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A new case of late-acting self-incompatibility in *Capparis* L. (Brassicaceae): *C. jacobinae* Moric. ex Eichler, an endemic andromonoecious species of the Caatinga, Pernambuco State, Brazil[1]

Luis Miguel Primo[2,4] and Isabel Cristina Machado[3]

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RESUMO – (Novo registro de auto-incompatibilidade de ação tardia em *Capparis* (Brassicaceae): *C. jacobinae* Moric. ex Eichler, uma espécie andromonóica endêmica da Caatinga, PE, Brasil). O sistema reprodutivo de *Capparis jacobinae* Moric. ex Eichler (Brassicaceae), uma espécie endêmica da Caatinga no Brasil, foi analisado através de polinizações controladas e observações do desenvolvimento dos tubos polínicos por meio de microscopia de fluorescência. De 105 flores autopolinizadas, apenas uma formou fruto (sucesso= 0,95%), ocorrendo a abscisão das demais em um intervalo de tempo uniforme, entre o oitavo e o décimo dia após a antese. Entretanto, tanto tubos polínicos procedentes de autopolinização quanto de polinização cruzada penetraram na micrópila, sendo a taxa de óvulos penetrados menor em flores autopolinizadas durante as 24 horas posteriores à polinização, igualando-se entre os dois tratamentos para 48, 72 e 96 horas posteriores à polinização. Além disso, foram realizadas duas estimativas indiretas do sistema reprodutivo, baseadas na razão pólen/óvulo e semente/óvulo, cujos resultados foram característicos de espécies xenógamas. Conclui-se, portanto, que *C. jacobinae* é auto-incompatível, apresentando sistema de auto-incompatibilidade de ação tardia, sendo este o terceiro registro deste mecanismo encontrado para o gênero e o primeiro encontrado em uma espécie de *Capparis* endêmica da Caatinga. É sugerido que este sistema de auto-incompatibilidade seja encontrado em outros representantes do mesmo gênero e família.

Palavras-chave: andromonoicismo, Capparaceae, razão pólen/óvulo, sistema sexual, tubos polínicos

ABSTRACT – (A new case of late-acting self-incompatibility in *Capparis* (Brassicaceae): *C. jacobinae* Moric. ex Eichler, an endemic andromonoecious species of the Caatinga, Pernambuco State, Brazil). We studied the reproductive system of *Capparis jacobinae* Moric ex Eichler (Brassicaceae), based on controlled hand-pollination and observation of pollen tube growth made in a fluorescence microscope. Of 105 self-pollinated flowers only one produced fruits (success = 0.95%), all the other flowers abscised at the same time, between the eighth and tenth day after anthesis. Nevertheless, self- and cross-pollinated pollen tubes reached the micropyle. The rate of penetrated ovules in self-pollinated flowers was lower during the first 24 h after pollination; thereafter this rate was similar between self- and cross-pollinated flowers for treatments of 48 h, 72 h and 96 h after pollination. In addition, we carried out two indirect estimates of the reproductive system, based on pollen/ovule and seed/ovule ratios, which resulted in typical features of xenogamous species. We concluded that *C. jacobinae* has a late-acting self-incompatibility system. This is the third record of this mechanism for the genus and the first for a species of *Capparis* endemic to the Caatinga. We suggest that this self-incompatibility system may occur in other species of the same genus and family.

Key words: andromonoecy, Capparaceae, pollen-ovule ratio, pollen tube growth, sexual system

Introduction

The Caatinga covers an area of about 1,000,000 km^2 mainly located in northeastern Brazil. It is characterized by low rainfall (usually below 800 mm/year) and by the occurrence of xerophytic deciduous vegetation, in general thorny, with succulent plants, varying from shrubs to trees with a seasonal herbaceous stratum (Sampaio 1995; Leal *et al*. 2003). The genus *Capparis* L. has 250 species (Mabberley 1993) and is represented in Brazil by about fifteen species that occur mainly in the Caatinga and Restinga environments (Barroso 1978; Fuks & Costa e Silva 2000).

