *A. fistulosus* in areas that present a high disturbance also contributes to their success (Elton 1958; Hobbs & Huenneke 1992). *Asphodelus fistulosus* forms large patches of vegetation causing a reduction of native species, impacting the biodiversity of the ecosystem (Elton 1958; Levine & D'Antonio 1999). The ornamental

use of *A. fistulosus* (Jeschke & Strayer 2006) and the lack of natural enemies (Keane & Crawley 2002) also favor invasion (Blumenthal 2006) increasing the availability of resources for pollinators and the possibility of pollination by exotic species (Simberloff & Holle 1999). The set of invasive traits described in *A. fistulosus* shows the invasive potential, especially given the wide range of attributes considered in the ideal weed that are expressed in the invaded range.

CONCLUSIONS

All reproductive phenophases of the species in both populations were found throughout the year, providing continuous availability of resources for floral visitors. However, flower and fruit production peaks differ between populations, suggesting that reproductive phenology responds to local conditions. The large number of flowers favors the presence of native visitors, which range from nectarivorous species of the Lepidoptera, and species of native bees (e.g., *Lasioglossum* sp. and *Ceratina* sp.) and exotic bees (e.g., *Apis mellifera*) that collect pollen and nectar. Our evidence supports Baker's law that self-pollinated species would be better colonizers. Furthermore, the mixed mating system of *A. fistulosus* guarantees variable offspring and dispersal to new habitats; and through autonomous pollination it generates progeny without the need for another individual to mate. The invasive potential of onionweed within the Chihuahuan Desert is favored by its mating system and phenological plasticity facilitating its expansion to other areas, prompting an urgent need to establish plans for its control.

ACKNOWLEDGMENTS

The first author is a student of the PhD Program Doctorado en Ciencias Biológicas y de la Salud - Universidad Autónoma Metropolitana Xochimilco (UAM-X), and the paper is part of his dissertation in partial fulfillment of the requirements for the graduate program. This research was funded by Consejo Nacional de Ciencia y Tecnología (CONACyT) that awarded a scholarship to O.S.G-E. (815924). Financial and logistical support was provided by the Instituto de Ecología, UNAM, SEP-CONACyT 221362 and the GEF 00089333 project “Enhancing National Capacities to manage Invasive Alien Species (IAS) by implementing the National Strategy on IAS” to M.C.M. and J.G. We thank Mariana Rojas-Arechiga for logistical support and comments, Isabel Briseño Sánchez, Diana Cárdenas Ramos, Esteban Munguía Soto, Omar Díaz Segura, José Aranda Pineda, Gerardo Manzanares Villasana and Linda Martínez Ramos for field assistance.

