

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

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Abstract

Background and aims – Understanding the traits that lead to the invasion potential of invasive alien species (IAS) provides insight for their management. The reproductive traits of IAS help us 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, South Africa, and North America.

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

Key results – Reproductive phenology showed continuous reproduction throughout the year. Floral morphology suggested a facultative autogamous breeding system, but the mating system was mixed with autonomous selfing. Flowers lasted 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 diverse pollinators, and the autonomous self-pollination implies that a single plant has the potential to develop a new population, which makes the control of this IAS a global challenge.

Keywords

breeding and mating system, floral visitors, invasive alien species, phenology

INTRODUCTION

Current severe environmental threats are brought about by changes in land use, climate change, and invasive alien species (IAS; Dirzo and Raven 2003), the latter being identified as one of the leading causes of species extinctions worldwide (Pejchar and Mooney 2009). Several hypotheses have been put forward to explain the success of biological invasions (Essl et al. 2015). For invasive plant species, a subgroup of these hypotheses links successful invasion to traits that allow these species to establish new populations

in their invaded range. Traits such as the ability of having sexual and asexual reproduction (Moravcová et al. 2015), multiple phenological strategies (Wolkovic and Cleland 2011), high germination rates (Gioria and Pyšek 2017), and a persistent seed bank (Gioria et al. 2021), facilitate the ability to become invasive and provide insight into the biology of IAS. These traits, many of which were partially described by Baker (1965) in his treatment of the perfect weed, usually confer the advantage of higher population growth than native species (Doody et al. 2009) and provide a working hypothesis expected to be found

in IAS. For many plants, the ecological characteristics that favour establishment success are poorly understood (Gallien and Carboni 2017). However, the identification of traits that confer invasive potential (Van Kleunen et al. 2010) are also an important component of risk assessment protocols (Pheloung et al. 1999) and a means of characterizing weedy species (Baker 1965; Sutherland 2004). Understanding the drivers of establishment and spread of IAS beyond their native range is key to predicting new invasions (Pyšek et al. 2020), although results do not always support the predictions.

Variation in mating and breeding systems of invasive plant species is broad (Barrett 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 and Fitter 1996; Barrett 2011). However, successful invasive plant species have a wide variety of mating systems, from self-compatibility (Jacquemart et al. 2015; Redmond and Stout 2018), self-incompatibility (Sutherland 2004; Friedman and Barrett 2008), and even mixed mating systems (Souza et al. 2016). There is also the argument that IAS 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; Stout and Tiedeken 2017) or in the absence of pollinators, favour species with autonomous self-pollination (Pannell et al. 2015). Even though most plants, including IAS, are pollinated by animals (Ollerton et al. 2011), self-compatibility and autonomous pollination reduce the dependence on biotic interactions (Van Kleunen and Johnson 2005; Van Kleunen et al. 2008) favouring 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 and Schürkens 2001; Mitchell et al. 2009).

Seed output in IAS is thought to be high (Díaz-Segura et al. 2020), and even though IAS invasions benefit from asexual reproduction in clonal spread (Guerra-García et al. 2015), there are successful IAS that rely entirely on sexual reproduction (Forman and Kesseli 2003). The overall behaviour 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), and it provides relevant information to understand the impacts of IAS in invaded ecosystems (Vilà et al. 2011). Hypotheses that help explain their success suggest that IAS shift flowering with climate change compared to native species (Wolkovich et al. 2013), invade habitats by having phenological differences with the native community (Wolkovich and Cleland 2014), and can germinate earlier, faster and respond to broader germination cues in their non-native than in their native range (Gioria

and Pyšek 2017). This variation in phenological phases and phenotypic plasticity 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 and Levine 2019).

Asphodelus fistulosus L. (Xanthorrhoeaceae) is a native herb from the south of Europe, found in the Mediterranean basin and Macaronesian region (Díaz-Lifante and Valdés 1996), a region that includes a wide variety of climates, mainly classified as temperate with no dry season and a mild/hot summer as well as temperate with dry and warm summers. The average annual precipitation is 1512 mm at the westernmost portion and decreases to 749 mm towards the east (Cropper 2013). It is a nitrophilous species, locally frequent in grasslands, steppes, and coastal sandbanks, preferably on alkaline and occasionally siliceous soils, in secondary habitats linked to human activity (Díaz-Lifante and Valdés 1996). *Asphodelus fistulosus* is considered invasive in Southeastern USA, Australia, India, South Africa, and New Zealand (Patterson 1996; Boatwright 2012), its introductions have been intentional for ornamental purposes (Bailey and Bailey 1976; Russel 2008) but the species can easily escape from cultivation (USDA 2016) and establish populations in disturbed, over-grazed habitats (Victoria State Department 2016). It impacts vegetation cover (Martínez-Cruz and Téllez-Valdés 2004) forming dense populations in arid and semi-arid environments and disturbed areas (Parsons and Cuthbertson 2001; Cullen 2012). The first reports of *A. fistulosus* in Mexico were from the northern arid environments (Conzatti 1946a, 1946b; Villaseñor and Espinosa-García 2004), and since then, the species has considerably increased its geographical distribution, and is now found in 15 out of 32 states (Guerrero-Eloisa 2017).

