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Reproductive biology of *Sphaeralcea* species with ornamental interest

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Abstract: The genus *Sphaeralcea* belongs to the Malvaceae family and has native species from South America. Their attractive morphological characteristics with ornamental value have not yet been explored. The objective of this work was to know the viability of pollen, stigma receptivity, type of pollination and combining ability of four *Sphaeralcea* species (*S. australis*, *S. bonariensis*, *S. crispa* and *S. mendocina*), with the aim to develop new ornamental varieties. Fructification, fertility, seed germination and survival seedlings on intraspecific and reciprocal interspecific offspring were assessed. The highest values of stigma receptivity and pollen viability were obtained at 2:00 PM for the four species. *S. mendocina* also showed high values of pollen viability at 4:00 PM .The species proved to be self-incompatible and allogamous, with different degrees of reproductive compatibility. The interspecific crosses of *S. mendocina* and the intraspecific of *S. crispa* did not produce descendants. The crosses between *S. australis* and *S. bonariensis* as maternal parent presented the best combining ability with good fruit production, seed germination and survival. This research provides useful information for the formulation and implementation of breeding strategies, to improve pollination efficiency, and to breed new *Sphaeralcea* varieties with ornamental potential.

1. Introduction

The Malvaceae family is worldwide distributed in regions with temperate and warm climate. In South America, are represented by 63 genus and 533 species of herbs, shrubs and trees, from these 315 are native, 202 endemic and 16 exotics (Zuloaga *et al.*, 2019). Some species are economically important, like various *Gossypium* species, including cotton. Others have medicinal properties (Martínez and Barboza, 2010) and ornamental interest (Krapovickas, 2003; Gutiérrez *et al.*, 2021). Some genera of Malvaceae with ornamental potential are *Pavonia*, *Lecanophora*, *Modiolastrum*, *Rynchosida* and *Sphaeralcea* (Ponce *et al*., 2006; Torres *et al*., 2008; Masini and Rovere, 2015; Gutierrez *et al*., 2021). In Argentina, the *Sphaerlacea* genus have native and herbaceous species with attractive characteristics for ornamental cultivation, such as *S. australis*, *S. crispa*, *S. mendocina* and *S. bonariensis* (Sriladda *et al*., 2012; Gutierrez *et al*., 2021). They are adapted to semi-arid conditions, and have tolerance to water stress, high and low temperatures and high insolation, which make them good candidates for breeding programs in urban ecosystems adapted to extreme weather conditions and for sustainable landscaping. Moreover, the use of native germplasm in breeding programs contributes to the conservation of biodiversity (Masini and Rovere, 2015). In general, native plants make more efficient use of environmental factors such as water and other climate factors, as well as edaphic and biological variables, which result in a lower maintenance demand and in a good performance under the restrictive local conditions.

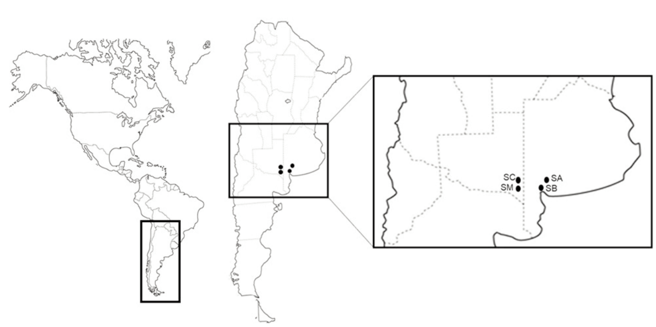
Knowledge of the plants reproductive biology is essential for classical breeding programs, because it allows better orientation and planning of the crosses. In the case of the species under study, their reproductive biology is unknown. This knowledge is essential to be used in pollinations, and to increase the chance of successful fertilization. Some of these aspects are pollen viability, stigma receptivity, pollination type and combining ability since these depend on successful reproduction. Pollen viability and stigma receptivity are aspects that plays an important role in successful hybridizations (Figueiredo *et al.,* 2020). Pollen viability is a measure of male fertility (Liu *et al*., 2021), viable pollen is critical to the process of reproduction and pollen longevity can be affected by temperature and relative humidity (Ren *et al*., 2019). Stigma receptivity is the ability to receive the pollen, therefore it directly affects the plant life cycle, allowing the pollen to adhere, hydrate and germinate (Shivanna and Sawhney, 1997). A detailed knowledge of these features will determine the best moment for pollination, to enable successful controlled pollination in breeding programs. Stigma receptivity is related to the activity of enzymes such as peroxidase, esterase and dehydrogenase (Galen and Plowright, 1987). Receptive stigmas have high enzyme activity, which can occur in different phases of flower development. The observation of the activity of these enzymes can be used to characterize stigma receptivity (Zhang *et al.,* 2021). For the pollination process to occur, the transfer of pollen to the stigma must happen during the period in which the stigma is receptive, otherwise, pollen cannot adhere and germinate.