The available data on the reproductive system of the genus *Capparis* indicate that its members are mainly self-incompatible (about 85% of the studied species). Only *C. flexuosa* L. (Ruiz-Zapata & Arroyo 1978) and *C. hastata* L. (Primo 2004; Tab. 1) were considered to be self-compatible, though in the Restinga (Carvalho 2002) and in semi-deciduous forests (Primo 2008) *C. flexuosa* was considered to be self-incompatible.

Observations on pollen tube growth in this genus were carried out for only two species: *C. pittieri* Standl. (Seavey & Bawa 1986) and *C. retusa* Grisenb. (Bianchi & Gibbs 2000), showing that the pollen tubes formed through self-pollination penetrated the ovule's micropyle. However, most of these ovules did not produce seeds, what was interpreted as a recognition-rejection of pollen tubes coming from self-pollination only when they were already inside the ovules. Species with this mechanism have a reproductive system with late-acting self-incompatibility (LSI) (*sensu* Seavey & Bawa 1986). This system, like conventional ones, such as sporophytic and gametophytic (where inhibition occurs in the stigma and style, respectively), may be distributed among species from phylogenetically related groups, such as genera or families (Gibbs & Bianchi 1999).

Taking into account this feature discussed by Gibbs & Bianchi (1999) and the two preceding occurrences of LSI in the genus, the present study aims to describe the reproductive system of *C. jacobinae* Moric. ex Eichler and to determine the nature of the incompatibility system through analysis of pollen-tube growth.

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[1] Part of the Master Dissertation of the first author

[2] Universidade Federal de Pernambuco, Programa de Pós-Graduação em Biologia Vegetal, Recife, PE, Brasil

[3] Universidade Federal de Pernambuco, Departamento de Botânica, Recife, PE, Brasil (imachado@ufpe.br)

[4] Corresponding author: luiprimo@yahoo.com.br

Material and methods

Study areas and species – Field work was carried out during two flowering cycles of *C. jacobinae*, from September 2002 to April 2003 and from October to December 2003, in two natural populations in the state of Pernambuco, Brazil: one in Arcoverde municipality (8°25'S, 37°02W) and the other in Vale do Catimbau, Buíque municipality (8°67'S, 37°01W). Each population was composed of approximately 40 individuals, distributed over an area of 10,000 m^2. The individuals of both populations formed groups of two or three, next to each other and joined by their canopies, or they grew in isolation. The distance between these groups or between isolated individuals was about 10 m.

Capparis jacobinae is widely distributed in the Caatinga and is endemic to this biome (Costa e Silva 2002). It is a shrubby species and has polystaminate brush-type flowers with an andromonoecious sexual system (Primo 2004; Primo & Machado unpublished data). The anthesis process is slow: it starts at 11:00 h and flowers are completely opened around 16:00 h. The flowering period lasts from August to March (Primo 2004; Primo & Machado unpublished data).

Voucher specimens of *C. jacobinae* were deposited in the Herbarium Geraldo Mariz at the Botany Department, Universidade Federal de Pernambuco (UFP 33764).

Reproductive system – To investigate the plant's reproductive system we carried out experiments using hermaphrodite flowers, which consisted of a control and four treatments: 1) Control: we marked hermaphrodite flowers (n = 99) of different individuals to test for the production of fruits under natural conditions; 2) Apomixis: we emasculated flowers of different individuals in pre-anthesis phase (n = 32), which were maintained bagged for one day; 3) Spontaneous self-pollination: we bagged flowers of different individuals in pre-anthesis phase (n= 33), and maintained them bagged for one day; 4) Manual self-pollination: we bagged flower buds of different individuals (n = 105) and, after flower opening and anther dehiscence, they were hand-pollinated with their own pollen and once more bagged and maintained this way for one day; 5) Manual cross-pollination: we emasculated and bagged flower buds of different individuals with indehiscent anthers (n = 72). Thereafter, these flowers received pollen from other individuals, and were bagged again. Each flower was pollinated with pollen grains from only one kind of donor flower, hermaphrodite or staminate, since there was no difference in the viability of pollen grains from these two flower types. The distance between individuals used in crossbreeding was ≥ 15 meters. In all treatments, the hermaphrodite flowers were subsequently monitored to verify whether fruits were produced.

