Article

POLLEN LIMITATION AND DEPENDENCE ON CROSS-POLLINATION IN BORAGE (*BORAGO OFFICINALIS* L.) IN THE PAMPAS REGION OF ARGENTINA

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Abstract—*Borago officinalis* L. is an insect-pollinated crop valued for its seed oil. While described as self-compatible, the extent to which its reproductive success depends on pollinator-mediated cross-pollination and whether it experiences pollen limitation in agricultural settings remain key questions for its sustainable cultivation. We experimentally evaluated the effect of five pollination treatments (natural pollination, autonomous self-pollination, artificial cross-pollination, anemophily, and apomixis) on fruit set and nutlet number in a borage experimental population in the Pampas region of Argentina. Artificial cross-pollination yielded the highest reproductive output, while autonomous self-pollination (including possible geitonogamous pollen transfer) and anemophily produced intermediate and similar results. Artificial cross-pollination increased fruit set by 284% and nutlet number per fruit by 338% compared to natural pollination, demonstrating strong pollen limitation despite the presence of managed honeybees. Apomixis was negligible. Our findings demonstrate that *B. officinalis* relies on cross-pollination to maximize reproductive success and that even in the presence of managed honeybees, pollen limitation can significantly reduce yield. This highlights the need to ensure adequate pollinator services for the cultivation of this species.

Keywords—Pollinators, yield, reproductive biology, oil crop

INTRODUCTION

Global demand for vegetable oils with specific nutritional and industrial properties has increased interest in specialty oilseed crops. Among these, borage (*Borago officinalis* L.), an annual herb native to the Mediterranean region (Asadi-Samani et al. 2014; Giménez & González Vera 2020), is valued for its seed oil rich in gamma-linolenic acid (GLA), an essential fatty acid with pharmaceutical, nutraceutical, and cosmetic applications (Montaner et al. 2000; Berti et al. 2002; Chiroque-Reyes et al. 2024). The plant produces actinomorphic, hermaphroditic flowers grouped in scorpioid cymes, each capable of developing up to four one-seeded nutlets (Osborne 1999).

However, maximizing seed yield in borage remains challenging due to two major factors: premature fruit abscission leading to seed loss (Montaner et al. 2002), and a strong dependence on insect pollinators. Although borage is self-compatible, its reproduction is characterized by marked protandry, as anthers dehisce before the stigma becomes receptive, which favours cross-pollination and limits autonomous selfing within individual flowers (Stawiarz et al. 2020; Montaner et al. 2000). Yet geitonogamous pollination among flowers of the same plant, facilitated by pollinator movement, can result in significant selfing rates (Montaner et al. 2001). The species is primarily entomophilous, with bees, particularly the European honeybee (*Apis mellifera*), as its main pollinators, attracted by nectar and pollen rewards (Giménez & González Vera 2020; Stawiarz et al. 2020). Consequently, inadequate pollination service may limit fruit and seed set, a phenomenon known as pollen limitation, which can constrain yields even in self-compatible crops and often necessitates the placement of honeybee hives near crops (NNFCC 2008; Falasca & Bernabé 2012; Stawiarz et al. 2020). Quantifying the extent of this limitation and the crop's dependence on pollinators is therefore essential for designing effective agronomic management, including decisions about pollinator conservation and hive placement.

In Argentina, borage is naturalized in several provinces (Falasca & Bernabé 2012), yet its reproductive biology and pollination requirements under local conditions remain largely unstudied. This knowledge gap hinders the development of evidence-based management practices to maximize seed production for the growing GLA market and to support pollinator conservation. To address this, the general objective of this study was to characterize the reproductive biology of borage under local cultivation conditions and to evaluate the contribution of insect pollination to its reproductive success. The specific objectives were: (1) to characterize the reproductive system of borage by evaluating the plant's capacity to form fruits with seeds via apomixis, autonomous self-pollination, cross-pollination, wind pollination, or insect pollination (see Box 1 for definitions); and (2) to evaluate in detail the dependence of different yield components (fruit set and number of nutlets per fruit) on pollination by floral visitors.