The aim of this study was to evaluate the reproductive biology of four native species of the genus *Sphaeralcea*, determining pollen viability, timing of stigma receptivity, pollination type and combining ability. The hypothesis we followed was that it is possible to determine aspects of the reproductive biology of the native germplasm of *Sphaeralcea*, with the ultimate objective to develop new ornamental varieties.

2. Materials and Methods

Collection area

The Pampas region is an extensive plain located to the east of Argentina between 31° and 39° south latitude. Aliaga *et al*. (2017) characterized the Pampas general climate, considering rainfall, air temperature, humidity, and wind speed as well as the altitude and the alternation between dry and wet events in the area. Based on these elements, they categorized the Southwest of Buenos Aires and the Southeast of La Pampa as semi-arid region. *Sphaeralceae* seeds were collected between December 2020 and March 2022 in different sites of this semi-arid region (Fig. 1). The sites were characterized by the occurrence of long periods of drought and isolated floods together with windy periods which affect severely the water availability (Aliaga *et al*., 2017).



Species (CODE)	Locality	Province	Location
Sphaeralcea australis (SA)	Tornquist	Buenos Aires	S38°40'76", W62°81'75"
Sphaeralcea bonariensis (SB)	Bahía Blanca	Buenos Aires	S38°45'29", W62°18'47"
Sphaeralcea crispa (SC)	Caleu Caleu	La Pampa	S38°48'29", W63°48'71"
Sphaeralcea mendocina (SM)	Caleu Caleu	La Pampa	S38°55'66", W63°49'76"

Fig. 1 - Geographic distribution and collection sites of studied populations of *Sphaeralcea australis*, *S. crispa*, *S. mendocina* and *S. bonariensis* in central Argentina, South America. For labels see the table.

Plant material and experimental design

The plant material was collected in the indicated area (Fig. 1) as seeds and preserved at 4°C dry with silica gel. The seeds were germinated after pre-germinative treatments to break dormancy (Gutierrez *et al*., 2019). After scarification, the seeds were placed in Petri dishes on filter paper moistened with distiller water in a germination chamber at 20°C (ISTA, 2019) with a 12 h photoperiod previously used in other Malvaceae (Erickson *et al*., 2016; Leperlier *et al*., 2020). Five plants of each *Sphaeralcea* species were grown in pots with commercial substrate (GROWMIX MultiPro®) in the greenhouse of the Center of Renewable Natural Resources from the Semi-Arid Region (CERZOS, CONICET - UNS), under controlled temperature (18-28°C), irrigation and relative humidity (55-85%).

During the day, when the flowers were in anthesis, pollen viability and stigma receptivity were studied at 8:00 h, 10:00 h, 12:00 h in the morning and at 2:00 h, 4:00 h, and 6:00 h in the afternoon.

The same experimental designs were used to evaluate pollen viability and stigma receptivity. Four species (treatments), five plants per species (replications) and three flowers per plant, were used to evaluate a total of 60 anthers and 60 stigmas in a completely randomized experiment.

Stigma receptivity

The Osborn method was used to evaluate the stigma receptivity, based on the reaction of the peroxidase enzyme. The stigma is classified as receptive when placing a drop of hydrogen peroxide at 40% on the flowers stigmas a bubble production is observed (Osborn *et al*., 1988). The reaction of stigma receptivity was examined with a stereomicroscope.