Manual pollination for the tests was carried out between 19:00 and 22:00 h. On non-pollinated staminate and hermaphrodite flowers, as well as on flowers submitted to self-pollination, we evaluated abscission time.

Aiming to test for the possibility of pollination leading to fruit production near the end of anthesis, we carried out manual cross-pollination between 04:30 and 05:00 h (n = 10), and thereafter we recorded whether fruits were produced.

In all treatments, the flowers were isolated from their visitors with semi-permeable paper bags closed with plastic-coated wires. We emasculated the flower buds with a sharp tip scissors. Anthers were cut immediately before dehiscence and filaments were left intact. Manual pollination was carried out by direct contact of the dehiscent anthers with the stigma.

We calculated the index of self-incompatibility (ISI) based on Bullock (1985) analyzing the percentage of fruit production from flowers submitted to manual self-pollination and cross-pollination. Fruits obtained in each treatment were also evaluated in terms of number of seeds.

A subsample of self-pollinated hermaphrodite flowers and another subsample of cross-pollinated flowers were fixed in FAA$_{70}$ 24, 48, 72 and 96 h after manual pollination (n = 4 to 6 pistils for each treatment and time). On these fixed flowers, we studied the percentage of ovules penetrated not only by pollen tubes originating from self-pollination but also by pollen tubes originating from cross-pollination. For this analysis we used fluorescent microscopy and staining with aniline blue (Martin 1959). We used χ^2 (Sokal & Rohlf 1995) to compare simultaneous treatments.

We tested for the viability of pollen grains in 10 hermaphrodite flowers and in 10 staminate flowers of five individuals, all collected just before anthesis, by staining the cytoplasm with acetic carmine 2% (Radford *et al.* 1974).

We also carried out two indirect estimates of the reproductive system, based on pollen/ovule and seed/ovule ratios, as suggested by Cruden (1977) and Wiens (1984), respectively. For the first estimate, we collected flower buds (n = 10 hermaphrodite flowers and n = 10 staminate flowers) of different individuals and fixed them in ethanol 70%. We then determined the average number of ovules per ovary and the average number of pollen grains per anther and per flower. To estimate the number of pollen grains, we placed the contents of all six anthers from 20 flower buds in pre-anthesis in a solution of 1 ml lactic acid and glycerin (3:1), following Lloyd (1972). Using this solution, we counted pollen grains using a Neubauer chamber, following Maeda (1985). The number of pollen grains per anther was multiplied by the number of stamens of each flower (Primo 2004; Primo & Machado unpublished data). Finally, we calculated the pollen/ovule ratio with the following formula:

$$\frac{\dfrac{\sum_{e} pe}{n_e} xR + \dfrac{\sum_{h} ph}{n_h}}{NO}$$

Where:
s = staminate flowers
h = hermaphrodite flowers
p_s = total number of pollen grains per staminate flower
n_s = total number of staminate flowers
R = ratio between staminate and hermaphrodite flowers [= 2.34 (Primo 2004; Primo & Machado unpublished data)]
p_h = total number of pollen grains per hermaphrodite flower
n_h = total number of hermaphrodite flowers
NO = number of ovules per flowers

The estimate of female fertility, i.e. the percentage of ovules that produced seeds (seed/ovule ratio), was calculated as the average number of seeds per fruit of the control group divided by the average number of ovules per flower (Wiens 1984).

