EXPECTED MATING SYSTEM, FLORAL DIVERSITY AND FLOWER VISITORS OF FIVE SPECIES OF IRIDACEAE OF THE ARGENTINE PAMPAS

Sistema de apareamiento esperado, diversidad floral y visitantes florales de cinco especies de Iridaceae de la región pampeana argentina

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RESUMEN

Las Iridáceas son una familia de plantas interesantes desde el punto de vista de la biología reproductiva debido a que la diversidad de estructuras florales de sus especies atrae una variedad de visitantes florales. Este trabajo describe algunos aspectos reproductivos de cinco especies de Iridáceas de la cuenca del río Salado en las pampas argentinas: *Cypella herbertii*, *Alophia lahue* y tres especies de *Sisyrinchium*. *C. herbertii* exhibe una interacción especializada con abejas colectoras de aceite, mientras que el resto de las especies estudiadas posee visitantes poco especializados. Para *A. lahue* y las especies de *Sisyrinchium* analizadas las estimaciones del sistema de apareamiento tienden a subestimar el grado de autogamia encontrado en experimentos previos. Observaciones de campo verificaron la producción de néctar en las flores de *C. herbertii* y sugieren que el éxito reproductivo de esta especie podría estar limitado por polen en una de las poblaciones estudiadas.

Palabras clave: Diversidad floral, flores de aceite, limitación por polen, relación polen-óvulo, sistema de apareamiento, visitantes florales

ABSTRACT

Iridaceae is an interesting plant family from the viewpoint of reproductive biology because the diverse floral structures of its species attract a gamut of different flower visitors. This work reports some reproductive aspects of five species of Iridaceae of the Salado river basin in the Argentine pampas: *Cypella herbertii*, *Alophia lahue* and three species of *Sisyrinchium*. *C. herbertii* exhibits a specialized interaction with oil-collecting bees, while the rest of the species studied had rather unspecialized visitors. For *A. lahue* and the species of *Sisyrinchium* analyzed estimations of expected mating system tend to underestimate the degree of autogamy found in previous experiments. Field observations verified the production of nectar in the flowers of *C. herbertii* and suggested that the reproductive success of this species might be pollen limited in one of the population studied.

Key words: Floral diversity, flower visitors, mating system, oil flowers, pollen limitation, pollen-ovule ratio

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INTRODUCTION

The plant family Iridaceae has a world-wide distribution and comprises nearly 1700 species in 82 genera (Mabberley 1998). This family is characterized by a high flower diversity; as a result, different species have been reported to attract a wide range of pollinators such as bees, beetles, short- and long-proboscis flies, butterflies, moths and Nectarinid birds (Bernhardt & Goldblatt 1998; Goldblatt & Manning 2006). The sub-Saharan species of Iridaceae, which are remarkably diverse (*ca*. 1050 spp. according to Goldblatt & Manning 2006), have grasped the attention of pollination biologists over the past 20 years and have produced many textbook examples of specialized interactions (Goldblatt *et al*. 1989; Goldblatt & Bernhardt 1990; Goldblatt *et al*. 1995; Johnson 1996; Goldblatt 1997; Steiner 1998; Goldblatt & Manning 2000; Johnson *et al*. 2003; Manning 2004). However, pollination of Iridaceae outside Africa has received scant attention (Cocucci & Vogel 2001; Freitas & Sazima 2003; Devoto & Medan 2004; Sapir *et al*. 2005).

Iridaceae of Argentina comprise 102 species in 23 genera (Anonymous 2008), and are well represented in the plains of the Salado river basin in southern South America. This area constitutes the main portion of the flooding pampas (León 1975; Cabrera 1976; León *et al*. 1979). Over the past century, these grasslands have been uninterruptedly grazed by cattle, and the present flora includes many adventitious species associated with grazing conditions (Sala *et al*. 1986).

The basic reproductive biology of most of the Iridaceae of the Salado grasslands, like the majority of the Iridaceae of Argentina (Cocucci & Vogel 2001), still remains understudied. However, a species of Iridaceae of these grasslands which has received some attention is *Cypella herbertii* (Lindl.) Herb. Previous studies have used the ratio of pollen grains to ovules in the flowers to predict *C. herbertii* would have a facultative xenogamous mating system (following Cruden 1977) and contrasted that prediction against the result of a glasshouse pollination experiment (Devoto & Medan 2004). Furthermore, it's been reported that, in addition to the oil produced at the base of the tepals, *C. herbertii* produces nectar in the connective tissue of the anthers (Roitman 1998). In this context, the main objective of this study was to describe the flower visitors and the expected mating system of five species of Iridaceae that occur in the natural grasslands of the Salado river basin in Argentina: *Cypella herbertii*, *Alophia lahue* (Molina) Espinosa, *Sisyrinchium platense* Johnst., *S. minus* Engelm. & Gray, and *S. minutiflorum* Klatt. A second objective was to further study some aspects of the reproductive biology of *Cypella herbertii*, specifically the production of nectar as a floral reward and its mating system under field conditions.