Pollen viability

The estimation of viable pollen was carried out with the Alexander technique (Alexander, 1980). The grain dyed in an intense violet color was taken as viable and the one that was colored green was taken as non-viable. Pollen grain counts were performed in an optical microscope of four random fields per preparation to estimate the percentage of pollen viability (%) = [(*Number of viable pollen grains*/*Number of total pollen grains*) x 100].

Mating system

The experimental trial to test the reproductive system in *Sphaeralcea* genus was based on four experiments and is seen in Table 1. In the greenhouse, the plants of experiments 2, 3, and 4 were isolated with a fine mesh in a cage that excludes potential pollinators. The plants of experiment 1 were used as control and located outside the cage.

For experiment 1, five plants of each species (*S. australis*, *S. crispa*, *S. mendocina* and *S. bonariensis)* were used and three flowers of each plant were marked the day before anthesis. The flowers were allowed to develop normally without any manipulation, as control. The developed fruits were properly identified and covered until harvest.

For experiment 2, five plants of each species were used, and three flowers of each plant were marked the day before anthesis. The fruits were properly identified and covered until fully developed and harvest.

For experiment 3, five plants of each species were used, and three flowers of each plant were marked the day before anthesis. The flowers were allowed to develop normally and without any type of manipulation to evaluate natural self-pollination. The developed fruit were properly identified and covered until harvest.

For experiment 4, inter-specific reciprocal and intra-specific crossing were performed between *S. australis*, *S. crispa*, *S. mendocina* and *S. bonariensis*

Table 1 - Experimental management on *Sphaeralcea australis*, *S. crispa*, *S. mendocina* and *S. bonariensis*. Normal seed set "+" and greatly reduced or zero seed set "-" (modified from Simpson, 2019)

Experimental management	Seed production	
1. Flowers left to develop normally, as control.	+ Fertile	− Infertile
2. Isolated flowers, then self-pollinated by hand.	+ Self-fertile	− Not self-fertile
3. Flowering plants in caged, then left freely.	+ Self-pollinating	− Not self-pollinating
4. Isolated flowers, then emasculated and outcrossed.	+ Outcrossing	− Not outcrossing

(Table 2). Five plants of each species were used, and three flowers for each plant were marked on the day before anthesis. The flower buds were emasculated, the anthers were removed prior to pollen release and reciprocal outcrossing were made once a day during the flowering period. Other flowers were used as male parent. After pollination, the flowers were properly identified and covered until fruit harvest.

The fruiting and fertility results of the four experiments were assessed by counting the seed set in relation to the number of pollinated flowers [Fructification (%) = (*number of fruits produced / number of pollinated flowers*) x 100] and assessment the full seed in relation to the total seed [Fertility (%) = (*number of full seeds/total number of seeds (full + empty)*) x 100]. A classification range based on fructification and fertility percentage was used, therefore 0 to 35% was considered low, 36 to 65% intermediate and 66 to 100% high.

Combining ability

The full seeds of the intra- and interspecific crosses of the previous experiments were subjected to mechanical scarification because native *Sphaeralcea* species present physical dormancy in its seeds (Gutierrez *et al*., 2019). Scarified seeds were then germinated in a culture chamber. The seeds that germinated were sown in seedling trays with commercial GROWMIX MultiPro® substrate and cultivated in the greenhouse under controlled light (shading net 50% of light extinction), temperature (18-28°C) and humidity (55-85%) conditions (early growth stage). The seedlings that developed three to four true leaves were transplanted into 7x7x9 cm pots with a substrate composed of 50% sandy soil, 35% peat, 10% perlite and 5% compost (advanced growth stage). Survival of germinated seeds and seedlings from intraspecific offspring (siblings) and reciprocal interspecific offspring (hybrids) were evaluated to quantify combining ability at each stage of development (early growth stage and advanced growth stage). A classification range was used for the percentages of germination and seedling survival as low (0 to 35%), intermediate (36 to 65%) and high (66 to 100%).

