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Floral morphology and reproduction mode determine feijoa (*Acca sellowiana*) as a facultative xenogamous species

*Morfologia floral e modo de reprodução determinam a feijoa (*Acca sellowiana*) como espécie xenógama facultativa*

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ABSTRACT
Different accessions from the active germplasm bank (São Joaquim, SC, Brazil) of feijoa or pineapple-guava (*Acca sellowiana*) were evaluated, with the aim of determining the number of pollen grains and ovules, including the pollen:ovule ratio and its association with the distance between stigma and stamens (SSD) and the distribution of stamens in the flower. The results demonstrated that 21.6%, 52.7% and 25.6% of the 73 accessions had an average SSD of less than 0.5 cm, 0.5 to 0.9 cm, and equal or more than 1.0 cm, respectively, thus fitting a 1:2:1 ratio among the three classes ($\chi 2 = 2.64$; $0.30<P<0.50$). An equal distribution of two types of stamens, radial and random, in the flower was also verified in a 1:1 ratio. This dual analysis also showed that the distribution of stamen types in the flower and SSD classes occurs independently. Radial type flowers had an average of 47.4 anthers, while flowers with random distribution had an average of 67.7. In flowers with random stamen distribution, more ovules were observed, as well as higher pollen:ovule ratio compared to flowers with radial stamen distribution. These results suggest that *A. sellowiana* exhibits a xenogamous mode of reproduction with a predominance of allogamy.
Keywords: pineapple-guava, pollen/ovule ratio, stamen distribution, stigma stamen distance.

RESUMO
Foram avaliados diferentes acessos do banco de germoplasma ativo (São Joaquim, SC, Brasil) de feijoa ou goiabeira-serrana (*Acca sellowiana*), com o objetivo de determinar o número de grãos de pólen e óvulos, incluindo a relação pólen:óvulo e sua associação à distância entre estigma e estames (SSD) e a distribuição dos estames na flor. Os resultados demonstraram que 21,6%, 52,7% e 25,6% dos 73 acessos apresentaram SSD inferior a 0,5 cm, entre 0,5 e 0,9 cm e igual ou superior a 1,0 cm, respectivamente. Portanto, enquadram-se na proporção de 1:2:1 entre as três classes ($\chi 2 = 2{,}64$; $0{,}30<P<0{,}50$). Também se verificou a distribuição igual de dois tipos de estames (radial e aleatório), na flor, na proporção de 1:1. Essa dupla análise também mostrou que a distribuição dos tipos de estames nas classes de flor e SSD ocorre de forma independente. As flores do tipo radial tiveram em média 47,4 anteras, enquanto as flores com distribuição aleatória tiveram em média 67,7. Em flores com distribuição aleatória de estames, observaram-se mais óvulos, bem como maior proporção pólen:óvulo em comparação com flores com distribuição radial de estames. Os resultados indicam que *A. sellowiana* apresenta um modo de reprodução xenógama com predominância de alogamia.
Palavras-chave: distância estigma-estame, estames, goiabeira-serrana, razão pólen:óvulo.

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INTRODUCTION

Although native to southern Brazil and northern Uruguay, feijoa [*Acca sellowiana* (O. Berg) Burret synonymous *Feijoa sellowiana*], known as goiabeira-serrana (Brazil) or guayabo del país (Uruguay) in its center of origin and pineapple-guava in other places, is still sparsely cultivated compared to other regions, such as Colombia and New Zealand, the two largest producers of the fruit in the world. However, feijoa plantings are increasing in both Santa Catarina and Rio Grande do Sul, southern states of Brazil, with the increasing availability of improved varieties (SANTOS *et al.*, 2022b). In this context, growers should understand its reproduction mode for breeding, in order to manage fruit production in a manner that yields high profit.

The flowering of feijoa occurs in October and November on the Santa Catarina plateau. As described by Mattos (1986) and Ramírez & Kallarackal (2017), feijoa flower buds appear singly or in clusters, with a maximum of five units, and are characterized by their pea grain-sized globulous shape. Its ornate flowers consist of four discreet sepals and four fleshy and deeply curved hood-shaped petals, white on the outside and glittery.