MATERIALS AND METHODS

Study sites

Salado river basin extends over 58 000 km^2 in Buenos Aires Province, Argentina. A temperate climate with a mean annual rainfall of nearly 1000 mm, poorly-drained halomorphic soils and summer droughts determine natural grasslands to be the dominant vegetation type of the region (León 1975; Cabrera 1976; León *et al*. 1979). The study was carried out in two field sites. All five focal species were present in both sites. The first site, located in a floodplain rangeland in the centre of the Salado basin (Estancia 'Las Chilcas', hereafter 'LC'; 36°30' Lat. S, 58°30' Long. W), was visited by two observers during five one-day trips spread from early October to early April in 1994-95 and again in 1995-96. The second site, which was closer to the northern limit of the basin (Estancia 'El Nazareno', hereafter 'EN'; 35°32' Lat. S, 58°00' Long. W), was visited by one observer for three consecutive days in November and seven days in December 2002, and for two days in October 2003. The change of location from LC to EN was owed to logistic reasons and, given the similarity between sites, there's no reason to expect differences in the field observations made.

Focal species

Cypella herbertii is one of several Iridaceae known to produce oils as a floral reward to their highly specific bee pollinators (Buchmann 1987; Vogel 1989). Its actinomorphic flowers have six orange-yellow tepals; the outer three being bigger (3-4.5 cm long) than the inner ones (0.9-1.4 cm long). *Alophia lahue* has actinomorphic oil-rewarding flowers with six blue tepals; the outer three being bigger (*ca*. 20 mm long) than the inner ones (*ca*. 10 mm). All studied species of *Sisyrinchium* have nectar-rewarding actinomorphic flowers, with six blue to light-blue equal-sized tepals: 5 mm long in *S. minus*, 4-5 mm in *S. minutiflorum*, and 12-15 mm in *S. platense*; this last species also has actinomorphic oil-rewarding flowers (Roitman 1998). All studied species produce flowers which last only one day. Full botanical descriptions and illustrations of the species studied here can be found in Cabrera (1968).

In each trip, observations were made on flower visitors during all the time the flowers remained open (times varied between species; see Results for details) by randomly walking through the population in an area of *ca*. 10 ha at LC and 5 ha at EN sites. Total sampling time is roughly 100 hours (all observers combined) for each site. Insects that contacted reproductive structures while foraging were recorded as flower visitors and captured for later identification. The presence and identity of pollen grains on the bodies of captured visitors was not verified. In addition, during each visit observations were made on approximate timing of flower opening and closure for each species. This was not based on following individually tagged flowers but on the aspect shown by the whole population of each species while the search for flower visitors took place. Additionally, the pollen-ovule ratio and the outcrossing index, OCI, following Cruden (1977) were calculated for all five species. These indexes provide a rough estimation of the expected mating system. To calculate pollen-ovule ratio the number of pollen grains from one anther and the number of ovules in the ovary were counted with a 20 × stereomicroscope on 10 flowers, and OCI was estimated from 15 flowers of each species. OCI ranges from 0 (cleistogamous species) to 4 (xenogamous species), and it is the sum of assigned values for three characteristics of the flowers: diameter, temporal separation of anther dehiscence and stigma receptivity, and spatial separation of stigma and anthers (Cruden 1977). The moment of stigma receptivity was determined in the laboratory by applying hydrogen peroxide (H_2O_2) to stigmas (Dafni 1992) of plants brought from the field and grown at the Lucien Hauman Botanical Garden (Faculty of Agronomy, Buenos Aires). Flower diameters of *C. herbertii* and *A. lahue* were based on the outer tepals.

To detect the presence of nectar in *C. herbertii* a glucose test was applied at EN site on the anthers exudate of this species (Hemoglucotest, Boehringer-Mannheim, Mannheim, Germany), and its equivalent sucrose concentration (in °Brix: g of solute per 100 g of solution; Bolten *et al*. 1979) was measured using a handheld refractometer modified for small volumes. These observations were carried out between 10:00 and 12:00 during the morning of a warm sunny day in October 2003 on 22 flowers randomly picked from different plants across the population.