REFERENCES

- Alegro, A., Bogdanović, S., Rešetnik, I., & Boršić, I. (2010). *Thladiantha dubia* Bunge (Cucurbitaceae), new alien species in Croatian flora. *Natura Croatica*, 19(1), 281-286.
- Bailey, L. H., & Bailey, E. Z. (1976). *Hortus third: a concise dictionary of plants cultivated in the United States and Canada* (No. BOOK). MacMillan Publishing Co..
- Baker, H. G. (1965). Characteristics and modes of origin of weeds. Characteristics and modes of origin of weeds., 147-172.
- Baker, H. G. (1967). Support for Baker's law-as a rule. *Evolution*, 21(4), 853-856.
- Baker, H. G. (1974). The evolution of weeds. *Annual review of ecology and systematics*, 5(1), 1-24.
- Barrett, S. C. (2002). The evolution of plant sexual diversity. *Nature Reviews Genetics*, 3(4), 274-284. <https://doi.org/10.1038/nrg776>
- Barrett, S. C. (2011). Why reproductive systems matter for the invasion biology of plants. *Fifty years of invasion ecology: the legacy of Charles Elton*, 1, 195-210.
- Batschelet, E. (1981). Circular Statistics in Biology. Ed. Academic Press Inc. Londres Inglaterra. 371 pp.
- Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, 9, 887-895. <https://doi.org/10.1111/j.1461-0248.2006.00934.x>
- Boatwright, J. S. (2012). *Asphodelus fistulosus* (Asphodelaceae, Asphodeloideae), a new naturalised alien species from the West Coast of South Africa. *South African Journal of Botany*, 79, 48-50. <https://doi.org/10.1016/j.sajb.2011.11.008>
- Briseño-Sánchez, M. I., Martínez-Peralta, C., & Mandujano, M. C. (2020). Population structure and reproductive biology of peyote (*Lophophora diffusa*, Cactaceae), a threatened species with pollen limitation. *The Journal of the Torrey Botanical Society*. <https://doi.org/10.3159/TORREY-D-18-00055.1>
- Burns, J. H., Pardini, E. A., Schutzenhofer, M. R., Chung, Y. A., Seidler, K. J., & Knight, T. M. (2013). Greater sexual reproduction contributes to differences in demography of invasive plants and their noninvasive relatives. *Ecology*, 94(5), 995-1004. <https://doi.org/10.1890/12-1310.1>
- Chittka, L., & Schürkens, S. (2001). Successful invasion of a floral market. *Nature*, 411(6838), 653-653. <https://doi.org/10.1038/35079676>
- Conzatti, C. (1946). *Flora Taxonomica Mexicana (Plantas Vasculares): Tomo I-II*.
- Corredor-Prado, J. P., Conti, D. D., Sezerino, A., Guerra, M. P., & Orth, A. I. (2015). Reproductive biology and absence of fruiting of *Aloe saponaria* (Aiton) Haw.(Xanthorrhoeaceae) outside its place of origin. *Revista Brasileira de Plantas Mediciniais*, 17(4 Suppl. 1), 713-721. https://doi.org/10.1590/1983-084X/14_023.
- Cruden, R. W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution*, 32-46. <https://doi.org/10.2307/2407542>
- Cullen, J. (2012). *Asphodelus fistulosus* L.—onion weed. *Biological control of weeds in Australia*. CSIRO, Canberra, 83-85.
- D'Antonio, C. M., Tunison, J. T., & Loh, R. K. (2000). Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecology*, 25(5), 507-522. <https://doi.org/10.1046/j.1442-9993.2000.01079.x>
- Dafni, A. (1992). Pollination ecology: A practical approach. New York, NY: Oxford University Press.

- Díaz-Segura, O., Golubov, J., Mandujano, M. C., & Zavala-Hurtado, J. A. (2020). Reproductive characteristics that favor invasiveness in *Leonotis nepetifolia* (L.) R. Br. *Plant Species Biology*, 35(4), 270-282. <https://doi.org/10.1111/1442-1984.12278>
- Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual review of Environment and Resources*, 28(1), 137-167. <https://doi.org/10.1146/annurev.energy.28.050302.105532>
- DiTomaso, J. M., Kyser, G. B., Oneto, S. R., Wilson, R. G., Orloff, S. B., Anderson, L. W., & Mann, J. J. (2013). Weed control in natural areas in the western United States. *Weed Research and Information Center, University of California*, 544.
- Doody, J. S., Green, B., Rhind, D., Castellano, C. M., Sims, R., & Robinson, T. (2009). Population-level declines in Australian predators caused by an invasive species. *Animal Conservation*, 12(1), 46-53. <https://doi.org/10.1111/j.1469-1795.2008.00219.x>
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London, UK: Methuen
- Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso A-C, Eschen R, Gallardo B, Galil B, García-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou K, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roques A, Roy H, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vilà M, Wilson JR, Zenetos A, Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. *BioScience* 65: 769–782. <https://doi.org/10.1093/biosci/biv082>
- Ferrero, V., Navarro, L., Castro, S., Loureiro, J., Sánchez, J. M., Carvallo, G. O., & Barrett, S. C. (2020). Global patterns of reproductive and cytotype diversity in an invasive clonal plant. *Biological Invasions*, 22(5), 1691-1703. <https://doi.org/10.1007/s10530-020-02213-9>
- Friedman, J., & Barrett, S. C. (2008). High outcrossing in the annual colonizing species *Ambrosia artemisiifolia* (Asteraceae). *Annals of Botany*, 101(9), 1303-1309. <https://doi.org/10.1093/aob/mcn039>
- Geerts, S., & Adedoja, O. (2021). Pollination and reproduction enhance the invasive potential of an early invader: the case of *Lythrum salicaria* (purple loosestrife) in South Africa. *Biological Invasions*, 1-11. <https://doi.org/10.1007/s10530-021-02549-w>
- Gioria, M., & Pyšek, P. (2017). Early bird catches the worm: germination as a critical step in plant invasion. *Biological Invasions*, 19(4), 1055-1080. <https://doi.org/10.1007/s10530-016-1349-1>
- Guerrero-Eloisa, O. S. (2017). Evaluación en el establecimiento y control mecánico de la especie exótica invasora *Asphodelus fistulosus* (L.) en el municipio de Cadereyta de Montes, Querétaro (Maestría). Universidad Autónoma Metropolitana - Xochimilco. 138pp.
- Herrera, I., & Nassar, J. M. (2009). Reproductive and recruitment traits as indicators of the invasive potential of *Kalanchoe daigremontiana* (Crassulaceae) and *Stapelia gigantea* (Apocynaceae) in a Neotropical arid zone. *Journal of Arid Environments*, 73(11), 978-986. <https://doi.org/10.1016/j.jaridenv.2009.05.004>
- Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, diversity, and invasion—Implications for conservations. *Conservation Biology*, 6, 324– 337. <https://doi.org/10.1046/j.1523-1739.1992.06030324.x>