The purpose of this study was threefold: (1) describe the flowering phenology of *A. 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 favour 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. The first site QRO was located close to Cadereyta de Montes, Queretaro, Mexico (20°47'24"N, 99°43'27"W), the type of soil is calcareous (Instituto Nacional de Estadística y Geografía 2021) with xeric scrub (Zamudio et al. 1992) in a semi-dry-temperate climate with summer rains (García 1988). The second site SLP was located in Guadalcázar, San Luis Potosí, Mexico (22°38'18"N, 100°26'13"W), the type of soil is lithosol consisting of submontane scrub vegetation, with a semi-

dry temperate climate having summer and winter rains (Torres-Colín et al. 2017). The linear distance between sites is 224 km and the study was performed between September 2018 and July 2019, while the pollination experiment was carried out in February 2020.

Phenology

A patch of vegetation invaded by *A. fistulosus* was identified in September 2018 at each site. We followed all individuals of *A. fistulosus* within 1 × 1 m plots at each site (N = 17 plots in QRO and N = 10 plots in SLP). The number of plots was based on the abundance of *A. fistulosus* individuals at each site, taking the loss of individuals over the period as well as availability of reproductive individuals into account. Sample size started at QRO = 1015 and SLP = 999 individuals and diminished over the study period to QRO = 791 and SLP = 856 individuals. All plants of *A. fistulosus* in each plot were tagged, mapped, and the frequency of their phenological phase recorded every two months from September 2018 to July 2019. We followed three phenophases (floral buds, flowers, and fruits) that were analyzed with circular statistics using a Rayleigh test to identify deviations from a uniform distribution for each site and a Watson-Williams two-sample test (U^2) to test for differences in phenophases between sites. All circular statistics by phenophases were run on Oriana v.4.0 (Kovach Computing Services 2011).

Meteorological data were obtained (average temperature and average precipitation) online (www.wunderground.com) from the nearest weather station (IQUERETA 15) for the study period. We correlated these environmental variables with the phenology observed in QRO.

Observation data from photographs that could identify the phenological states (floral buds, flowers, and fruits) of *A. fistulosus* in the citizen science portal iNaturalist Mexico (Naturalista 2023) were made for the states of Queretaro and San Luis Potosi. These phenophases were analyzed with circular statistics using a Rayleigh test run on Oriana v.4.0 (Kovach Computing Services 2011).

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 individuals 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 07h00 to 18h00 with 15-minute breaks for each period of observation. The identity (species or morphospecies) of the visitor, activity (catalogued as pollen or nectar collection), and time of observation were recorded for each visit (Dafni 1992). Visitors were captured for identification in ethyl acetate lethal chambers

(Márquez 2005). A Shannon diversity index (H') based on the frequency of floral visitors was calculated for each site and compared between sites with a Hutcheson t test.

Anthesis was followed in QRO (February 2019) and SLP (March 2019) in three plots. Fifteen flowers of three different individuals were followed for corolla aperture and measured with a digital calliper (to the nearest 0.05 mm) in 15-minute intervals from 07h00 to 18h00. Stigmas were considered receptive by a change in colouration (light pink to dark pink) and moisture on the stigmatic surface, while anther dehiscence was detected with the presence of pollen. Circular statistics were used to describe floral behaviour where the mean angle (μ) represented 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 (09h00) and sampled at 18h00. Nectar concentration 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 (blocks) 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® v.16.0.0 (JMP 2021).

Floral morphological traits were taken to determine the breeding system. The out-crossing index (OCI) and pollen/ovule ratio (P/O; Cruden 1977) were estimated using (a) corolla aperture (mm), (b) presence of dichogamy (temporal separation of sexual functions), and

Table 1. Results of the circular statistical analysis for the occurrence of seasonality in the reproductive phenological patterns of *Asphodelus fistulosus* observed in Cadereyta, QRO, and Guadalcázar, SLP. The Rayleigh test assesses deviations from a uniform distribution.

