



Reproductive performance of southern highbush blueberry cultivars (*Vaccinium corymbosum* L.) in northeastern Argentina*

Desempeño reproductivo de cultivares de arándano *southern highbush* (*Vaccinium corymbosum* L.) en el nordeste argentino

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* Recepción: 23 de junio, 2026. Aceptación: 18 de septiembre, 2026. This work derives from the doctoral thesis entitled “Biología reproductiva de arándanos (*Vaccinium corymbosum* L.) en la Mesopotamia argentina”, carried out as part of the Doctorado en Recursos Naturales at the Universidad Nacional del Nordeste, Argentina.

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Abstract

Introduction. Southern highbush blueberry cultivars (SHB, *Vaccinium corymbosum* L.) have enabled the expansion of blueberry production into warmer, subtropical regions. In these environments, understanding cultivar-specific reproductive responses is essential to improve parental selection and breeding efficiency. **Objective.** To evaluate the key components of the reproductive performance of southern highbush blueberry cultivars under subtropical conditions of northeastern Argentina. **Materials and methods.** This study evaluated pollen production and *in vitro* pollen germination across year × location × cultivar combinations, and fruit set and number of well-developed seeds per fruit across year × location × pollination treatment combinations, in the SHB cultivars ‘Emerald’ and ‘Snowchaser’ grown in Concordia and Bella Vista, Argentina, during 2023 and 2024. Data were analyzed by analysis of variance, and mean comparisons were performed using Tukey’s test ($p \leq 0.05$). **Results.** Pollen production varied among years and cultivar × location combinations, with generally higher values in 2024, ranging from 8,638.89 to 26,194.44 tetrads per flower. *In vitro* pollen germination was affected by cultivar, location, year, and their interactions, with the lowest values observed for ‘Emerald’ in Bella Vista and ‘Snowchaser’ in Concordia during 2024. Fruit set was lowest in ‘Emerald’ × ‘Emerald’ and in pollination treatments using ‘Snowchaser’ as the female cultivar in Concordia in 2024, whereas the highest number of well-developed seeds per fruit was recorded in ‘Snowchaser’ × ‘Snowchaser’ in Concordia in 2024. **Conclusions.** The findings indicate that reproductive behavior in southern highbush blueberry cultivars under subtropical conditions is shaped by genotype, environmental conditions, and their interaction. The contrasting responses of reproductive traits indicate that reproductive success cannot be inferred from a single reproductive attribute.

Keywords: Ericaceae, pollen production, pollen germination, cross-pollination, fruit set, seed development.



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Resumen

Introducción. Los cultivares de arándano *southern highbush* (SHB, *Vaccinium corymbosum* L.) han permitido expandir la producción hacia regiones subtropicales. En estos ambientes, comprender sus respuestas reproductivas es fundamental para mejorar la selección de parentales y el mejoramiento genético. **Objetivo.** Evaluar los principales componentes del desempeño reproductivo de cultivares SHB bajo condiciones subtropicales del nordeste argentino. **Materiales y métodos.** Se evaluaron la producción y la germinación *in vitro* del polen en combinaciones de año × localidad × cultivar, y el cuajado de frutos y el número de semillas bien desarrolladas por fruto en combinaciones de año × localidad × tratamiento de polinización, en los cultivares SHB ‘Emerald’ y ‘Snowchaser’ cultivados en Concordia y Bella Vista durante 2023 y 2024. Los datos se analizaron mediante análisis de varianza y prueba de Tukey ($p \leq 0,05$). **Resultados.** La producción de polen varió entre años y combinaciones cultivar × localidad, generalmente con mayores valores en 2024, y osciló entre 8638,89 y 26194,44 tétradas por flor. La germinación *in vitro* del polen fue afectada por el cultivar, la localidad, el año y sus interacciones, con los valores más bajos registrados para ‘Emerald’ en Bella Vista y ‘Snowchaser’ en Concordia durante 2024. El cuajado de frutos fue menor en ‘Emerald’ × ‘Emerald’ y en los tratamientos de polinización con ‘Snowchaser’ como cultivar femenino en Concordia durante 2024, mientras que el mayor número de semillas bien desarrolladas por fruto se registró en ‘Snowchaser’ × ‘Snowchaser’ en Concordia durante 2024. **Conclusiones.** Los hallazgos indican que el comportamiento reproductivo de cultivares SHB bajo condiciones subtropicales está condicionado por el genotipo, las condiciones ambientales y su interacción. Las respuestas contrastantes de los distintos componentes reproductivos indican que el éxito reproductivo no puede inferirse a partir de un único atributo reproductivo.