Box 1. Key reproductive biology terms used in this study

Apomixis: A reproductive process in which seeds are formed without meiosis or fertilization, resulting in offspring genetically identical to the maternal plant.

Autonomous self-pollination (autogamy): Fertilization of ovules by pollen from the same flower, occurring without the involvement of pollinators or external pollen vectors.

Geitonogamy: Transfer of pollen between different flowers of the same individual plant; although functionally a form of selfing, it typically depends on pollinators and can influence mating patterns and genetic diversity.

Xenogamy (cross-pollination): Transfer of pollen between flowers of different individuals, resulting in outcrossing and increased genetic recombination.

Anemophily: Pollination mediated by wind, involving the passive transport of pollen grains through the air from anthers to stigmas.

MATERIALS AND METHODS

STUDY SITE AND PLANT MATERIAL

The study was conducted during the spring and summer of 2010 at the experimental field of the Faculty of Agronomy, University of Buenos Aires (FAUBA) (34°35'37"S, 58°29'07"W), located in the Rolling Pampas region of central Argentina. The area has a temperate humid climate with mean annual temperatures around 17 °C and average annual precipitation close to 1000 mm, mainly concentrated in spring and summer. Soils in the region are deep and fertile Mollisols typical of the Pampas, supporting intensive agricultural production.

The experimental field is located in a landscape with active apiculture. During the study period, approximately 40 managed honeybee (*Apis mellifera*) colonies were present within 400 m of the experimental plot (L. Landi and A. Basilio, personal communication, March 2026), and no other commercial apiaries were established in the immediate vicinity.

Twenty borage plants were cultivated from seeds manually collected in autumn 2010 from a spontaneous population in Marcos Paz (Buenos Aires Province, Argentina). Seeds were stored at room temperature in sealed glass jars until use.

For the experiment, seeds were sown in trays with sterilized soil under controlled temperature and humidity conditions until reaching the seedling stage with three to four well-expanded true leaves. This stage ensures robust seedlings capable of withstanding transplanting. Subsequently, they were transplanted to an experimental plot of 8 m × 2 m with a spacing of approximately 50 cm between plants.

EXPERIMENTAL DESIGN AND POLLINATION TREATMENTS

To quantify the contribution of different pollination mechanisms to the reproductive success of *B. officinalis*, we implemented a series of experimental treatments designed to isolate each potential pathway. This methodology, standard in reproductive biology studies (Dafni et al. 2005; Kearns & Inouye 1993), allows us to characterize the species' reproductive system and evaluate its dependence on pollinators.

Borage flowers are protandrous: anthers dehisce at anthesis (male phase), while the stigma becomes receptive approximately 24 h later, after the style has elongated (Montaner et al. 2001; Stawiarz et al. 2020). Receptivity lasts 1–2 days. The experimental design consisted of five pollination treatments, each aimed at isolating a specific reproductive mechanism.

Treatments were randomly assigned to either individual flowers or entire inflorescences, depending on the treatment (see below). For manipulative treatments requiring daily access (artificial cross-pollination and apomixis), inflorescences were covered with exclusion bags (made of non-woven material Tyvek®) before any flowers had opened. Bags were removed daily to check for newly opened flowers. Upon opening (anthesis, defined as fully opened flowers with completely expanded corolla and freshly dehisced anthers), each flower was tagged and subjected to its designated treatment. For bagged treatments applied to entire inflorescences (anemophily and autonomous self-pollination), selected inflorescences were covered with the corresponding bags (wide-mesh net or exclusion, respectively) before anthesis and remained covered throughout the experiment. The five treatments were as follows:

- Artificial cross-pollination (xenogamy): Flowers were emasculated at anthesis (day 1) by removing anthers with sterile forceps to prevent self-pollination. On the following day (day 2), when stigmas had become receptive, they were manually pollinated using a brush loaded with pollen mixed from freshly dehisced anthers of at least three different donor plants.
- Apomixis: Flowers were emasculated at anthesis (day 1) and immediately covered with exclusion bags; they remained bagged throughout the experiment.
- Autonomous self-pollination (autogamy): Flowers were covered before anthesis with exclusion bags that prevent insect access but allow air exchange, and left undisturbed.
- Anemophily: Flowers were covered before anthesis with wide-mesh net bags (≈ 2 mm) designed to exclude insects while permitting airflow and potential wind-borne pollen.
- Natural pollination (control): Flowers were tagged at anthesis and left fully exposed to ambient pollinators and wind.

Each treatment was replicated across multiple flowers per plant to account for individual variability. Due to differences in experimental approach, the number of flowers per plant varied among treatments. For treatments applied to entire inflorescences (anemophily and autonomous self-pollination), all flowers within the selected inflorescences were included. Based on the number of inflorescences used per plant (approximately 3–4 for anemophily and 2–3 for autonomous self-pollination) and the total flower counts per treatment, this resulted in an average of 38.1 flowers per plant for anemophily and 22.9 for autonomous self-pollination. For manipulative treatments requiring individual flower handling (artificial cross-pollination and apomixis), flowers were treated as they opened on previously bagged inflorescences, yielding an average of 17.6 flowers per plant for artificial cross-pollination and 7.6 for apomixis. For natural pollination, individual flowers were tagged at anthesis across the plants, averaging 6.9 flowers per plant.

The total number of replicates (flowers) per treatment was: Apomixis (N = 152), Autonomous Self-Pollination (N = 457), Anemophily (N = 762), Natural Pollination (N = 138), and Artificial Cross-Pollination (N = 352). This disparity was incorporated and controlled for statistically using mixed models.

DATA COLLECTION AND ANALYSIS

At fruit maturity, before nutlet abscission, we manually harvested all marked fruits and recorded reproductive data from each flower in the different treatments.

For each treated flower, two reproductive variables were recorded:

- Presence or absence of fruit set (binary variable: 0 = no fruit, 1 = with fruit).
- Number of nutlets per fruit (count variable).

For the fruit set, a generalized linear mixed model (GLMM) with a binomial distribution and logit link was used. The model included 'treatment' (five levels) as a fixed effect and a random intercept for 'maternal plant' to model the dependence between flowers from the same plant.

Parameter estimation was performed by maximum likelihood with Laplace approximation.

Since one treatment exhibited near-perfect success (probability close to 1), inference focused on the marginal means of each treatment on the probability scale. We report 95% confidence intervals for these probabilities and performed pairwise comparisons with Sidak adjustment; both tests and intervals were obtained on the same probability scale to ensure coherence.

For the number of nutlets, a Poisson GLMM with a log link and the same random intercept for maternal plant was fitted. Model adequacy was verified using diagnostics based on simulated residuals (uniformity, outliers, and dispersion), and the absence of relevant overdispersion was confirmed.

For both response variables (fruit set and number of nutlets), the global effect of the treatment was assessed using a likelihood ratio test (LRT), comparing the model with the treatment to a null model maintaining the same random effect structure (χ^2 with 4 d.f.). To assess the explanatory power of the models, we calculated marginal and conditional R^2 values following the method of Nakagawa and Schielzeth (2013) for generalized linear mixed models.

All analyses were performed in the R statistical environment (R Core Team 2024), using the packages glmmTMB (v. 1.1.13; Brooks et al. 2017), DHARMa (v. 0.4.7; Hartig 2024), emmeans (v. 2.0.2; Lenth & Piaskowski 2026), multcomp (v. 1.4.30; Hothorn et al. 2008), multcompView (v. 0.1-11; Graves et al. 2026), and MuMIn (v. 1.48.11; Bartoń 2025).