Considering the flower's morphology, an important factor for pollination is the distance between the stigma and stamens (SSD), implying the attraction of exclusive pollinators (DEGENHARDT *et al.*, 2001). More specifically, pollinating agents with smaller body sizes, such as domestic bees and native species of the Meliponini tribe, which is characterized by small workers, would be more suitable for accessions that present smaller distances between stigma and stamens. In this case, access points with distances of up to 0.4 cm would be suitable for smaller pollinators, whereas SSD outside this range would accommodate a greater diversity of pollinators, such as birds.

In addition to this characteristic, the arrangement of stamens in the flower is also variable and may occur radially or randomly. This fact could also affect pollination, since flowers with radially arranged stamens may be located closer to the stigma, making it more likely that insects collecting pollen grains from anthers would come in contact with the stigma. Furthermore, the arrangement of the stamens in the flower and the distance between the stigma and stamens are neither variable within plants nor dependent on the phenological stage of the flower (DUCROQUET *et al.*, 2000; DEGENHARDT *et al.*, 2001).

To be selected as a new cultivar, one plant must show characteristics superior to other plants of the same species in its natural state, in terms of productivity and production stability. In addition, usually, for an allogamous species, such as feijoa, cross-pollination can provide the required physiological vigor and increment in seed and fruit production. Previous reports demonstrated that while the percentage of formed fruit per 100 flowers (fruit set) in branches excluding pollinators was 5.1% or less, fruit set in the branches with free access to pollinators varied between 10.4% to 90.9% (SANTOS *et al.*, 2022a). In addition, the number of seeds and pulp yield are positively correlated in hand self-pollination (SÁNCHEZ-MORA *et al.*, 2022). Thus, pollination is a crucial issue in the reproductive biology of this species.

Previously, Degenhardt *et al.* (2001) evaluated the distance between the stigma and stamens and the arrangement of the stamens in the flower for 15 genotypes of feijoa. However, the present study was done with five times more genotypes and additional traits related to the mode of reproduction. Currently, the Active Germplasm (AGB) maintained by Santa Catarina State Agricultural Research and Rural Extension Agency (Epagri), which is located at the Experimental Station of São Joaquim, Santa Catarina, holds 313 characterized accessions that can be used to perform basic studies and breeding (SAIFERT *et al.*, 2020). Taking advantage of this resource, the present study aimed to determine: 1) the variation in the distance between stigma and stamens, 2) the pattern of distribution of stamens in the flower, and 3) the number of pollen grains and ovules in flowers of different accessions of feijoa from the AGB of São Joaquim.

MATERIAL AND METHODS

STUDY AREA

The bioassays were carried out at the São Joaquim Experimental Station (EESJ), which is part of the Epagri, situated at an altitude of approximately 1,350 m, latitude of 28°16’ 40S and longitude of 49°56’ 09 W (EPAGRI, 2025). Average annual temperature is 13.5°C, and average annual precipitation is 1,585 mm (EPAGRI, 2025). Soil can be characterized as humic, dystrophic, alic Cambisol, clayey texture, basaltic substrate (SANTOS *et al*., 2013). The surroundings of the Feijoa Active Germplasm Bank (AGB) exhibit secondary vegetation in an advanced stage of succession, including adult *Araucaria angustifolia* trees on two sides, an area covered with native grassland on the third side, and physical facilities of the experimental area on the fourth side, which borders the city of São Joaquim.

GERMPLASM

From the Feijoa AGB collections (SAIFERT *et al*., 2020), 73 accessions were used for the floral morphology characterization in the present study. Each accession consists of three plants originating from vegetative propagation, spaced 3 m in a row and 5 m between rows.

MORPHOLOGY OF STIGMAS AND ANTHERS

Initially, the distance between the stigma and stamen (SSD) was measured in 30 flowers taken at random from each of the 73 accessions. According to SSD values, the accessions were classified as small – from 0 to 0.4 cm, medium – from 0.5 to 1.0 cm, or large – larger than 1.0 cm, as proposed by Degenhardt et al. (2001). Afterwards, the distribution patterns of the stamens in the same flowers were classified as random or radial. Statistical analysis consisted of mean and standard deviation of SSD values in 30 flowers of each accession and the χ^2 test to assess: (a) whether the proportion was (a) 1:1:1 or 1:2:1 in the three SSD classes; (b) whether the proportion was 1:1 in the stamen distribution patterns and (c) if these two variables could be considered independent.