Site	Phenophase	Z test	Mean vector (r)	Rayleigh test (p)
Cadereyta (QRO)	Floral buds	13.68	0.25	< 0.001
	Flower	1.67	0.17	= 0.188
	Fruits	160.24	0.52	< 0.001
Guadalcázar (SLP)	Floral buds	46.54	0.35	< 0.001
	Flower	20.09	0.35	< 0.001
	Fruits	137.64	0.48	< 0.001

(c) herkogamy (spatial separation of sexual functions). Five flowers of 65 individuals were collected and stored in FAA (Formaldehyde Alcohol Acetic Acid). A digital calliper (0.05 mm) was used to measure the following: corolla aperture (CA), minimum anther-stigma distance (ASD), and flower length (FL). To estimate the number of pollen grains per flower (GP), 65 anthers were collected before pollen release and stored in 5-ml Eppendorf tubes

with ethanol. 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 was obtained by dissecting the ovarian chamber and counting the ovules present in each of the 65 flowers.

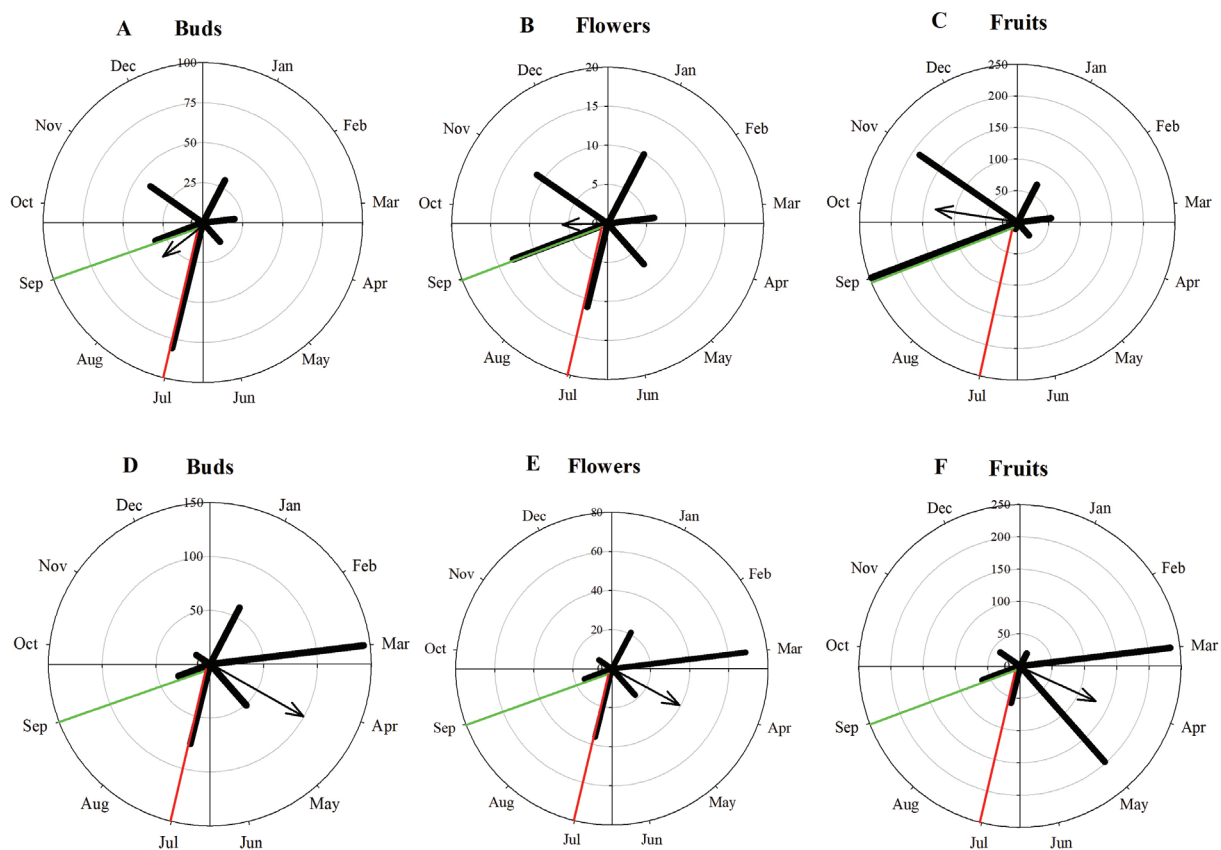


Figure 1. Circular plots of the phenophases of the reproductive structures (floral buds, flowers, and fruits) of *Asphodelus fistulosus*. Upper plots correspond to the QRO site (A–C) and lower plots to the SLP site (D–F). Bars represent the frequency of each phenophase, the arrow the magnitude of the mean vector (r). Green lines indicate the start and red lines the finish of phenology observations at both sites.