Finally, the high abundance of *C. herbertii* at EN allowed the conduction of a field pollination experiment that aimed to establish the mating system of this species under natural conditions. This was done to contrast against previous estimations of the mating system of *C. herbertii* based on glasshouse experiments (Devoto & Medan 2004). The experiment consisted of four treatments: natural pollination (n = 15 flowers), anther removal with no pollination to rule out the occurrence of agamospermy (n = 14), hand self-pollination (n = 22), anther removal with hand cross-pollination (n = 32). Two previous studies had shown a very low reproductive success in *C. herbertii* following automatic self-pollination (Roitman 1998; Devoto & Medan 2004), so no test for this was performed in the present study. Except for natural pollination, all flowers were immediately bagged after manipulation to prevent contamination with pollen from an unwanted source. Fruit set (%) of these four treatments was measured as (N° of fruits produced / N° of flowers pollinated) × 100. In addition, the occurrence of natural pollination in this population of *C. herbertii* was assessed once in each of the two trips to EN site. This was done by counting in a sub-sample of the population the number of flowers that had pollen on their stigmas at 12:00 h. This observation was possible in the field because the greenish pollen grains are clearly visible against the black-velvety background of the stigmatic surface.

RESULTS

Flowers of *C. herbertii* start opening early in the morning (*ca*. 7:00 h) and may remain open until 18:00 h. The strong yellow colour of the flowers tends to fade to a very pale yellow during the day, particularly in hot sunny days. Flowers of *Sisyrinchium* spp. start opening around 8:00 and by 17:00 h are almost completely closed. Flowers of *Alophia lahue* remain open between 8:00 and 16:00 h. The occurrence of protandry or protogyny was observed in none of the studied species, being all adichogamous (with no time lag between receptivity of stigma and release of pollen).

Thirteen different insect species were recorded visiting flowers of the focal species (Table 1). The most conspicuous visitor was the bee *Chalepogenus roitmani* which was seen actively collecting oil from the base of the tepals of *C. herbertii* and was also recorded once on a flower of *S. platense*. These bees squeeze their body between the anthers and the inner tepals to reach the oil producing structures in *C. herbertii*, and in so doing passively transfer pollen from the anthers to the stigma. It was repeatedly observed in the field that one visit of *C. roitmani* to previously unvisited flowers of *C. herbertii* was enough to deposit a very visible amount of pollen on at least one of the three stigmatic surfaces of the flower. The flowers of all other species were mostly visited by rather unspecialized insects ranging from small beetles feeding on floral tissues (Melyridae and Curculionidae), flies feeding on pollen (e.g. Syrphidae), and small bees collecting pollen (Halictidae) (Table 1).

Table 1. Flower visitors to species of Iridaceae in the Salado river basin, Argentina.

Plant species	Order	Family	Visitor species
Cypella herbertii	Hymenoptera	Anthophoridae	*Chalepogenus roitmani*
		Halictidae	*Dialictus* sp.
			Augochlorella (*Ceratalictus*) sp.
	Coleoptera	Cantharidae	*Chauliognathus cf. scriptus*
		Curculionidae	Unidentified species
		Melyridae	*Astylus quadrilineatus*
		Meloideae	*Tetraonyx* sp.
Alophia lahue	Hymenoptera	Apidae	*Apis mellifera*
		Halictidae	*Dialictus* sp.
			Augochlora sp. 1
			Augochlora sp. 2
	Diptera	Syrphidae	*cf. Allograpta* sp.
			Toxomerus sp.
			Palpada sp.
	Coleoptera	Melyridae	*Astylus quadrilineatus*
		Curculionidae	Unidentified species
Sisyrinchium platense	Hymenoptera	Anthophoridae	*Chalepogenus roitmani*
	Diptera	Syrphidae	*Toxomerus* sp.
Sisyrinchium minus *S. minutiflorum*	Hymenoptera	Halictidae	*Dialictus* sp.
	Diptera	Syrphidae	*cf. Allograpta* sp.

The estimation of mating systems based on pollen-ovule ratio suggests *A. lahue* is xenogamous, whereas the three species of *Sisyrinchium* can be expected to behave as facultative xenogamous (Table 2). Estimations of mating systems based on OCI suggest *A. lahue* and *S. platense* are facultative xenogamous, whereas *S. minus* and *S. minutiflorum* are facultative autogamous.

Table 2. Characteristics of five species of Iridaceae of the Salado river basin in Buenos Aires Province, Argentina.

Species	Pollen-Ovule ratio	OCI	Expected reproductive system
Alophia lahue	4580	3	FX
Cypella herbertii	6245	3	FX
Sisyrinchium platense	570	3	FX
Sisyrinchium minus	1680	2	FA
Sisyrinchium minutiflorum	830	2	FA

FA = facultative autogamous, FX = facultative xenogamous; OCI = outcrossing index

The production of nectar on the connective tissue of the anthers of *C. herbertii* was confirmed. The sticky exudates had a mean sucrose concentration of 11.8% (range = 10.0 -14.0; n = 22 flowers). The assessment of the occurrence of natural pollination in *C. herbertii* at EN site in November 2002 showed that none of 96 flowers checked had visible pollen on their stigmas at 12:00 pm, whereas in the second trip in December 2002, 78 of 81 flowers had abundant pollen on their stigmas at the same time of the day. Field pollination experiments on *C. herbertii* produced the following fruit set: natural pollination = 13.3%, agamospermy = 0%, hand self-pollination = 84.6%, hand cross-pollination = 87.5%.