Table 2 - Combinations of interspecific reciprocal and intraspecific crosses that originated the hybrid and sibling offspring, respectively

Female parent (♀)	x	Male parent (♂)
Interspecific reciprocal crosses		
S. australis		*S. crispa*
S. australis		*S. mendocina*
S. australis		*S. bonariensis*
S. bonariensis		*S. crispa*
S. bonariensis		*S. australis*
S. bonariensis		*S. mendocina*
S. crispa		*S. australis*
S. crispa		*S. mendocina*
S. crispa		*S. bonariensis*
S. mendocina		*S. crispa*
S. mendocina		*S. australis*
S. mendocina		*S. bonariensis*
Intraspecific crosses		
S. australis		*S. australis*
S. bonariensis		*S. bonariensis*
S. crispa		*S. crispa*
S. mendocina		*S. mendocina*

3. Results

Stigma receptivity

The four species of *Sphaeralcea* had different behaviors in terms of stigma receptivity, reaching different maximum percentages and at different times of the day. *S. bonariensis* showed high values at 8:00 am and sustained over time until 2:00 PM when it was 100%. *S. australis and S. crispa* had similar behaviors with two high peaks of receptivity, at 8:00 am and the maximum at 2:00 PM (99% *S. australis* and 93% *S. crispa*). *S. mendocina* during the morning hours showed a different behavior from the rest, with very low stigma receptivity values with an exponential growth between 12:00 to 2:00 PM where it reached the highest percentage of receptivity (92%). After 2:00 PM, when all the species had their maximum peaks of stigma receptivity, the values began to decrease in different ways. For *S. australis* and *S. bonariensis* the decrease was marked, reaching values of 0% at 6:00 PM. For *S. crispa* and *S. mendocina* it was gradual until 6:00 PM, when receptivity was null (Fig. 2).

Pollen viability

The four species of *Sphaeralcea* obtained high percentages of pollen viability, although these values varied throughout the day and between species. The highest values were recorded at 2:00 PM for *S. australis* (99%), *S. bonariensis* (99%) and *S. crispa* (98%), with no statistically significant differences between

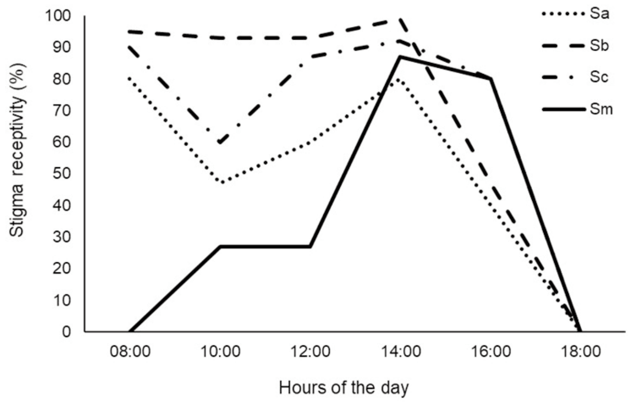


Fig. 2 - Stigma receptivity percentage in *Sphaeralcea australis* (Sa), *S. bonariensis* (Sb), *S. crispa* (Sc) and *S. mendocina* (Sm) flowers in function of time of the day.

them, and at 4:00 PM for *S. mendocina* (99%). At 12:00 PM the percentages were also high for all species and the lowest values were recorded at 6:00 PM for all species (Fig. 3).

Mating system

All combinations, inter and intraspecific crosses, managed to form fruits (Table 3) except *S. mendocina* x *S. bonariensis*. In the case of self-pollinations, fruits were not observed.

The species used as female parent produced differences in the percentage of fruit production. The values were low when *S. crispa* was used as female (7 to 33%), intermediate when it was *S. mendocina* (47 to 53%) and high (67 to 100%) with *S. australis* and *S. bonariensis*. In the intraspecific crosses, the same pattern was repeated, showing low fruiting percentages for *S. crispa* (13%), intermediate in *S. mendocina* (40%) and high in *S. australis* (67%) and *S. bonariensis* (87%).