Table 2. Results of the circular statistical analysis for the occurrence of seasonality in the reproductive phenological patterns of *Asphodelus fistulosus* observed in Queretaro and San Luis Potosí States using iNaturalist observations from 2013 to 2022. The Rayleigh test assesses deviations from a uniform distribution.

State	Phenophase	Z test	Mean vector (r)	Rayleigh test (p)
Queretaro	Floral buds	7.3	0.46	< 0.001
	Flower	7.78	0.48	< 0.001
	Fruits	4.85	0.43	< 0.001
San Luis Potosí	Floral buds	3.32	0.19	0.036
	Flower	1.56	0.12	0.209
	Fruits	0.14	0.04	0.867

RESULTS

Phenology

Reproductive phenophases at the two studied populations in the Chihuahuan desert (QRO and SLP) were studied throughout the 11-month study period (Table 1).

Asphodelus fistulosus showed floral bud production in summer in QRO and in spring in SLP, flowering peaked during autumn in QRO and in spring in SLP (Fig. 1). Fruit production was observed in autumn in QRO and in spring in SLP. The phenological pattern of floral buds ($U^2 = 162.131$, $p < 0.001$), flowers ($U^2 = 299.098$, $p < 0.001$), and fruits ($U^2 = 1443.044$, $p < 0.001$) did not match between the sites. The frequency of phenophases did not