Results and discussion

The results of controlled pollination experiments (Tab. 2) indicate that *C. jacobinae* is self-incompatible, with ISI = 0.013, since out of 105 self-pollinated flowers, only one produced fruits (success = 0.95%), which is consistent with the data of Ruiz-Zapata & Arroyo (1978). The lack of fruit production by apomixis and spontaneous self-pollination indicates that *C. jacobinae* depends on pollen vectors for reproduction. Moreover, the lack of fruit production through manual cross-pollination carried out at the end of anthesis (04:30-05:00 h.) suggests that these vectors have crepuscular/nocturnal activity, as observed by Primo (2004) and Primo & Machado (unpublished data).

Because *Capparis jacobinae* has staminate and hermaphrodite flowers on the same individual, this is the second record of andromonoecy for the genus (Primo 2004; Primo & Machado unpublished data); the first was *C. pittieri* (Bawa & Beach 1981). The occurrence of andromonoecy in the family has already been mentioned for *Cleome* (Brassicaceae), and there are records of trimonoecy in *C. rosea* (Carvalho 2002) and *C. spinosa*

Table 2. Results of manual pollination and control in *Capparis jacobinae* Moric. ex Eichler (Brassicaceae). ISI = Self-incompatible index.

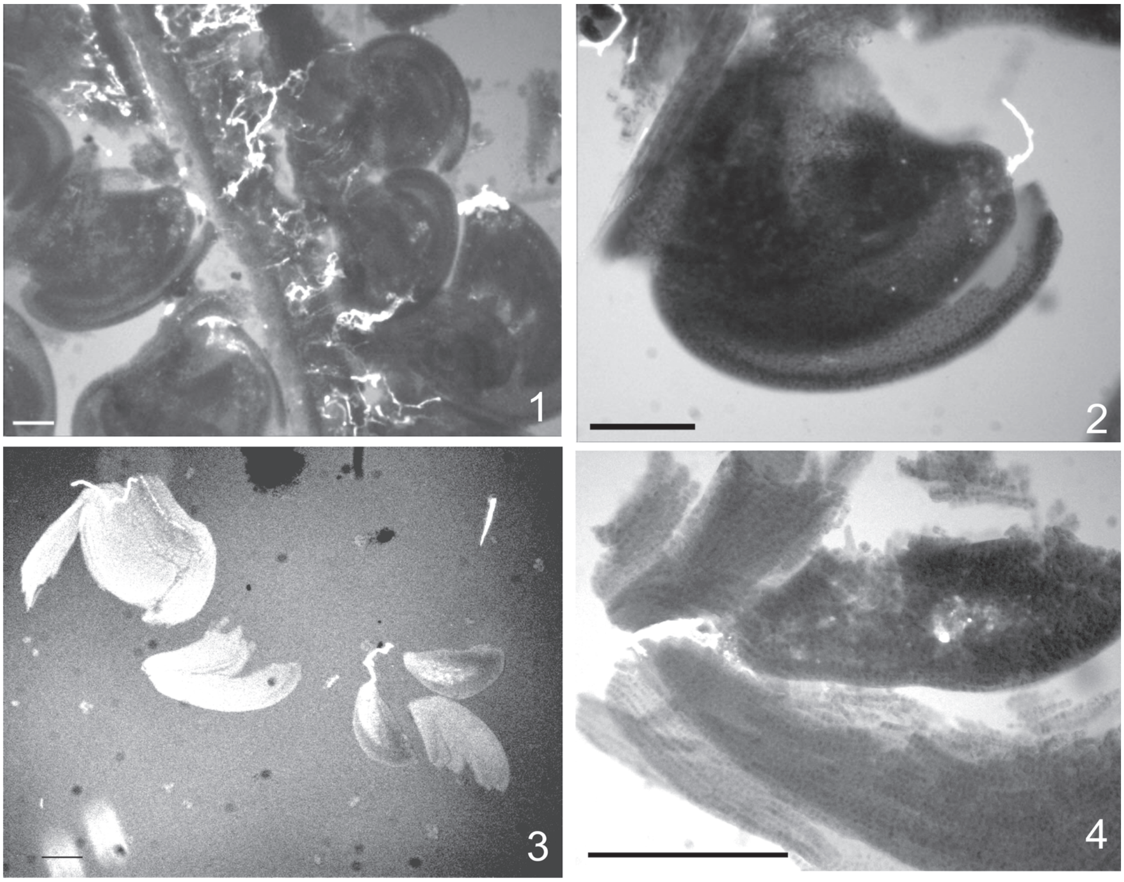
	Control	Spontaneous self-pollination	Apomixis	Manual self-pollination	Cross-pollination	ISI
Nº individuals	21	10	11	16	15	
Flowers/fruits	99/21	33/0	32/0	105/1	72/51	
(% success)	(21,21)	(0)	(0)	(0,95)	(70,83)	0,013
Average nº seeds/fruit*	13,55	—	—	—	17,15	