Regarding fertility, most of the interspecific cross-

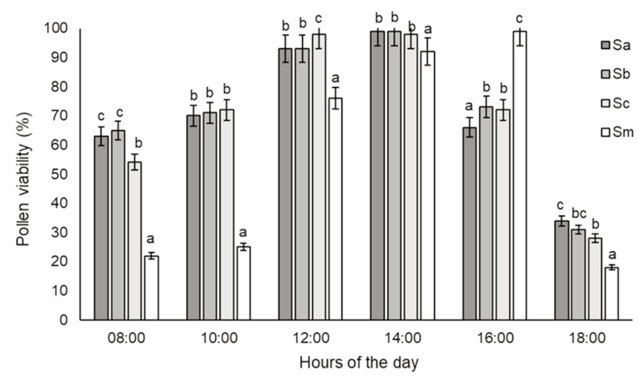


Fig. 3 - Pollen viability percentage in *Sphaeralcea australis* (Sa), *S. bonariensis* (Sb), *S. crispa* (Sc) and *S. mendocina* (Sm) flowers at different times of the day. Means with different letters indicate significant differences with the Fisher's LSD Test, p<0.05. Each vertical bar represents mean ± standard error.

Table 3 - Number of pollinated flowers (NPF), number of fruits produced (NFP), fructification percentage (FP), number of full seeds (NFS), number of empty seeds (NES) and seed fertility percentage (SFP) for intraspecific and interspecific reciprocal crosses between *S. australis* (Sa), *S. bonariensis* (Sb), *S. crispa* (Sc), and *S. mendocina* (Sm)

(♀ x ♂)	NPF	NFP	FP (%)	NFS	NES	SFP (%)
			Interspecific reciprocal crosses			
SaxSb	15	15	100	277	43	83.1
SaxSc	15	15	100	188	43	78.3
SaxSm	15	10	66.7	90	68	55.7
SbxSm	15	8	53.3	18	115	4.5
SbxSc	15	15	100	367	43	89.5
SbxSa	15	10	66.7	179	14	90.2
ScxSb	15	2	13.3	14	0	78.6
ScxSm	15	1	6.7	1	9	10
ScxSa	15	5	33.3	68	6	90.5
SmxSc	15	7	46.7	30	8	78.9
SmxSa	15	7	46.7	58	12	79.7
			Intraspecific crosses			
SaxSa	15	10	66.7	121	74	62.1
SbxSxb	15	13	86.7	283	17	94.3
ScxSc	15	2	13.3	21	9	70
SmxSm	15	6	40	63	8	86.7

es yielded high percentages of full seed production with values between 78 to 91%. However, in the cross of *S. australis* x *S. mendocina* it was intermediate (56%) and it was low for *S. bonariensis* x *S. mendocina* (4%) and *S. crispa* x *S. mendocina* (10%). For intraspecific crosses, fertility was high for *S. bonariensis* (94%), *S. mendocina* (89%) and *S. crispa* (70%) and intermediate for *S. australis*.

Combining ability

The germination percentage after mechanical scarification was high for all crosses except for *S. australis* x *S. australis*, which showed intermediate values (Table 4). Seedling survival decreased throughout development in all descendants, with high and intermediate values predominating in the first growth stage (plant tray) and the majority being low in the advanced stage of development (pot). In the case of the hybrid, the offspring from *S. australis* x *S. bonariensis* showed the highest values of final survival (56%). In the intraspecific crosses, the highest values of descendant survival were from *S. australis* x *S. australis* (66%). The crosses that failed to develop live seedlings were *S. bonariensis* x *S.*

4. Discussion and Conclusions

The methods used by Osborn *et al.* (1988) and Alexander (1980) to evaluate stigma receptivity and pollen viability, respectively, were effective to achieve successful crosses in the genus *Sphaeralcea*.

Stigma receptivity is a highly variable trait among species of the plant kingdom. There are species such as *Carica papaya* L. where the flowers are receptive before the floral opening and until the closing (Parés *et al.*, 2002), others such as *Passiflora edulis* are receptive during anthesis until flowers closed (Ángel Coca *et al.*, 2011). Our results for the genus *Sphaeralcea* showed that *S. australis*, *S. crispa* and *S. bonariensis* had high stigma receptivity at flowers opening, except for *S. mendocina*, which obtained positive results after they opened, and the bubbling was null before flower closure (6:00 PM) for all species. Ambient heat can serve to attract insects to an open flower through volatilization of floral scent during anthesis, and also helps to maintain a period of maximum stigma receptivity (Consiglio and Bourne, 2001). In our results, stigma receptivity was high between 12:00 PM and 2:00 PM which are coinci-