- Hong, L., Shen, H., Ye, W.H., Cao, H.L., Wang, Z.M. (2007). Self-incompatibility in *Mikania micrantha* in South China. *Weed Res* 47:280–283. <https://doi.org/10.1111/j.1365-3180.2007.00575>.
- Jeschke, J. M., & Strayer, D. L. (2006). Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology*, 12, 1608–1619. <https://doi.org/10.1111/j.1365-2486.2006.01213.x>
- Jacquemart, A. L., Somme, L., Colin, C., & Quinet, M. (2015). Floral biology and breeding system of *Impatiens balfourii* (Balsaminaceae): an exotic species in extension in temperate areas. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 214, 70-75. <https://doi.org/10.1016/j.flora.2015.06.001>
- Janzen, D. H. (1971). Seed predation by animals. *Annual review of ecology and systematics*, 2(1), 465-492.
- JMP®, Version 16.0.0>. SAS Institute Inc., Cary, NC, 1989–2021.
- Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, 17, 164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Knight, T. M., Steets, J. A., Vamossi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Duda M.R., Johnston, R.J., Mitchell, M.O. & Ashman, T. L. (2005). Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.*, 36, 467-497. <https://doi.org/10.1146/annurev.ecolsys.36.102403.11532>
- Kovach, W. L. (2011). Oriana – Circular statistics for windows, ver. 4. Wales: Kovach Computing Services, Pentraeth.
- Lach, L. (2008), Floral visitation patterns of two invasive ant species and their effects on other hymenopteran visitors. *Ecological Entomology*, 33: 155-160. <https://doi.org/10.1111/j.1365-2311.2007.00969.x>
- Levine, J. M., & D'Antonio, C. M. (1999). Elton revisited: A review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26. <https://doi.org/10.2307/3546992>
- Lifante, Z. D. (1996). Reproductive biology of *Asphodelus aestivus* (Asphodelaceae). *Plant Systematics and Evolution*, 200(3), 177-191. <https://doi.org/10.1007/BF00984934>
- Lucardi, R. D., Wallace, L. E., & Ervin, G. N. (2020). Patterns of genetic diversity in highly invasive species: cogongrass (*Imperata cylindrica*) expansion in the invaded range of the southern United States (US). *Plants*, 9(4), 423. <https://doi.org/10.3390/plants9040423>
- Márquez, J. (2005). Técnicas de colecta y preservación de insectos. *Boletín Sociedad Entomológica Aragonesa*, 37:385–408.
- Martínez-Cruz, J., & Téllez-Valdés, O. (2004). Listado florístico de la Sierra de Santa Rosa, Guanajuato, México. *Botanical Sciences*, (74), 31-49. <https://doi.org/10.17129/botsci.1685>
- Mitchell, R. J., Flanagan, R. J., Brown, B. J., Waser, N. M., & Karron, J. D. (2009). New frontiers in competition for pollination. *Annals of botany*, 103(9), 1403-1413. <https://doi.org/10.1093/aob/mcp062>
- Morales, C. L., Sáez, A., Garibaldi, L. A., & Aizen, M. A. (2017). Disruption of pollination services by invasive pollinator species. Impact of biological invasions on ecosystem services, 203-220. https://doi.org/10.1007/978-3-319-45121-3_13