Palabras clave: Ericaceae, producción de polen, germinación de polen, polinización cruzada, cuajado de frutos, desarrollo de semillas.

Introduction

Blueberry (*Vaccinium* spp.; Ericaceae) is one of the most widely cultivated berry crops worldwide (Brazelton et al., 2025). The expansion of blueberry production into warmer, non-traditional regions has been enabled by southern highbush blueberry (SHB, *Vaccinium corymbosum* L.) cultivars, which have adapted to low-chill conditions (Fang et al., 2020). The sustainability of this production system relies on the continuous development of improved cultivars with enhanced productivity, environmental adaptation, and fruit quality (Edger et al., 2022; Ru et al., 2024).

In Argentina, however, cultivar development remains limited. Varietal replacement has progressed more slowly than in other producing countries, and more than 90 % of registered cultivars originate from foreign breeding programs (Aggio et al., 2022; Instituto Nacional de la Semilla, 2026). Consequently, strengthening regional breeding strategies is essential to develop genotypes that are adapted to local production conditions and commercial requirements (Chu et al., 2025).

The efficiency of breeding programs depends on the selection of suitable parental genotypes, which in turn depends on their reproductive performance. Reproductive performance in plants encompasses multiple processes, including pollen production, *in vitro* pollen germination, pollination success, and seed formation (Pandey, 2022). In *Vaccinium*, pollen production and germination have been shown to be strongly influenced by genotype (Chakrabarti et al., 2025; Doi et al., 2021; Leposavić et al., 2017), and pollen performance has been associated with the formation of well-developed seeds per fruit (Vander Kloet, 1983).

High pollen production is considered a favorable trait for yield in bee-pollinated species such as *Vaccinium* spp. (Brevis et al., 2006; Dogterom et al., 2000; Doi et al., 2021). It is also relevant in breeding programs, where pollen

availability may influence the efficiency of controlled crosses. Pollen production is influenced by both genotype and growing conditions (Danti et al., 2022; Dölek Gencer et al., 2023), and genotypic differences among cultivars have been reported in *V. corymbosum* (Chakrabarti et al., 2025).

In vitro pollen germination provides a functional measure of pollen performance by reflecting its ability to produce a pollen tube under controlled conditions and is widely used to assess pollen quality (Althiab-Almasaud et al., 2024). It is influenced by conditions during microsporogenesis and pollen maturation (Lohani et al., 2025; Iovane & Aronne, 2022), with responses varying among genotypes (Hedhly et al., 2005; Čolić et al., 2025). These developmental processes involve coordinated metabolic and cellular functions, including carbohydrate balance and energy availability, membrane and cell wall integrity, ion transport, and redox homeostasis (Lohani et al., 2025). Variation in these processes can contribute to differences in pollen germination.

Fruit set of *V. corymbosum*, defined as the proportion of flowers that develop into fruit, is influenced by cultivar-specific reproductive traits and pollen source (Liu et al., 2022; Martin et al., 2025). Cross-pollination often results in higher reproductive success than self-pollination (Taber & Olmstead, 2016; Vander Kloet, 1983). Pollen source also influences the number of seeds per berry, with cross-pollination generally increasing seed production, although the magnitude of this effect depends on the specific genotype combination (Doi et al., 2018; 2021). Because reproductive performance depends on both fruit set and seed formation, evaluating responses to self- and cross-pollination across genotype combinations is essential for parental selection in breeding programs.