*The control was calculated with 18 fruits of 12 individuals; and cross-pollination was calculated with 13 fruits of nine individuals.

(Machado *et al.* 2006). Andromonoecy has been interpreted as a favorable sexual system when the pollination system requires huge amounts of pollen. This sexual system would have been developed in the plants' life history to increase the level of cross-pollination and recombination through higher resource allocation on paternal reproductive success (pollen donation) (Heithaus *et al.* 1974; Bawa & Beach 1981; Ramirez *et al.* 1984). Although the trimonoecious and andromonoecious individuals of *Cleome spinosa* are self-incompatible (Machado *et al.* 2006), Ruiz-Zapata & Arroyo (1978) recorded a strong association between andromonoecy and self-incompatibility in another tropical plant community.

The viability of pollen grains in *Capparis jacobinae* is high, not only in bisexual flowers (99.2 %) but also in staminate flowers (99.8 %), showing that both kinds of flower may be acting as pollen donors. Regarding the female function, there is an average of 30.5 ovules per hermaphrodite flower, with the P/O ratio = 108647.37 and the seed/ovule ratio = 0.44. According to Cruden (1977), this high P/O ratio is characteristic of xenogamous species. In the same way, according to the criterion of Wiens (1984), the seed/ovule ratio varies from 0 to 1, where the lowest values belong to allogamous species. A ratio of 0.44 would indicate that the seeds are produced mainly by cross-pollination. Bullock (1985) points out that a species is self-incompatible when it shows values of ISI < 0.25. Therefore, *C. jacobinae* has at least three characteristics that classify it as self-incompatible.

In *Capparis jacobinae*, both the ovules of flowers submitted to self-pollination and the ovules of flowers submitted to cross-pollination were reached by pollen tubes (Fig. 1-4). The abscission time in flowers submitted to self-pollination was similar; all fell between the eighth and the



Figures 1-4. Ovules of *Capparis jacobinae* Moric. ex Eichler (Brassicaceae) penetrated by pollen tubes (arrows) after pollination. 1-2. Self-pollination 96 h. 3. Cross-pollination 24 h. 4. Cross-pollination 96 h. Bars = µm.

tenth day after anthesis, except for two developing fruits, from the same individual, that fell 23 and 36 days after self-pollination (Fig. 5). Otherwise, the abscission of staminate and hermaphrodite flowers that have not been pollinated occurred between the third and the fifth day after anthesis (Fig. 5). Different from endogamous depression, in which the accumulation of many lethal recessive alleles causes the abscission of self-pollinated flowers, late-acting self-incompatibility (LSI) is an active recognition-rejection mechanism that is genetically controlled by a few loci (Lipow & Wyatt 1999; 2000).

However, we frequently observed chaotic growth of pollen tubes in pistils of self-pollinated flowers, which go in several directions before penetrating the micropyle (Fig. 1). The percentage of penetrated ovules differs ($\chi^2 = 4.53$; p= 0.03) among treatments during the first 24 h after pollination, when there are a higher number of ovules penetrated by pollen tubes originating from cross-pollination (Tab. 3).