- Moravcová, L., Pyšek, P., Jarošík, V., & Pergl, J. (2015). Getting the right traits: reproductive and dispersal characteristics predict the invasiveness of herbaceous plant species. *PloS one*, 10(4). <https://doi.org/10.1371/journal.pone.0123634>
- Morellato, L. P. C., Alberti, L. F., & Hudson, I. L. (2010). Applications of circular statistics in plant phenology: a case studies approach. In *Phenological research* (pp. 339-359). Springer, Dordrecht. https://doi.org/10.1007/978-90-481-3335-2_16
- McNeely, J. (2001). Invasive species: a costly catastrophe for native biodiversity. *Land Use and Water Resources Research*, 1.
- Novak, S. J. (2005). Genetic bottlenecks in alien plant species: influence of mating systems and introduction dynamics. *Species invasions: insights into ecology, evolution and biogeography*, 201-228.
- Obeso, J. R. (1992). Pollination ecology and seed set in *Asphodelus albus* (Liliaceae) in northern Spain. *Flora*, 187, 219-226. [https://doi.org/10.1016/S0367-2530\(17\)32225-9](https://doi.org/10.1016/S0367-2530(17)32225-9)
- Ojija, F., Arnold, S. E., & Treydte, A. C. (2019). Impacts of alien invasive *Parthenium hysterophorus* on flower visitation by insects to co-flowering plants. *Arthropod-Plant Interactions*, 13(5), 719-734. <https://doi.org/10.1007/s11829-019-09701-3>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, 120(3), 321-326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Pannell JR, Auld JR, Brandvain Y, Burd M, Busch JW, Cheptou P-O, Conner JK, Goldberg EE, Grant A-G, Grossenbacher DL et al. 2015. The scope of Baker's law. *New Phytologist* 208: 656–667. <https://doi.org/10.1111/nph.13539>
- Parsons, W. T., Parsons, W. T., & Cuthbertson, E. G. (2001). *Noxious weeds of Australia*. CSIRO publishing.
- Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in ecology & evolution*, 24(9), 497-504.
- Pheloung, P. C., Williams, P. A., & Halloy, S. R. (1999). A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of environmental management*, 57(4), 239-251. <https://doi.org/10.1006/jema.1999.0297>
- Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, 50(1), 53-65. [https://doi.org/10.1641/0006-3568\(2000\)050\[0053:EAECON\]2.3.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2)
- Powell, K. I., Krakos, K. N., & Knight, T. M. (2011). Comparing the reproductive success and pollination biology of an invasive plant to its rare and common native congeners: a case study in the genus *Cirsium* (Asteraceae). *Biological Invasions*, 13(4), 905-917. <https://doi.org/10.1007/s10530-010-9878-5>
- Pyšek, P., Jarošík, V., & Kučera, T. (2003). Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. *Conservation Biology*, 17(5), 1414-1424. <https://doi.org/10.1046/j.1523-1739.2003.02248.x>
- Pyšek, P., & Richardson, D. M. (2008). Traits associated with invasiveness in alien plants: where do we stand?. In *Biological invasions* (pp. 97-125). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-36920-2_7