NUMBER OF ANTHERS, POLLEN GRAINS AND OVULES

The number of pollen grains was estimated in flowers in nine accessions, three of each SSD class, totaling 27 plants. Using a methodology similar to that proposed by Kearns & Inouye (1993), four flowers were collected from each accession, and the number of stamens was counted in each flower. Then, five anthers were collected from each flower, stored individually in 1.5 ml tubes, and diluted in 1.0 ml of 85% lactic acid. In the laboratory, the four 1.5 µL samples were then collected with the aid of a micro-pipette. Each sample was placed on a slide, and all pollen grains were counted under an optical microscope at 100x magnification. The number of pollen grains in each anther (N) was estimated by multiplying the average number of pollen grains in the anther sample (X) by the volume of lactic acid in which the dilution was carried out (1000 ml) and then, dividing this value, is the product between the volume of lactic acid in the sample (1.5 ml) and the number of anthers in each tube (5). This calculation is given as N = X.133.33. To estimate the number of pollen grains produced per flower, the average number of pollen grains per anther was multiplied by the number of anthers per flower.

POLLEN:OVULE RATIO

The pollen:ovule ratio was determined in flowers of nine accessions, three from each SSD class and respective anthers. Four flowers were collected from each accession, and then the ovary was removed from each flower, placed in a plastic bag, and stored in a refrigerator. Under a glass slide, each gynoecium was cut into four transverse slices, and from each of the four sections, all ovules were counted under a microscope. The number of ovules counted in each section was added together to get the total number per flower. To calculate the pollen: ovule ratio, we followed Cruden (1977), who used the following formula: P/O= average number of pollen grains per flower/number of ovules.

The mean and standard deviation for the number of stamens, pollen grains and ovules per flower were estimated. The data, stratified or not by SSD class and type of stamen distribution in the flower, were also subjected to Analysis of Variance and the SNK 5% mean separation test (SOKAL & ROHLF, 1981).

RESULTS

DISTANCE BETWEEN STIGMA AND STAMENS AND DISTRIBUTION OF STAMENS IN THE FLOWER

The distance between stigma and stamens, as determined in 30 flowers collected from 73 AGB accessions in São Joaquim, varied from 0.2 to 1.3 cm. Based on standard deviation values, the variation between flowers on the same plant was relatively small (table 1). Then, grouping the accessions by distance class between stigma and stamens, the results demonstrated that 20.5% had an average distance of less than 0.5 cm. Most accessions (52.1%) presented an intermediate distance, and 27.4% presented an average distance greater than 1.0 cm (table 2).

Deviations of the three SSD classes to the 1:1:1 proportion were statistically significant (χ^2= 12.03; P<0.005), indicating that SSD is proportionally different. Indeed, the 1:1:1 ratio had previously been found by Degenhardt et al. (2001), albeit in a reduced sample of 15 accessions. Our alternative ratio of 1:2:1 revealed that the deviations were not statistically significant in data collected in the present study (χ^2 = 0.81; 0.50<P<0.90), confirming that one half of the tested feijoa accessions belong to the SSD medium class with intermediate distance values between stigma and stamens.

Table 1 – Mean and standard deviation of distance between stigma and stamens (SSD) evaluated in 30 flowers from 73 accessions from the Feijoa Active Germplasm Bank, São Joaquim, SC.

Accession #	Provenance	SSD (cm)	Accession #	Provenance	SSD (cm)
50	Videira	0.68±0.11	277	São Joaquim	1.00±0.11
50[A]	Fraiburgo	0.70±0.10	291	São Joaquim	0.50±0.07
53	Videira	0.90±0.10	294	Lages	0.90±0.10
66	Caçador	0.80±0.08	300	São Joaquim	0.25±0.08
79	Frei Rogério	0.40±0.09	301	Lages	0.30±0.11
85	Campos Novos	1.15±0.16	321	Lages	0.70±0.09
98	Videira	0.57±0.10	331	Lages	1.10±0.10
99	Videira	0.80±0.08	332	Lages	0.90±0.08
101	Lages	0.70±0.07	370	Bom Jardim	0.86±0.13
103	São Joaquim	0.40±0.10	373	Bom Jardim	0.50±0.07
110	São Joaquim	0.7±0.10	374	Bom Jardim	0.22±0.09
117	São Joaquim	0.50±0.07	376	Lages	0.67±0.09
118	São Joaquim	1.10±0.12	377	Bom Jardim	0.70±0.08
119	São Joaquim	0.90±0.11	379	São Joaquim	1.00±0.07
124	São Joaquim	0.40±0.09	387	São Joaquim	0.80±0.08
124[A]	São Joaquim	1.20±0.16	393	Videira	0.40±0.12
125	São Joaquim	1.19±0.16	401	Lages	1.10±0.13
135	Videira	0.50±0.09	451	Nova Zelândia	1.30±0.12
138	Lages	0.50±0.08	452	Califórnia	1.00±0.07
138[A]	Lages	0.40±0.13	453	USA	1.30±0.13

to be continued...