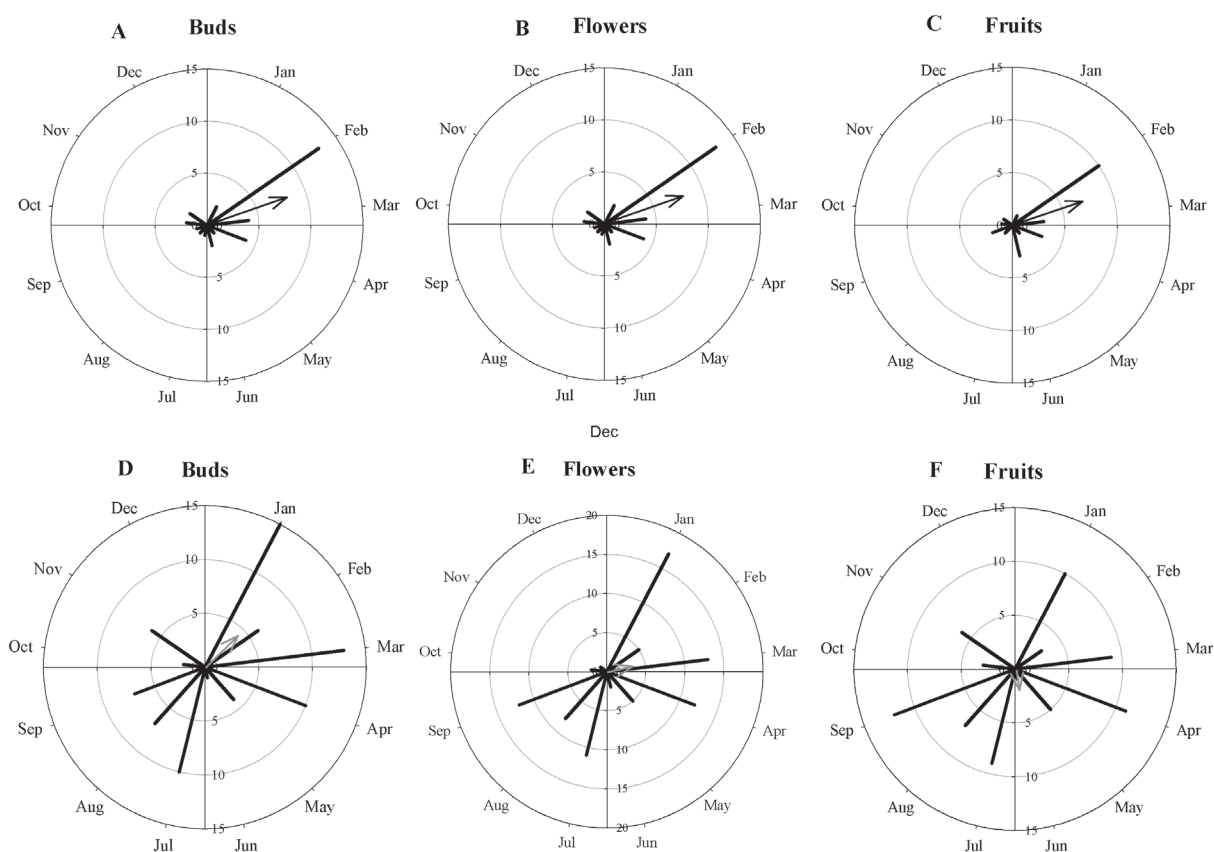


Figure 2. Circular plots of the phenophases of the reproductive structures (floral buds, flowers, and fruits) of *Asphodelus fistulosus* using Citizen Science observations in Mexico. Upper plots correspond to the Queretaro State (A–C) and lower plots to San Luis Potosí State (D–F). Bars represent the frequency of each phenophases, the arrows the magnitude of the mean vector (r).

Table 3. Floral visitors, activity (N = nectar, P = pollen), origin (NA = North America, A = America, E = exotic), and time spent on flowers (seconds) of *Asphodelus fistulosus* at two sites in the southern Chihuahuan Desert (QRO and SLP).

Order	Family	Genus	Species	Activity	Mean time spent in activity (s)	Site	Origin
Coleoptera	Melyridae	<i>Trichochrous</i>	–	N, P	113	QRO	NA
Hymenoptera	Apidae	<i>Ashmeadiella</i>	–	N	3	QRO	A
Hymenoptera	Apidae	–	–	N	8 15	QRO SLP	–
Hymenoptera	Apidae	<i>Ceratina</i>	–	N, P	20	QRO	–
Hymenoptera	Apidae	<i>Apis</i>	<i>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	–
Hymenoptera	Halictidae	–	–	N,P	12	QRO	–
Lepidoptera	–	–	–	N	7	SLP	–
Lepidoptera	Geometridae	<i>Metanema</i>	<i>inatomaria</i>	N	6	SLP	A
Lepidoptera	Hesperiidae	<i>Copaeodes</i>	<i>minima</i>	N	7	QRO	A
Lepidoptera	Lycaenidae	<i>Echinargus</i>	<i>isola</i>	N	27	SLP	NA
Lepidoptera	Lycaenidae	<i>Hemiargus</i>	<i>ceraunus</i>	N	13	QRO	A
Lepidoptera	Lycaenidae	<i>Leptotes</i>	<i>marina</i>	N	8	QRO	NA
Lepidoptera	Nymphalidae	<i>Anthanassa</i>	<i>texana</i>	N	4	QRO	NA
Lepidoptera	Nymphalidae	<i>Agraulis</i>	<i>vanillae</i>	N	6	SLP	A
Lepidoptera	Nymphalidae	<i>Texola</i>	<i>elada</i>	N	3	QRO	NA
Lepidoptera	Pieridae	<i>Catasticta</i>	<i>nimbice</i>	N	10	QRO	A

Table 4. 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

differ between years in QRO ($\chi^2 = 5.4293$, d.f. = 2, $p = 0.0662$) but did in SLP ($\chi^2 = 159.72$, d.f. = 2, $p < 0.001$) with more plants in bud than expected in 2019 ($p < 0.001$) and more fruiting plants than expected in 2018 ($p < 0.001$).

The phenology results suggest that floral buds, flowers, and fruits are influenced by at least one environmental variable in QRO. Floral buds showed 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 ($r = 0.38$, $p < 0.001$).

Phenophases observed on the citizen science platform (iNaturalist Mexico) showed all reproductive phenophases present year-round. QRO showed a synchronous production of buds, flowers, and fruits with a peak in winter (Fig. 2), and SLP had a more homogeneous

distribution of buds, flowers, and fruits year-round (Fig. 2, Table 2).

Floral visitors and flowering time

During the 10 observation periods at each site, 13 species of floral visitors were identified in QRO belonging to Hymenoptera (six spp.), Coleoptera (one sp.), and Lepidoptera (six spp.), and eight species were registered in SLP belonging to Formicidae (one sp.), Apidae (two spp.), Halictidae (one sp.), and Lepidoptera (four spp.) (Table 3). The diversity calculated for floral visitors was $H' = 0.923$ (QRO) and $H' = 0.330$ (SLP); a Hutcheson t test showed that QRO was significantly more diverse than SLP ($t = 18.45$, d.f. = 768, $p < 0.0001$). The exotic bee *Apis mellifera* Linnaeus, 1758 was the only common species

at both sites and individuals of the genus *Lasioglossum* Curtis, 1833 were also found at both sites, but we were unable to identify the specimens to a lower taxonomic level.