Therefore, we recorded three reproductive features in *Capparis jacobinae* that place it in a late-acting self-incompatibility system: first, the abscission of self-pollinated flowers occurs even if the pollen tubes reach the embryonic sacs (cf. Fig. 1 and 2), a phenomenon that does not exist in the sporophytic and gametophytic systems. Similar results were observed in *Capparis pittieri* and in *C. retusa* (Seavey & Bawa 1986; Bianchi & Gibbs 2000), two species that exhibit LSI.

Second, the difference between the passive mechanism of endogamous depression and the mechanism of active rejection of LSI is that the abscission of all self-pollinated flowers occurs over a short period and in all populations (Seavey & Bawa 1986; Lipow & Wyatt 1999). In *Capparis jacobinae* we observed in both populations, during the two flowering episodes, that the self-pollinated flowers fell in a well-defined period, between the eighth and the tenth day (Fig. 5).

The third evidence to be considered is the rhythm of ovule penetration by pollen tubes after self-pollination and cross-pollination (Tab. 3), which is similar to other species that have the LSI mechanism, such as *Capparis retusa* (Capparaceae) (Bianchi & Gibbs 2000), *Chorisia chodatii* Hassl., *C. speciosa* St. Hill. (Bombacaceae), *Tabebuia caraiba* (Mart.) Bur., *T. ochracea* (Cham.) Standl. (Bignoniaceae) (Gibbs & Bianchi 1992), *Dolichandra cynanchoides* Cham., *Tabebuia nodosa* (Grisenb.) Grisenb. (Bignoniaceae) (Gibbs & Bianchi 1999) and *Spathodea campanulata* Beauv. (Bignoniaceae) (Bittencourt *et al*. 2003).

Therefore, because *Capparis jacobinae* is the third record of LSI within the genus, it reinforces the hypothesis that the late-acting self-incompatibility mechanism could be distributed among species from phylogenetically close groups (Gibbs & Bianchi 1999). New studies with this approach on *Capparis* species and on the family Brassicaceae may reveal new occurrences of LSI.

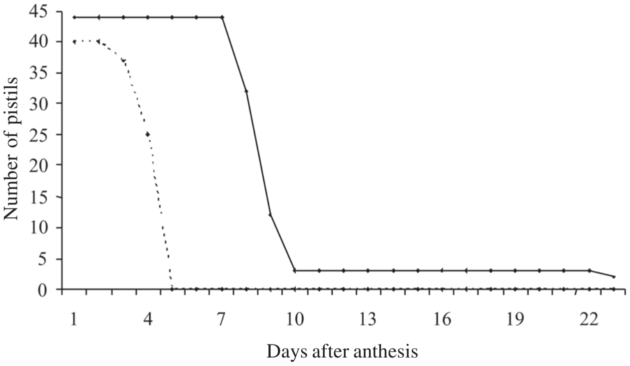


Figure 5. Abscission time of pistils of non-pollinated hermaphrodite flowers (.....) and of self-pollinated hermaphrodite flowers (——) in *Capparis jacobinae* Moric. ex Eichler (Brassicaceae).

Table 3. Percentage of ovules penetrated by pollen tubes in *Capparis jacobinae* Moric. ex Eichler (Brassicaceae), in accordance with two treatments carried out at different times after pollination (* hours after pollination).

Treatment	24*			48*			72*			96*		
	Ovaries (n.)	Penetrated ovules (%)	Non-penetrated ovules (%)	Ovaries (n.)	Penetrated ovules (%)	Non-penetrated ovules (%)	Ovaries (n.)	Penetrated ovules (%)	Non-penetrated ovules (%)	Ovaries (n.)	Penetrated ovules (%)	Non-penetrated ovules (%)
Self-pollination	6	7,3	92,7	4	33,03	66,97	5	63,9	36,1	5	68,2	31,8
	χ^2 = 4,53; p = 0,03			χ^2 = 0,99; p = 0,32			χ^2 = 0,37; p = 0,54			χ^2 = 1,03; p = 0,31		
Cross-pollination	5	16	84	4	43,6	56,4	4	73,1	26,9	5	88,8	11,2

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