Continuation of table 1

Accession #	Provenance	SSD (cm)	Accession #	Provenance	SSD (cm)
141	Tangara	1.24±0.14	456	Nova Zelândia	1.10±0.11
148	Fraiburgo	0.30±0.09	457	Nova Zelândia	1.00±0.07
152	Ponte Alta	0.80±0.09	501	Fraiburgo	1.00±0.06
159	Palmas	0.60±0.10	504	Fraiburgo	0.40±0.11
212	Lages	1.00±0.13	508	Caçador	0.40±0.07
222	Lages	0.75±0.09	509	Videira	0.62±0.08
223	Painel	1.10±0.13	511	Caçador	0.50±0.09
229	Lages	0.34±0.12	512	Caçador	0.65±0.09
231	Urupema	0.90±0.10	520	Fraiburgo	0.80±0.07
240	Urupema	0.90±0.10	521	Fraiburgo	0.40±0.09
242	Urupema	0.70±0.07	522	Caçador	0.60±0.07
244	Urupema	0.40±0.07	528	Videira	0.70±0.08
247	Painel	0.80±0.08	707	Lebon Régis	0.80±0.09
249	Lages	0.80±0.07	735	Curitibanos	0.50±0.09
250	Lages	0.70±0.08	740	Ponte Alta	0.30±0.08
260	Painel	1.10±0.11	755	Papanduvas	1.20±0.14
276	Lages	1.20±0.10			

An equal radial and random distribution of stamens was found, fitting a proportion of 1:1 (χ^2 = 0.013; 0.90<P<0.95) (table 2).

Dual analysis of the two characteristics revealed that SSD is equally distributed between the radial and random pattern of stamens (table 2). In addition, the three SSD classes and the stamen distribution were segregated independently (χ^2=0.959; 0.50<P<0.90).

Table 2 – Number of accessions by distance between stigma and stamens (SSD) and by distribution of stamens in the flower, São Joaquim, SC.

SSD	Range (cm)	Number of accessions	Number of accessions per stamen pattern of distribution	
			Radial	Random
Small	0 – 0.4	15	7	8
Medium	0.5 – 0.9	38	18	20
Large	1.0 – 1.4	20	12	8
Total		73	37	36

NUMBER OF ANTHERS, POLLEN GRAINS AND OVULES

Analysis of Variance (data not shown) revealed statistical significance for both number of anthers and pollen:ovule ratio in the context of stamen distribution pattern in the flower, but not in the different SSD classes. Average values for the number of pollen grains were statistically significant not only among SSD classes but also between radial and random stamen distribution in the flower. The number of ovules was statistically significant among SSD classes. Out of these four characteristics evaluated, we identified a significant interaction between SSD classes and type of stamen distribution and the number of anthers.

When stamen distribution is radial, the average number of anthers per flower was 67.7, statistically higher than when stamen distribution is random in the flower with an average of 47.4 anthers (table 3). However, no statistically significant difference was observed between the average number of anthers per flower for the three SSD classes.

The average number of pollen grains per flower ranged from 436,800 to 1,925,333 (n=36). Flowers with stamens distributed randomly throughout the flower produce more pollen grains

(1,105,938) than flowers with stamens distributed radially (732,927). This difference is statistically significant based on the greater number of anthers that occur in flowers with randomly distributed stamens (table 3).

Table 3 – Average number of anthers, pollen grains, ovules and pollen grains:ovule ratio relative to SSD and type of stamen distribution in the flower (n = 36).