RESULTS

The effects of five pollination treatments on the reproductive success of *B. officinalis* were evaluated based on data from 1,861 flowers across 20 maternal plants. The pollination treatment had a highly significant overall effect on both the probability of fruit set (Likelihood Ratio Test: χ^2 = 1007.2, $P < 0.001$; Table 1) and the number of nutlets per fruit (LRT: χ^2 = 1301.8, $P < 0.001$; Table 2).

FRUIT SET

The probability of fruit formation varied significantly among treatments (Binomial GLMM with random maternal plant effect; Fig. 1 & Table 1). Artificial cross-pollination resulted in a probability of fruit set that was significantly higher than all other treatments (pairwise differences in probability between 0.740 and 0.989, $P < 0.0001$

Table 1. Results of the Generalized Linear Mixed Model (GLMM) for the probability of fruit set in *Borago officinalis*. Estimates are on the logit scale.

Treatment	Estimate	SE	Z	P
Apomixis	-2.229	0.735	-3.03	0.002
Autonomous self-pollination	-2.279	0.219	-10.411	<0.001
Anemophily	0.542	0.29	1.87	0.061
Natural pollination	1.235	0.193	6.387	<0.001
Artificial cross-pollination	24.905	4057.184	0.006	0.995

Table 2. Results of the Generalized Linear Mixed Model (GLMM) for the number of nutlets per fruit in *Borago officinalis*. Estimates are on the log scale.

Treatment	Estimate	SE	Z	P
Apomixis	-2.665	0.717	-3.72	<0.001
Autonomous self-pollination	-1.728	0.124	-13.984	<0.001
Anemophily	0.294	0.205	1.433	0.152
Natural pollination	1.12	0.125	8.944	<0.001
Artificial cross-pollination	2.597	0.12	21.572	<0.001