Table 4 - Number of full seeds (NFS), germination percentage (GP), number of seedlings in early growth stage (NSEGS), survival percentage of early growth stage (SPEGS), number of seedlings in advanced growth stage (NSAGS) and survival percentage of advanced growth stage (SPAGS) for intraspecific and interspecific reciprocal crosses between *S. australis* (Sa), *S. bonariensis* (Sb), *S. crispa* (Sc), and *S. mendocina* (Sm)

(♀ x ♂)	NFS	GP (%)	NSEGS	SPEGS (%)	NSAGS	SPAGS (%)
Interspecific reciprocal crosses						
SaxSb	277	88.8	181	73.6	102	56.4
SaxSc	188	83.5	139	88.5	12	8.6
SaxSm	90	100	90	100	35	38.9
SbxSm	18	100	9	50		0
SbxSc	367	80.5	186	67.4	70	37.6
SbxSa	179	100	77	43	7	9.1
ScxSb	14	100	13	92.9	3	23.1
ScxSm	1	100	0	0	-	
ScxSa	68	69.1	30	63.8		0
SmxSc	30	71.4	7	35	1	14.3
SmxSa	58	92.6	20	40		0
Intraspecific crosses						
SaxSa	121	63.6	64	85.3	42	65.6
SbxSxb	283	82.3	120	51.5	47	39.2
ScxSc	21	100	11	55	0	0
SmxSm	63	73.8	42	93.3	6	14.3

dent with the time of day when the maximum ambient temperatures were recorded, with an average of 30.4°C (National Meteorological Service, https://www.smn.gob.ar/).

In some species high temperatures affect pollen viability (Rao *et al*., 1992; Radice *et al*., 2020; Iovane *et al.*, 2022). In *Sphaeralcea*, there is still no evidence of how environmental factors affect pollen viability, but our results are indirect evidence that pollen would not be affected by high summer temperatures. One possible explanation for these results is that they are native species adapted to local climate conditions and therefore high temperatures do not generate the thermal stress that affects viability during pollen development or in its mature state. The results of this research indicate that the pollinations that take place between 12:00 PM and 2:00 PM have a greater probability of generating fruits and seeds, since it is when most of the open flowers are receptive, and the viability of pollen is optimal.

These species demonstrated to be self-incompatible and allogamous, with different degrees of reproductive compatibility and combining ability between them. The *S. mendocina* x *S. bonariensis* cross produced aborted fruits and were not able to produce offspring. The crosses *S. bonariensis* x *S. mendocina*, *S. crispa* x *S. mendocina*, *S. mendocina* x *S. australis* and *S. crispa* x *S. crispa* managed to produce viable seeds that germinated, but with no descendants since the seedlings were not fully develop. These effects are probably the product of reproductive incompatibility between the species since they have different chromosome numbers, *S. mendocina* is 2n = 30 and the rest of the *Sphaeralcea* are 2n = 10 (Krapovickas, 1949). It would be interesting to achieve offspring with the germplasm of *S. mendocina* since it has very attractive and particular ornamental features such as the color of the leaves with shades in the range of gray and pink flowers (Gutiérrez *et al*., 2021). The null survival of the intraspecific crosses for *S. crispa* could be due to the rapid loss of vigor of the seeds, since at the time of germination they were smaller plants with a very weak appearance.

Except for *S. bonariensis* x *S. mendocina* and *S. australis* x *S. mendocina* crosses, which were not compatible due to chromosomal differences; the crosses with the best combining ability were those that had *S. australis* and *S. bonariensis* as maternal parent with good fruit production. Regarding combining ability, the crosses with the best survival offspring were *S. australis* x *S. bonariensis* and *S. australis* x *S. australis*. Both produced the greatest quantity and quality of descendant plants that prospered over time and had adequate growth and development. These novel results will allow us to improve the pollination efficiency and to design a strategic plan for the ornamental improvement of *Sphaeralcea genus*

Our study provides the first data on the reproductive biology and mating system of *Sphaeralceae* genus belonging to four native species, which provides valuable information for the formulation and implementation of new approaches for genetic improvement programs. This facilitates the development of new varieties of *Sphaeralcea* hybrids with ornamental qualities.

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