STAMEN DISTRIBUTION IN THE FLOWER						
	Anthers per flower			**Pollen grains per flower (*1000)**		
SSD	Random	Radial	Average	Randon	Radial	Average
Small	63.7aA	43.2bB	53.5A	1027.0	706.4	866.7B
Medium	59.6aA	52.2bA	55.9A	976.0	541.5	758. B
Large	61.7aA	46.7bAB	54.2A	1314.8	950.9	1132. A
Average	61.7a	47.4b	54,5	1105.9a	732.9b	919.4
CV (%)		9.9%			24.2%	

	Ovule per flower			**Pollen:ovule ratio**		
SSD	Random	Radial	Average	Random	Radial	Average
Small	225.5	191.0	208.2B	4554.4	3698.3	4180.4A
Medium	215.0	181.0	198.0B	4539.4	2991.9	3903.1A
Large	260.0	264.7	262.3A	5057.1	3592.3	4398.3A
Average	233.5a	212.2a	222,8	4810.2a	3511.0b	4160.6
CV (%)		16.8%			29.3%	

Means followed by different letters, lowercase in rows and uppercase in column, within the same characteristic differ statistically by the Student–Newman–Keuls (SNK) 5% test. Distance between stigma and stamens.

On the pistil, the number of ovules per flower varied from 144 to 304 (n=36), which is indicative of the seed production potential of these plants for the next generation. As an example of the greater quantity of pollen grains, the large SSD class presented mean values for the number of ovules per flower (262) significantly higher than the means of the other two classes, which were not statistically significant between them.

POLLEN:OVULE RATIO

The average pollen:ovule ratio was 4160.6 (table 3). Flowers with radial stamen distribution have a lower number of ovules per flower, as well as a lower pollen:ovule ratio than flowers with a random stamen distribution. It will be recalled that the number of anthers, number of pollen grains per anther and number of ovules were statistically significant for the three classes of SSD. However, no statistically significant difference was found in pollen:ovule ratio between flowers with different SSD and number of anthers.

DISCUSSION

DISTANCE BETWEEN STIGMA AND STAMENS AND DISTRIBUTION OF STAMENS IN THE FLOWER

Since the variation of the SSD values between flowers on the same plant was relatively small, it is possible to infer phenotypic homogeneity on this characteristic in the same feijoa plant, thus allowing the classification of plants based on these distances. Our study confirmed previous ones regarding the existence of three phenotypic classes of SSD (DEGENHARDT *et al.*, 2001).

However, the data generated by the present work showed statistical deviations in the 1:1:1 proportion among the SSD classes, previously found by Degenhardt *et al.* (2001). The alternative ratio of 1:2:1 emerged probably because the sample size in the present study was larger (n=73) than the previous one by (n=15; DEGENHARDT *et al.*, 2001). In addition, in the present study, there were representatives from both the feijoa types, Brazilian and Uruguayan (SAIFERT *et al.*, 2020). Thus, most of the Feijoa AGB accessions belong to the SSD medium class, with intermediate distance values between stigma and stamens.

Regarding the radial and random distribution of stamens, our results fit a proportion of 1:1, which did not differ from previous studies in the same trait (DEGENHARDT *et al.*, 2001). Thus, feijoa follows the most common pattern in angiosperms, i.e., the occurrence of a reduced number of stamens arranged radially in the flower (ENDRENS, 1994).

NUMBER OF ANTHERS, POLLEN GRAINS AND OVULES

Usually, each stamen in the analyzed flowers contained only one anther. However, it is not uncommon to find stamens with two anthers. Owing to the appearance of the flower and the number of anthers, the feijoa flower could be classified as a “brush-flower” type flower that can be pollinated by birds (PROCTOR *et al.*, 1996).

The number of anthers, ovules and pollen grains in feijoa flowers was variable, being a difference of 4.4 times between the higher and lowest value. In flowers with radial stamen distribution, the average number of anthers per flower was higher than when stamen distribution was random.

While the number of anthers per flower was not distinct among the three SSD classes, the number of anthers per flower was fewer in flowers with radial distribution type, compared to flowers with randomly distributed stamens. In fact, the flowers of plants in the large SSD class have a statistically higher number of pollen grains than those found in the two other SSD classes. No plausible biological reason for this has been advanced. However, our working hypothesis is that this could be associated with one or more characteristics, such as color intensity or sugar content of the petals (not yet evaluated), which would be attractive to pollinating birds. We also point out that a greater number of anthers is not always indicative of a greater number of pollen grains per flower. This is evident for flowers in the medium SSD class with radial distribution of stamens.