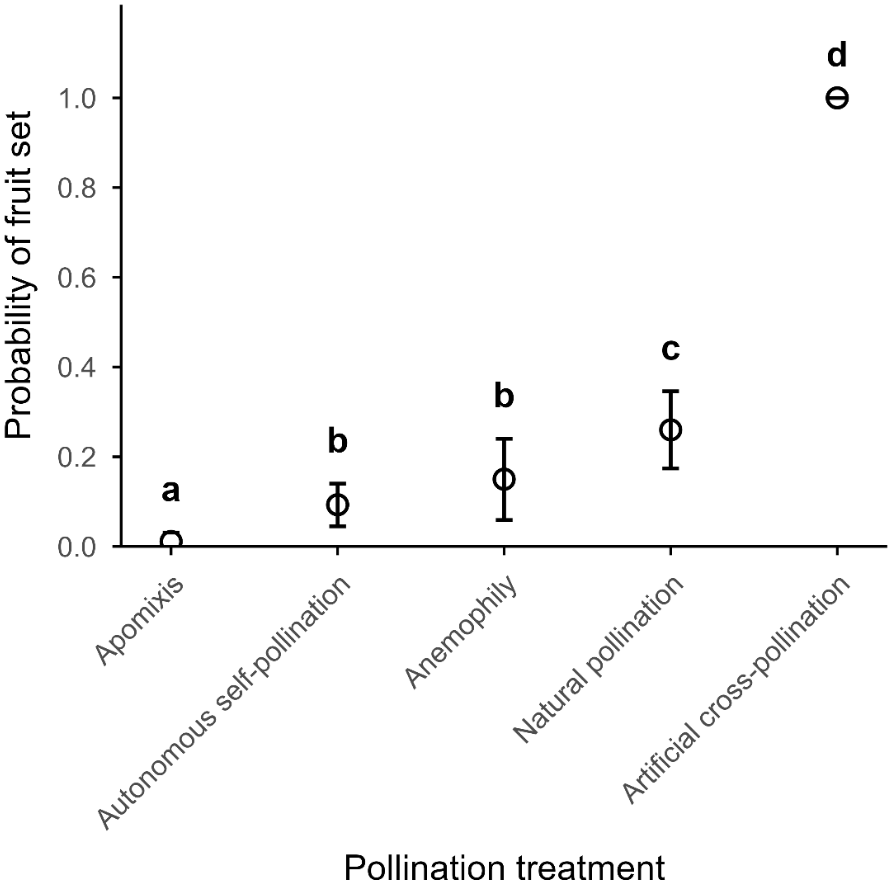

Figure 1. Probability of fruit set in *Borago officinalis* flowers under five pollination treatments. Points show marginal means estimated from a binomial Generalized Linear Mixed Model (GLMM) with a random intercept for maternal plant; error bars represent 95% simultaneous confidence intervals on the probability scale. Different letters indicate statistically significant differences based on pairwise comparisons with Sidak adjustment.

in all cases; Fig. 1). The model explained a substantial proportion of the variance, with a marginal R^2 of 0.619 and a conditional R^2 of 0.791, indicating that while pollination treatment was the main driver, variation among maternal plants also contributed to the observed patterns.

Natural pollination led to a higher fruit set probability than autonomous self-pollination (difference = 0.167, $P < 0.0001$), anemophily (difference = 0.111, $P = 0.0195$), and apomixis (difference = 0.249, $P < 0.0001$). Both anemophily (difference = 0.139, $P = 0.0008$) and autonomous self-pollination (difference = 0.082, $P = 0.0002$) resulted in higher fruit set than apomixis. No significant difference was observed between autonomous self-pollination and anemophily (difference = 0.057, $P = 0.623$).

NUMBER OF NUTLETS PER FRUIT

The number of nutlets per fruit also differed significantly among treatments (Poisson GLMM; Fig. 2 & Table 2), with no evidence of overdispersion. Artificial cross-pollination yielded a significantly higher number of nutlets than all other treatments (pairwise differences between 1.841 and 2.373, $P < 0.0001$; Fig. 2). The model explained a moderate proportion of the variance, with a marginal R^2 of 0.390 and a conditional R^2 of 0.574.

Fruits from the natural pollination treatment contained more nutlets than those from autonomous self-pollination (difference = 0.367, $P < 0.0001$), anemophily (difference = 0.306, $P < 0.0001$), and apomixis (difference = 0.532, $P < 0.0001$). Both anemophily (difference = 0.226, $P < 0.0001$) and autonomous self-pollination (difference = 0.165, $P < 0.0001$) produced more nutlets per fruit than apomixis. No significant difference was found between autonomous self-pollination and anemophily (difference = 0.061, $P = 0.8666$).

Overall, artificial cross-pollination consistently produced the highest reproductive output, with a fruit set probability of 1.00 and an average of 2.39 nutlets per fruit. In contrast, natural pollination yielded only 0.26 fruit set (74 percentage points lower) and 0.54 nutlets (77% lower), representing a 284% increase in fruit set and a 338% increase in