- Rambuda, T. D. & Johnson, S. D. 2004: Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? -*Diversity and Distributions* 10: 409-416. <https://doi.org/10.1111/j.1366-9516.2004.00100.x>
- Redmond, C. M., & Stout, J. C. (2018). Breeding system and pollination ecology of a potentially invasive alien *Clematis vitalba* L. in Ireland. *Journal of Plant Ecology*, 11(1), 56-63. <https://doi.org/10.1093/jpe/rtw137>
- Ruiz, J. L. (2003). Polinizadores potenciales de *Asphodelus* spp. en los Pirineos y en el macizo Cazorla-Segura (Huesca y Jaén, España)(Insecta). *mellifera*, 6, 4.
- Russel, G. (2008). Eradication program for onion weed in Arizona: Environmental assessment.
- Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., & Weller, S. G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, 32(1), 305-332.
- Santos, G. M. D. M., Aguiar, C. M., Genini, J., Martins, C. F., Zanella, F. C., & Mello, M. A. (2012). Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biological Invasions* 14(11), 2369-2378. <https://doi.org/10.1007/s10530-012-0235-8>
- Simberloff, D., & Holle, B. V. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, 1, 21-32. <https://doi.org/10.1023/A:1010086329619>
- Smith, A. L., Hodkinson, T. R., Vilellas, J., Catford, J. A., Csörgő, A. M., Blomberg, S. P., ... & Buckley, Y. M. (2020). Global gene flow releases invasive plants from environmental constraints on genetic diversity. *Proceedings of the National Academy of Sciences*, 117(8), 4218-4227. <https://doi.org/10.1073/pnas.1915848117>
- Souza, V. C. D., Andrade, L. A. D., & Quirino, Z. G. M. (2016). Floral biology of *Sesbania virgata*: an invasive species in the Agreste of Paraíba, northeastern Brazil. *Rodriguésia*, 67, 871-878. <https://doi.org/10.1590/2175-7860201667402>
- Stout, J. C., Kells, A. R., & Goulson, D. (2002). Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation*, 106(3), 425-434. [https://doi.org/10.1016/S0006-3207\(02\)00046-0](https://doi.org/10.1016/S0006-3207(02)00046-0)
- Stout, M. J., Thaler, J. S., & Thomma, B. P. (2006). Plant-mediated interactions between pathogenic microorganisms and herbivorous arthropods. *Annu. Rev. Entomol.*, 51, 663-689. <https://doi.org/10.1146/annurev.ento.51.110104.151117>
- Stout, J. C., & Tiedeken, E. J. (2017). Direct interactions between invasive plants and native pollinators: evidence, impacts and approaches. *Functional Ecology*, 31(1), 38-46. <https://doi.org/10.1111/1365-2435.12751>
- Sutherland, S. (2004). What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia*, 141(1), 24-39. <https://doi.org/10.1007/s00442-004-1628-x>
- USDA (United States Department of Agriculture). (2016). Invasive Species for the Tonto National Forest.
- Van Kleunen, M., & Johnson, S. D. (2005). Testing for ecological and genetic Allee effects in the invasive shrub *Senna didymobotrya* (Fabaceae). *American Journal of Botany*, 92(7), 1124-1130. <https://doi.org/10.3732/ajb.92.7.1124>
- Van Kleunen, M., & Johnson, S. D. (2007). Effects of self-compatibility on the distribution range of invasive European plants in North America. *Conservation Biology*, 21(6), 1537-1544. <https://doi.org/10.1111/j.1523-1739.2007.00765.x>