In the present study, the number of pollen grains per flower was lower than the values found in other myrtaceous species (FIDALGO & KLEINERT, 2009), such as *Eugenia speciosa*, but 2.2, 7.2, 8.1, 29.0 and 180 times higher when compared to *Gomidesia schaueriana*, *Myrcia splendens*, *Psidium cattleyanum*, *Myrcia. racemosa* and *M. multiflora*, respectively. Compared to other species of *Psidium* genus reported by Oliveira *et al.* (2021), the number of pollen grains per feijoa flower was 5 to 6 times fewer than that found in *P. guajava*, but similar or higher than the distinct *Psidium cattleyanum*, and *P. guineense* genotypes.

Similarly, the number of ovules per flower obtained in feijoa flower in the present study was higher than the number of ovules per flower found in other Myrtaceae species reported by Fidalgo & Kleinert (2009), e.g., *E. speciosa* (5), *G. schaueriana* (8), *M. multiflora* (7), *M. racemosa* (9), *M. splendens* (4), and *P. cattleyanum* (127). Given the variation among and within *Psidium* species (OLIVEIRA *et al.*, 2021), the number of ovules per flower we found in feijoa was similar, higher or half that of *P. guineense*, *P. cattleyanum* and *P. guajava*, respectively. Overall, the number of ovules per flower in feijoa found in the present work fit the range reported by other species and genera of the Myrtaceous family.

Taking into account the results obtained in the present work, *Acca sellowiana* can be included among the species that have numerous ovules per flower. Species with few ovules per flower require a smaller load of pollen grains deposited on the stigma when compared to species with numerous ovules (RAMÍREZ, 1995).

POLLEN:OVULE RATIO

The pollen:ovule ratio values obtained in feijoa flower in the present study were smaller than those of *E. speciosa* (58250), *G. schaueriana* (50630), *M. splendens* (31630) and *M. racemosa* (7920), but higher than the values found in *M. multiflora* (1290) and *P. cattleyanum* (900) (FIDALGO & KLEINERT, 2009).

Pollen:ovule ratio is typically related to the mode of pollination and the reproductive system, since an increase in the number of pollen grains in plants with cross-pollination can substantially benefit their reproductive success, as a component of the fitness, mainly for an allogamous species (BERTIN, 1989) like feijoa. In this context, Oliveira *et al.* (2021) classified *P. cattleyanum* and *P. guajava* as having a xenogamous mode of reproduction since the pollen:ovule ratio exhibited by distinct genotypes for each species varied from 3,900 to 24,000 and from 5,300 to 8,100, respectively. The same authors also attributed the facultative xenogamous mode of reproduction to *P. guineense* based on its pollen:ovule ratio close to 2,000. Similarly, Fidalgo & Kleinert (2009) classified *P. cattleyanum* (pollen:ratio = 900) as facultative xenogamous.

Xenogamous species have a greater number of pollen grains than autogamous species and, thus, have a higher pollen:ovule ratio. According to the classification of Cruden (1977), a species that has a pollen:ovule ratio similar to that of feijoa can be classified as facultative xenogamous, in that it will preferentially cross-pollinate but may also exhibit self-compatibility. This is the case of feijoa since it showed a late self-incompatibility system (FINATTO *et al*., 2011) in 53.3% of the accessions maintained in the Active Germplasm Bank (n=313), while 46.7% were self-compatible with different degrees of self-compatibility based on the number of formed fruits (SÁNCHEZ-MORA *et al*., 2022).

CONCLUSION

Based on the obtained results, it is possible to separate feijoa accessions according to the distances between stigma and stamens into three distinct classes. The distances between stigma and stamens were in the proportion of 1:2:1, revealing that most of the accessions belong to the intermediate distance class.

The flowers presented two forms of stamen distribution, radial and random, and these occurred in a 1:1 ratio. The distance between stigma and stamens and the distribution of stamens in the flower occur independently.

The number of anthers and pollen grains per flower varied according to the distribution of stamens. Random-type flowers have more anthers and pollen grains than flowers with a radial distribution of stamens. Based on pollen:ovule ratio, feijoa, like most myrtaceous species, can be classified as having a facultative xenogamous mode of reproduction.

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CONTRIBUTION OF AUTHORS

CF, AIO and RON planned and designed the experiments. CF performed field evaluations. CF and MRF performed data analyses. CF, MRF and RON wrote the first draft of the manuscript. RON and AIO controlled the funding acquisition. All authors revised and contributed to the submitted version of the manuscript.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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