The activities (collecting nectar or pollen) were divided into the Lepidoptera that exclusively collected nectar, while the Hymenoptera collected both nectar and pollen (Table 3). At both sites, visitors were mostly active at midday, but the exotic bee *A. mellifera* was active throughout the 10-h observation period (Fig. 3). Flowering lasted approximately 11 h (07h00–18h00), 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 and pollen release coinciding with the peak of visitor activities (10h00–12h00) (Fig. 4). The average production of nectar was 0.15 μ l ($\pm$ SE = 2.778)

per day, and due to the small quantity, it was not possible to measure sugar concentration. When measuring nectar, we identified the presence of springtails (subclass Collembola), very likely consuming nectar that may have influenced the quantity of nectar sampled.

Mating and breeding system

Asphodelus fistulosus produced fruits without pollinators, had the capacity for autonomous pollination, and was self-compatible. Pollination experiments showed high fruit set with no differences among treatments ($\chi^2 = 9.17$, d.f. = 6, $p = 0.164$), which indicates a mixed mating system. Floral morphometric data (Table 4) 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

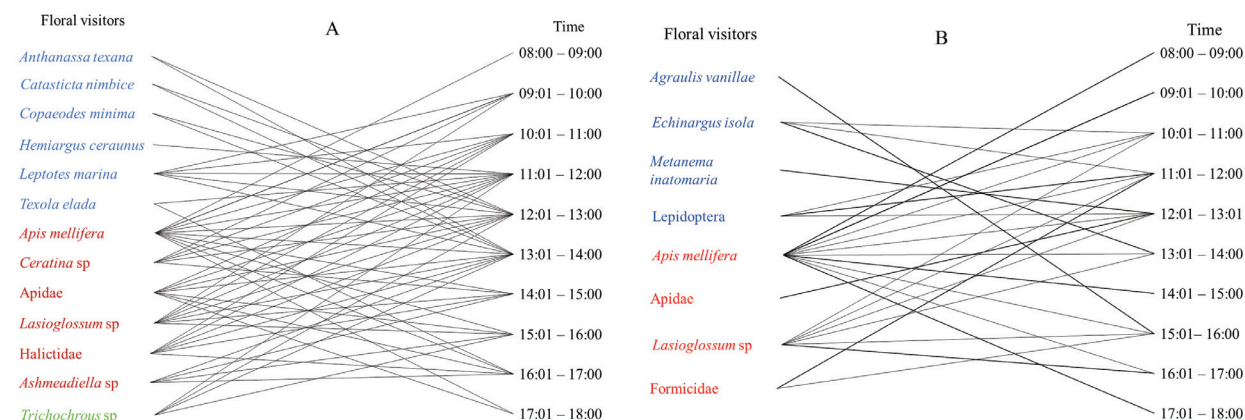


Figure 3. Time of day and floral visitors of *Asphodelus fistulosus* for (A) QRO and (B) SLP. The colour represents the family: blue = Lepidoptera, red = Hymenoptera, green = Coleoptera.