DISCUSSION

This study added information on the flower visitors of five species of Iridaceae which are common in the temperate grasslands of the Salado river basin in Buenos Aires, Argentina. Except for *C. herbertii* and its specialized interaction with oil-collecting bees, all species studied seem to have rather unspecialized interactions with a variety of flower visitors. It's interesting to discuss this pattern in the context of the floral diversity, particularly floral symmetry, presented by species of Iridaceae world-wide. Symmetry is a floral cue strongly associated to the composition of the visitor assemblage of a given plant taxon (Giurfa *et al.* 1999) and its importance is particularly significant in Iridaceae. In this family the spectra of visitors differs widely between predominantly actinomorphic taxa and those that are predominantly zygomorphic: while pollination by pollen-collecting female bees, scarab beetles and short-tongued flies is overrepresented among actinomorphic genera, pollination by nectar-collecting bees, long-proboscid flies, birds, butterflies and moths, which are all long-tongued visitors, is under-represented (Goldblatt & Manning 2006). These differences are partially due to the absence of a flower tube that can be visited by pollinators with extended mouthparts. In this context, except for *C. herbertii*, the Iridaceae of the Salado grasslands seem to fit well the pattern of 'actinomorphic flowers visited by short-tongued pollinators'. *Cypella herbertii* seems to be an exception because the secretion of floral oils and its utilization by oil-collecting bees has opened one unique pollination niche for the species and is an innovation perhaps as specialized as the development of tubular zygomorphic floral morphologies (Buchmann 1987; Goldblatt & Manning 2006). It would be interesting to explore the evolutionary and biogeographic processes that fostered the development of long-tubed, zygomorphic flowers in Africa while totally prevented their evolution in the Iridaceae of the Salado grasslands. In addition, future studies should focus on finding if in the Salado grasslands there are species of flower visitors capable of exploiting the floral oil rewards produced by *A. lahue* and *Sisyrinchium*.

Regarding the several insects recorded on the flowers of the species studied, it remains to be determined which of them actually transport pollen on their bodies and effectively act as pollinators of their host plants. Furthermore, future studies should also address the possibility and potential consequences of heterospecific pollen transfer (McLernon *et al*. 1996) in the Iridaceae of the Salado grasslands given the fact that these species have largely overlapping flowering periods (Roitman 1998) and share some of their flower visitors.

Estimations of mating system based on pollen-ovule ratio and OCI suggest the species of Iridaceae studied range from facultative xenogamous to facultative autogamous. However, except for *C. herbertii*, all species showed a rather high fruit set following spontaneous and hand self-pollination (Roitman 1998) which suggests they behave as autogamous. This incongruence could be partly explained by the occurrence of late acting autogamy as a mechanism of reproductive assurance (Klips & Snow 1997; Traveset 1999), and should receive further attention in future studies. However, the difference between predicted and actual mating system could also be owed, as suggested by previous criticism (Charnov 1979, 1982; Cruden *et al*. 1996), to the inability of the pollen-ovule ratio to accurately predict a species' mating system.

The high fruit set following spontaneous self-pollination reported for flowers of *A. lahue* and the species of *Sisyrinchium* (Roitman 1998) suggests that their short-term dependence on pollinators is rather low, although the long-term consequences of scarcity of pollinators should still be considered (Charlesworth & Charlesworth 1987; Lynch 1991; Bond 1994). In the case of *C. herbertii*, however, spontaneous self-pollination had a low efficiency in terms of fruit set (Roitman 1998; Devoto & Medan 2004), and field observations suggested a high temporal variability in pollinator activity (as shown by the highly variable number of stigmas with pollen recorded on two different dates). Furthermore, field experiments in *C. herbertii* showed natural pollination produced a lower fruit set than hand self- and cross pollination. This suggests the reproductive success of the population of *C. herbertii* at EN site could be pollen limited (Larson & Barrett 2000; Wilcock & Neiland 2002). Future studies should focus on the influence of the combined effect of low spontaneous fruit set, pollinator unpredictability and possible pollen limitation on the reproduction of *C. herbertii*. Finally, further studies should also explore the actual contribution of *C. herbertii's* specialized flower visitors to reproduction, and whether the production of nectar in the flowers attracts visitors that actually contribute to pollination.

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