- Van Kleunen, M., Manning, J. C., Pasqualetto, V., & Johnson, S. D. (2008). Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *The American Naturalist*, 171(2), 195-201. <https://doi.org/10.1086/525057>
- Van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology letters*, 13(2), 235-245. <https://doi.org/10.1111/j.1461-0248.2009.01418.x>
- Victoria State Department. 2016. Invasiveness Assessment-Onion weed (*Asphodelus fistulosus*) in Victoria
- Villaseñor, J. L., & J. Espinosa-Garcia, F. (2004). The alien flowering plants of Mexico. *Diversity and distributions*, 10(2), 113-123. <https://doi.org/10.1111/j.1366-9516.2004.00059.x>
- Wang, N., Li, W., Zhou, B., & Yan, X. (2016). Invasiveness, clonal form and geographical origin of invasive clonal plant species in China. *Biodiversity Science*, 24, 12–19. <https://doi.org/10.17520/biods.2015190>
- Williamson, M., & Fitter, A. (1996). The varying success of invaders. *Ecology*, 77(6), 1661-1666. <https://doi.org/10.2307/2265769>
- Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90(8), 2068-2076. <https://doi.org/10.1890/08-1245.1>
- Wolkovich, E. M., & Cleland, E. E. (2011). The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment*, 9(5), 287-294. <https://doi.org/10.1890/100033>
- Wolkovich, E. M., Davies, T. J., Schaefer, H., Cleland, E. E., Cook, B. I., Travers, S. E., & Davis, C. C. (2013). Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany*, 100(7), 1407-1421. <https://doi.org/10.3732/ajb.1200478>
- Wolkovich, E. M., & Cleland, E. E. (2014). Phenological niches and the future of invaded ecosystems with climate change. *AoB plants*, 6. <https://doi.org/10.1093/aobpla/plu013>
- Yan, X. H., Zhou, B., Yin, Z. F., Wang, N., & Zhang, Z. G. (2016). Reproductive biological characteristics potentially contributed to invasiveness in an alien invasive plant *Bidens frondosa*. *Plant Species Biology*, 31(2), 107-116. <https://doi.org/10.1111/1442-1984.12092>
- Zeng, J. J., Zhou, B., & Wang, N. (2021). Comparing the reproductive biological characteristics of the alien invasive *Coreopsis lanceolata* to those of the non-invasive alien congener *Coreopsis tinctoria*. *Plant Species Biology*. <https://doi.org/10.1111/1442-1984.12323>
- Zhang, Z. Q., Zhang, Y. H., & Sun, H. (2011). The reproductive biology of *Stellera chamaejasme* (Thymelaeaceae): A self-incompatible weed with specialized flowers. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 206(6), 567-574. <https://doi.org/10.1016/j.flora.2011.01.008>

Table 1. Floral visitors and activity (N = nectar, P = pollen) and origin (NA = North America, A = America, E= exotic) on *Asphodelus fistulosus* flowers and mean time spent in the flowers (seconds).

Order	Family	Genus	Species	Activity	Mean time spent in activity (s)	Site	Provenance
Coleoptera	Melyridae	<i>Trichochrous</i>	-	N, P	113	QRO	NA
Hymenoptera	Apidae	<i>Ceratina</i>	-	N, P	20	QRO	-
Hymenoptera	Apidae	<i>Apis</i>	<i>A. mellifera</i>	N, P	11 16	QRO SLP	E
Hymenoptera	Formicidae	-	-	N, P	15	SLP	-
Hymenoptera	Halictidae	<i>Lasioglossum</i>	-	N, P	11 7	QRO SLP	-
Lepidoptera	Geometridae	<i>Metanema</i>	<i>M. inatomaria</i>	N	6	SLP	A
Lepidoptera	Hesperiidae	<i>Copaeodes</i>	<i>C. minima</i>	N	7	QRO	
Lepidoptera	Lycaenidae	<i>Echinargus</i>	<i>E. isola</i>	N	27	SLP	NA
Lepidoptera	Lycaenidae	<i>Hemiargus</i>	<i>H. ceraunus</i>	N	13	QRO	A
Lepidoptera	Lycaenidae	<i>Leptotes</i>	<i>L. marina</i>	N	8	QRO	NA
Lepidoptera	Nymphalidae	<i>Anthanassa</i>	<i>A. texana</i>	N	4	QRO	NA
Lepidoptera	Nymphalidae	<i>Agraulis</i>	<i>A. vaniallae</i>	N	6	SLP	A
Lepidoptera	Nymphalidae	<i>Texola</i>	<i>T. elata</i>	N	3	QRO	NA
Lepidoptera	Pieridae	<i>Catasticta</i>	<i>C. nimbe</i>	N	10	QRO	A

Table 2. Floral morphological measurements (mean \pm SE) of *Asphodelus fistulosus* (N = 65 flowers) from different individuals for each site (QRO and SLP).

Floral trait	QRO	SLP
Perianth width (mm)	16.77 \pm 0.22	15.80 \pm 0.21
Spatial separation of stamens-stigmas (mm)	0.30 \pm 0.12	0.16 \pm 0.28
Stigma height (mm)	6.24 \pm 0.12	5.56 \pm 0.05
Number of ovules	6	6
Pollen grains per flower	2304 \pm 61	2268 \pm 72

Table 3. Production of fruits (fruit set) after *Asphodelus fistulosus* pollination experiments in QRO. N = sample size (number of flowers); mean \pm SE for each treatment.