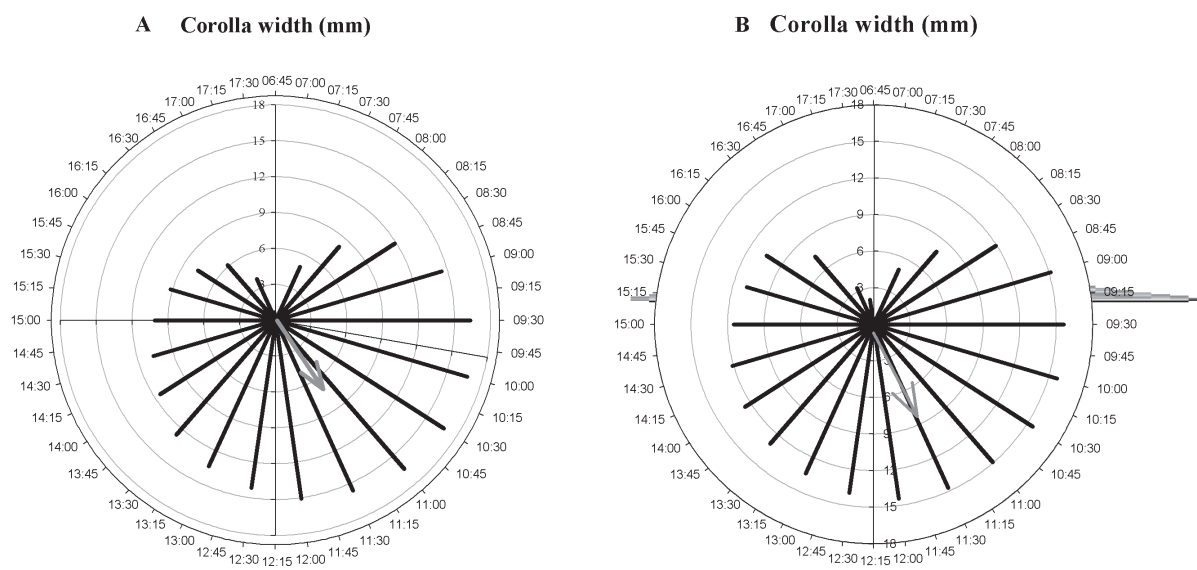


Figure 4. Circular plots of the corolla width of flowers followed (A) at the QRO site and (B) at the SLP site. Bars represent the mean corolla width every 30 min and the arrow the magnitude of the mean vector (r).

Table 5. Fruit set of pollination experiments on *Asphodelus fistulosus* 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

(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 ($\chi^2 = 9.17$, d.f. = 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 5).

DISCUSSION

Reproductive traits in IAS are considered important components in their invasion potential (Baker 1974). Phenological events can be advantageous for invasion in several ways providing information on the success of IAS (Baker 1974): the potential to change phenophases in response to different habitats, anticipated or delayed flowering, and extended or continuous phenophases (Wolkovich and Cleland 2011, 2014; Wolkovich et al. 2013). IAS have been shown to extend flowering periods that confer advantages over native plant species (Pyšek et al. 2003; Pyšek and Richardson 2008), with examples across the taxonomic spectrum such as in *Bidens frondosa* L. (Yan et al. 2016), *Leonotis nepetifolia* (L.) R.Br. (Díaz-Segura et al. 2020), and *Coreopsis lanceolata* L. (Zeng et al. 2021). Using *A. fistulosus* citizen science data from 170 observations for both sites (QRO = 42 observations, SLP = 128 observations), reproductive phenophases could be seen year-round with a peak in mid-winter for QRO (buds, flowers, and fruits). In SLP, two of the phenophases (flowers and fruits) did not show a clear peak, they were distributed uniformly year-round, but buds did show a marginally significant peak during winter. Comparing the study and citizen science data there is no clear relationship for either site. These differences could be a response to local conditions, frequency of observations, and geographic coverage of observations, which highlights the importance of citizen science data for large-scale phenological data and the relevance of small-scale phenological data that

shows the effects of local conditions on phenological stages. The continuous reproductive pattern suggests a wide niche breadth (Wolkovich and Cleland 2011) that enables reproductive events year-round, similar to other IAS found in the Brazilian savannas (Xavier et al. 2019), a trait that enhances the potential for invasion.

A second component in the success of IAS that is reflected in phenological events is phenotypic plasticity. At the study sites in the Chihuahuan Desert, *A. fistulosus* reproduction peaked during two different seasons (summer in QRO and spring in SLP), while data from other countries suggest flowering peaks in summer in the USA (DiTomaso et al. 2013) and during spring in South Africa (August–October; Boatwright 2012). In the native Mediterranean range of *A. fistulosus*, flowering occurs between December and June (Boatwright 2012), while congeners are known to flower during March–May for *A. albus* Mill. (Obeso 1992) and June to September for *A. aestivus* Brot. in Spain and May to April in Portugal (Díaz-Lifante 1996). There is therefore evidence that phenologically, *A. fistulosus* and quite likely its congeners follow two strategies: extended flowering periods as well as the potential to easily change phenophases depending on local conditions.