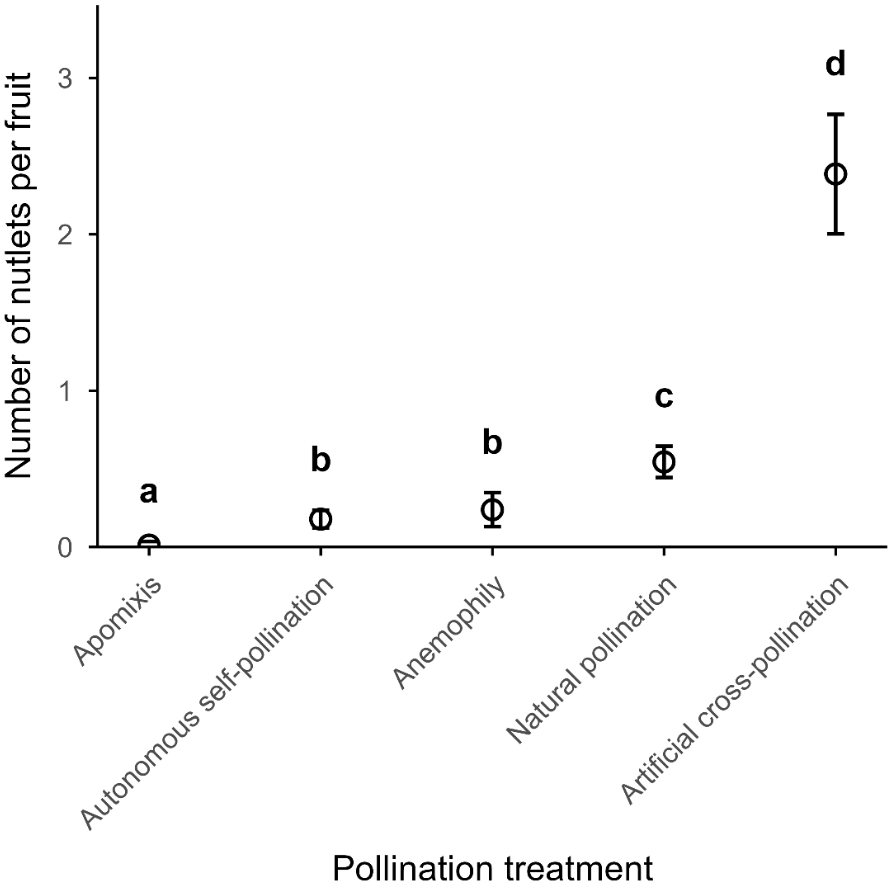

Figure 2. Number of nutlets per fruit in *Borago officinalis* under five pollination treatments. Points show marginal means estimated from a Poisson GLMM with a random intercept for maternal plant; error bars represent 95% confidence intervals. Different letters indicate statistically significant differences based on pairwise comparisons with Sidak adjustment.

nutlet number when moving from natural to cross-pollination. Autonomous self-pollination and anemophily performed even more poorly, with fruit set reductions of 91% and 85%, and nutlet reductions of 93% and 90%, respectively, relative to the cross-pollination maximum. Apomixis was negligible, contributing less than 2% of the maximum reproductive success.

DISCUSSION

This study provides a clear experimental characterization of the reproductive system of *B. officinalis* in the Pampas region of Argentina. Our results demonstrate that while borage possesses a self-compatible and facultatively xenogamous system, its reproductive success is maximized by cross-pollination and is currently limited by pollen receipt under natural conditions.

REPRODUCTIVE SYSTEM: FACULTATIVE XENOGAMY WITH LIMITED AUTOGAMY

Our manipulative experiment confirms that borage exhibits a facultatively xenogamous reproductive system. The high fruit set and nutlet number achieved through artificial cross-pollination establish the upper limit of reproductive potential and underscore the superiority of cross-pollen transfer (Leach et al. 1993). In contrast, the significantly lower success under autonomous self-pollination indicates a limited capacity for autogamy. This is likely a consequence of the marked protandry documented in the species, where anthers dehisce before the stigma becomes receptive, creating a temporal barrier to self-fertilization within the same flower (Stawiarz et al. 2020). The near-zero fruit set in the apomixis treatment definitively rules out agamospermy as a reproductive pathway for this species.

The intermediate success of the autonomous self-pollination treatment confirms the presence of self-compatibility, as some fruitset did occur, likely through geitonogamy or delayed selfing. In borage, protandry reduces the likelihood of self-fertilization within a single flower but does not prevent geitonogamous pollination. Plants produce multiple flowers simultaneously, and bees commonly visit several flowers on the same individual before moving to neighbouring plants, facilitating the transfer of self-pollen among flowers of the same plant (Montaner et al. 2001). Experimental studies have shown that this process can lead to high selfing rates in *B. officinalis*, with most seeds produced under open pollination originating from geitonogamous fertilization. Our results are consistent with this mechanism: although autonomous self-pollination produced lower fruit and seed set than cross-pollination, its non-negligible reproductive success suggests that within-plant pollen transfer may contribute to reproduction when cross-pollen availability is limited.