Pollination treatment	N	Fruit set
Control	40	0.85 \pm 0.36
Supplementary pollen	42	0.71 \pm 0.45
Artificial self-pollination	44	0.84 \pm 0.36
Autonomous self-pollination	40	0.82 \pm 0.38
Artificial cross pollination	44	0.65 \pm 0.47
Natural (control) cross pollination	43	0.67 \pm 0.47
Geitonogamy	41	0.75 \pm 0.44

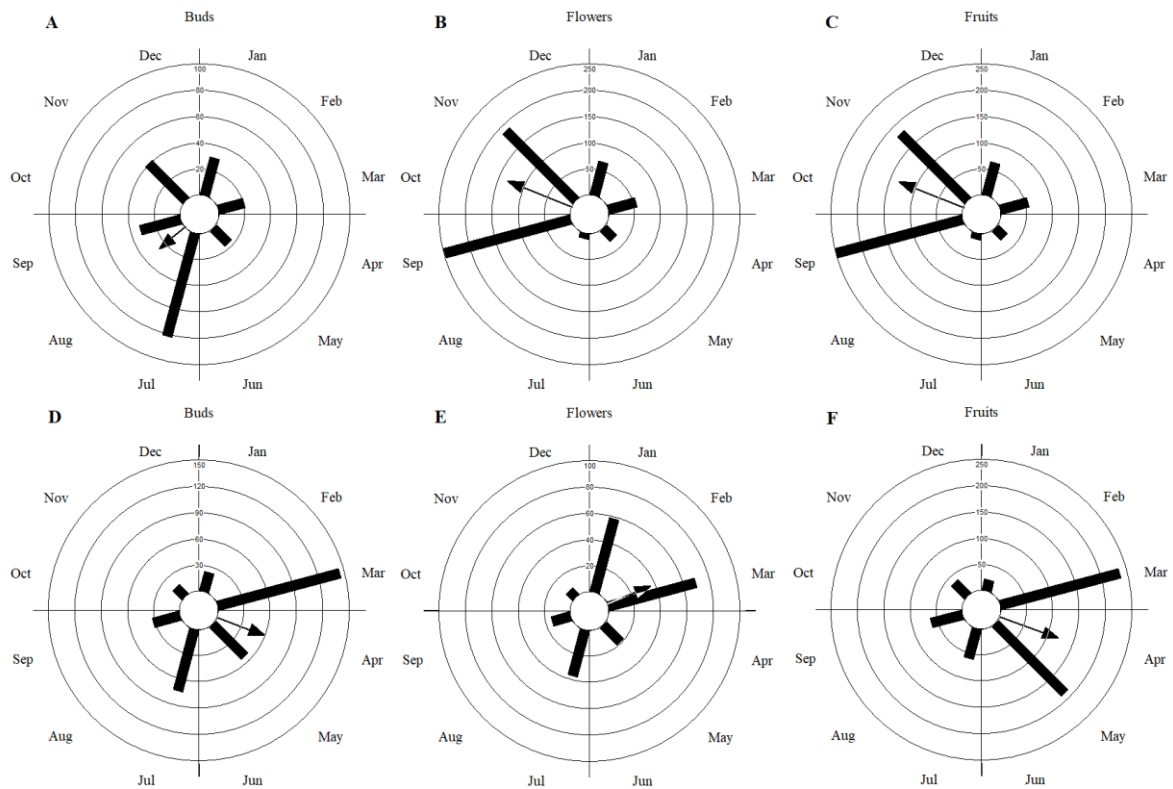


Figure 1. Circular plots of the reproductive structures phenophases (floral buds, flowers and fruits). Upper plots correspond to the QRO site (A-C) and lower plots to GCZ (D-F). Bars represent the frequency of each phenophases, the arrow the magnitude of the mean vector (r).