As a possible consequence of extended flowering periods, there is also an enhanced attraction towards floral visitors (Ojija et al. 2019). Extended flowering 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. 2003; this study). The floral resources generated by a single individual of *A. fistulosus* can be significant, producing 30–60 flowers per plant (Oscar Sandino Guerrero-Eloisa pers. obs.) and this abundance of floral resources can potentially divert native pollinator species from visiting native flora (Powell et al. 2011; Yan et al. 2016) and even increase visitor frequency in congeneric sympatric species (Zeng et al. 2021). Generalist pollination systems are thought to favour the invasive potential of IAS (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 also including *Xylocopa* Latreille, 1802, *Bombus* Latreille, 1802, *Anthidium* Fabricius, 1805, *Chelostoma* Latreille, 1809, and *Megachile* Latreille, 1802 (Obeso 1992; Díaz-Lifante 1996). Lara (2009) describes 11 species (ten bees and one beetle) as flower visitors and potential pollinators of *A. fistulosus* in its native range, including five *Bombus* species, four *Xylocopa* species, *Apis mellifera*, and *Agapanthia asphodeli* Latreille, 1804. Lara (2015) describes two species as confirmed pollinators of *A. fistulosus* (*Xylocopa cantabrita* Lepeletier, 1841 and *Apis mellifera*), our study showed that *A. mellifera* was the most common visitor that would mean a first step in invasive species favouring the success of another IAS (invasion meltdown; Simberloff and 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 its negative effect on native plants and positive effects on invasives (Morales et al. 2017). Secondly, *A. mellifera* is not usually an efficient pollinator of native plants (Santos et al. 2012) and is resilient to disturbance (Winfrey et al. 2009). The presence of *A. mellifera* in Mexico is widespread with feral, Africanized (Barrios et al. 1990) and managed colonies brought about through apiculture (Labougle and Zozaya 1986). 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 IAS is certainly present. These interactions not only benefit the exotic species, but may also cause competition with native plant species for floral visitors (Stout and Tiedeken 2017). Of the native pollinator species found on *A. fistulosus* in the present study, *Lasioglossum* sp. (native to America) and *Trichochrous* sp. have been reported as frequent visitors of 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 and Adedija 2021). Lara (2015) describes 17 butterfly species as potential pollinators (four families) in the native range of *A. fistulosus* and in this study, nine species from five families were present. In both studies, the Nymphalidae and Pieridae families were found in the native range as well as in the places where *A. fistulosus* invades.

Not only is the length of the flowering period relevant for IAS success but also floral longevity, because these determine on one hand the seasonality in the reproductive 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 IAS (single flower), with evidence in species with anthesis that can last 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* N.E.Br., and 6–11 d in *Kalanchoe daigremontiana* Raym.-Hamet & H.Perrier (Herrera and 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). Short-lived floral resources that are spread over a long time period can favour recurrent visitors, which maximize the amount and activity of the floral visitors and promotes outcrossing due to the number of receptive flowers in the 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, according to which selfing species would be better colonizers (Baker 1967). The evidence supporting this hypothesis seems to be quite widespread among IAS (Baker 1967). 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 an outcrossing and a 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 and Johnson 2007) through inbreeding (Novak and Mack 2005; Sakai et al. 2001) but floral visitors can favour outcrossing, generating more vigorous recombinant seeds. Evidence of this is contradictory, some IAS species are highly successful through entirely clonal reproduction (Corredor-Prado et al. 2015; 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 IAS possess self-incompatibility (17 species in South Africa; Rambuda and Johnson 2004) among others such as *Mikania micrantha* Kunth (Hong et al. 2007) and *Ambrosia artemisiifolia* L. (Friedman and Barrett 2008). Self-compatibility would favour continuous seed production, population maintenance, and some degree of dispersal (Herrera and Nassar 2009; Zhang et al. 2011; Zeng et al. 2021) and the continuous availability of floral buds, flowers, and fruits in *A. fistulosus* and its 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 increase its invasive success, the establishment of *A. fistulosus* in areas that present a high disturbance regime also contributes to their success (Elton 1958; Hobbs and Huenneke 1992). *Asphodelus fistulosus* forms large patches of vegetation causing a reduction of native species, impacting the biodiversity of the ecosystem (Elton 1958; Levine and D'Antonio 1999). The ornamental use of *A. fistulosus* (Jeschke and Strayer 2006) and the lack of natural enemies (Keane and Crawley 2002) also favour invasion (Blumenthal 2006), increasing the availability of resources for pollinators and the possibility of pollination by exotic species (Simberloff and 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 differed between populations, suggesting that reproductive

phenology responded to local conditions. The large number of flowers favoured the presence of native visitors, which ranged from nectarivorous species of Lepidoptera, species of native bees (e.g., *Lasioglossum* sp. and *Ceratina* sp.), to exotic bees (*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. The invasive potential of onionweed within the Chihuahuan Desert is favoured by its mating system and phenological plasticity facilitating its expansion to other areas, prompting an urgent need to establish plans for its control.

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