POLLEN LIMITATION AND THE ROLE OF POLLINATORS

A key finding of our study is the evidence for strong pollen limitation, which occurred despite the proximity of managed honeybee (*Apis mellifera*) hives. This indicates that the service provided by the local pollinator community was insufficient to maximize fruit and seed set, a phenomenon observed in other agricultural systems (Garibaldi et al. 2014). The results from the anemophily treatment suggest that wind plays a negligible role, reinforcing the critical dependency on insect pollinators for effective pollen transfer.

The similar, intermediate performance of autonomous self-pollination and anemophily treatments suggests that neither mechanism alone contributes substantially to reproductive success under open pollination. Therefore, the yield observed under natural conditions likely reflects a combination of processes, including autonomous selfing, cross-pollination mediated by insects, and potentially geitonogamous pollen transfer among flowers of the same plant facilitated by pollinator movements. However, the substantially lower reproductive output relative to artificial cross-pollination indicates that cross-pollen receipt under field conditions was still sub-optimal.

AGRONOMIC IMPLICATIONS AND FUTURE DIRECTIONS

From an agronomic perspective, our findings have direct implications for borage cultivation. The mere presence of beehives does not guarantee adequate pollination services. To maximize seed yield for GLA production, management practices must actively ensure a high rate of cross-pollination. To enhance pollination services, we recommend strategies supported by empirical evidence, such as increasing semi-natural habitat around fields to support wild bee populations (Kennedy et al. 2013; Garibaldi et al. 2014) and optimizing the density and spatial arrangement of honeybee colonies during flowering (Cunningham et al. 2016).

This study has limitations that point to fruitful future research. First, using seeds from a single population prevents the detection of potential genetic variation in the reproductive system (Leach et al. 1993). Second, the experiment was conducted under optimal conditions without resource competition, which may not fully reflect field dynamics where abiotic stress can alter plant-pollinator interactions (Descamps et al. 2018; Bishop et al. 2020). Third, the lack of pollinator visitation data prevents a direct correlation between visitor activity and reproductive success (Sáez et al. 2018). Finally, as a single-year study, it does not capture interannual variability in pollinator assemblages (Petanidou et al. 2008) or the resulting variation in fruit and seed set that may occur across years.

Future research should focus on quantifying the minimum visitation rate required to achieve a high yield, which would allow for precise management recommendations. Furthermore, it would be highly relevant to investigate whether the mode of pollination influences seed quality, particularly the oil and GLA content. In other oilseed crops like sunflower and oilseed rape, insect pollination has been shown to enhance not only yield but also the oil concentration of seeds (Bommarco et al. 2012; Jilo et al. 2025). Determining if cross-pollinated seeds are of superior quality would provide a compelling economic argument for investing in pollinator conservation within borage production systems.

CONCLUSION

This study demonstrates that borage in the Pampas region experiences pollen limitation under natural conditions, resulting in reduced fruit set and seed production relative to its potential. While the species is self-compatible, cross-pollination maximizes reproductive output, and wind pollination contributes negligibly. These results highlight the importance of effective pollinator services, beyond the mere presence of managed honeybees, for improving yields in this emerging oilseed crop.

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AUTHOR CONTRIBUTION

MD conceived the ideas and designed the methodology. MD supervised the field work. MM and MD analysed the data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

GENERATIVE AI DISCLOSURE STATEMENT

The authors used ChatGPT (OpenAI) to improve the clarity and grammar of the English. All scientific content, interpretations, and conclusions are solely those of the authors.

DATA AVAILABILITY STATEMENT

The dataset and R scripts used to reproduce all analyses, tables, and figures are publicly available at Zenodo (https://doi.org/10.5281/zenodo.19112475)

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