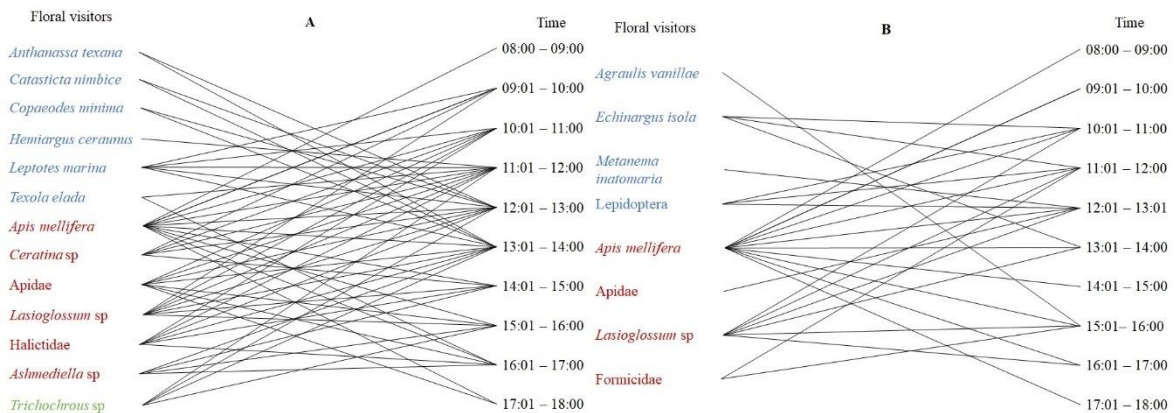


Figure 2. Time of day and floral visitors of *Asphodelus fistulosus* for (A) QRO and (B) GCZ. The color represents the family blue= Lepidoptera, red = Hymenoptera, green = Coleoptera.

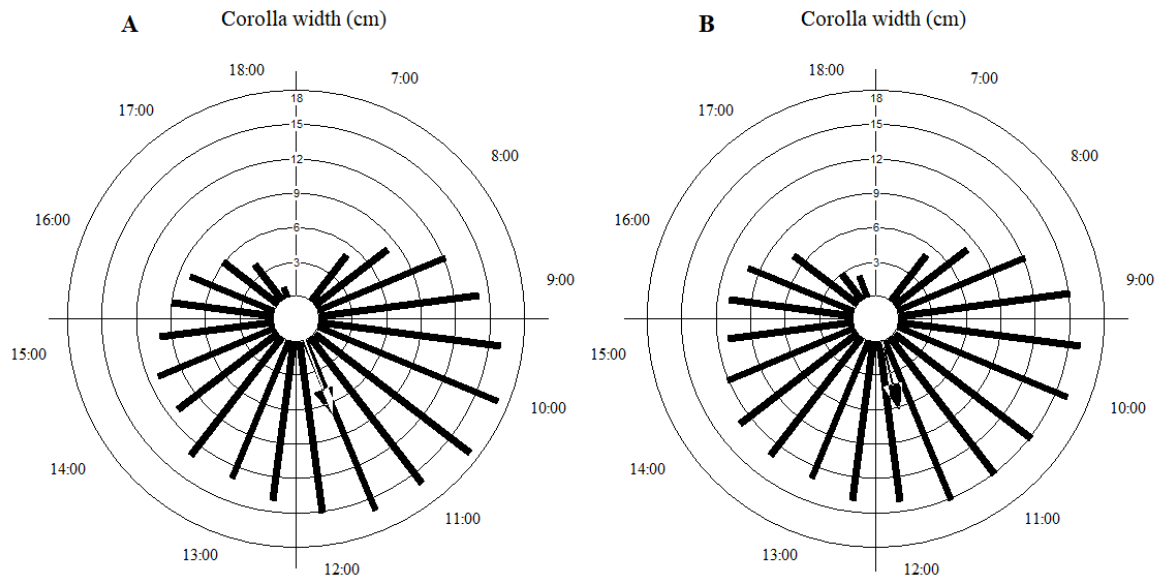


Figure 3. Circular plots of the corolla width. (A) of flowers followed at the QRO site and (B) for the GCZ site. Bars represent the frequency of each phenophases, the arrow the magnitude of the mean vector (r).