Temperature is one of the main environmental factors regulating plant reproductive development, and deviations from the optimal thermal range can negatively affect male reproductive performance. Both low and high temperatures may disrupt critical processes in pollen development, including meiosis, tapetum function, microspore development, pollen maturation, and pollen tube growth. These alterations frequently result in reduced pollen production, lower pollen viability and germination, impaired fertilization, and ultimately decreased fruit and seed set (Begcy et al., 2024; Lohani et al., 2025).

In northeastern Argentina, SHB reproductive development occurs during winter and early spring (Pannunzio et al., 2023), when environmental conditions differ among production areas. Historical climatic records indicate that Bella Vista (Corrientes) experiences warmer conditions during the flowering period (M. A. Almiron, personal communication, March 10, 2025), whereas Concordia (Entre Ríos) is characterized by lower temperatures and higher relative humidity during the same period (S. O. Ramos, personal communication, May 21, 2025). These climatic differences provide a contrasting environmental framework for evaluating the reproductive performance of different cultivars across locations.

In Argentina, ‘Emerald’ and ‘Snowchaser’ are important SHB cultivars, particularly following the varietal shift toward licensed cultivars (Recalde et al., 2025; Rivadeneira, 2020). ‘Emerald’ is vigorous and productive, whereas ‘Snowchaser’ is an early-flowering cultivar adapted to evergreen management (Williamson et al., 2019). According to their original descriptions, both cultivars exhibit low to moderate levels of self-compatibility (Lyrene, 2008a, 2008b). In northeastern Argentina, both cultivars have been shown to produce binucleate and morphologically normal pollen grains (Recalde et al., 2025). However, morphological normality alone does not necessarily reflect pollen functionality, which ultimately depends on its ability to germinate, effect fertilization, and contribute to seed formation (Cascallares et al., 2020).

Understanding the reproductive performance of SHB cultivars under subtropical conditions is therefore relevant for identifying efficient parental combinations in breeding programs. Reproductive performance is defined not only by fruit set but also by the ability to produce well-developed seeds. Therefore, this study aimed to evaluate the key components of the reproductive performance of southern highbush blueberry cultivars under subtropical conditions of northeastern Argentina.

Materials and methods

Plant material and study sites

The southern highbush blueberry cultivars (*V. corymbosum*) ‘Emerald’ and ‘Snowchaser’ were studied at two blueberry-producing locations in northeastern Argentina. At the beginning of the study, ‘Emerald’ plants were 13 years old and ‘Snowchaser’ plants were 9 years old at both locations. Field sampling and controlled pollinations were conducted in Concordia (Entre Ríos Province, Argentina; 31°19’S; 58°05’W) and Bella Vista (Corrientes Province, Argentina; 28°26’S; 58°57’W) during the 2023 and 2024 growing seasons.

In Concordia, the climate is humid subtropical, with a mean annual temperature of 19 °C and average annual precipitation of 1,300 mm (Ramos et al., 2018; S. O. Ramos, personal communication, May 21, 2025), whereas Bella Vista has a mean annual temperature of 20.7 °C and annual precipitation close to 1,400 mm, with marked seasonal variation (M. A. Almiron, personal communication, March 10, 2025). Soils in Concordia are deep and sandy, with low organic matter content and a slightly acidic pH (5.0–5.5) (Perkul & Clozza, 2025). In Bella Vista, soils are sandy loam, with low fertility and limited water retention capacity (Maidana et al., 2020).

At both locations, plants were grown in commercial fields on raised beds covered with black plastic mulch. Frost protection was provided by overhead sprinkler irrigation. Standard agronomic management practices for blueberry production in northeastern Argentina were followed.

Experimental design

A completely randomized design was implemented with a factorial arrangement defined by year (2023–2024), location (Concordia and Bella Vista), and cultivar or pollination treatment, depending on the response variable analyzed. Nine experimental units (EU) were established for each combination of factors. Each EU consisted of a group of three plants grown under uniform agronomic conditions within each site. All measurements were conducted at the EU level, while individual flowers, fruits, or pollination events within each EU were considered subsamples and were not treated as independent replicates. The same experimental structure was used for all measured variables, with differences arising only in the factor combinations included in each analysis.

Pollen production and *in vitro* pollen germination

Flowers sampled for pollen production estimation were collected at the pre-anthesis stage, when the corolla was fully developed and closed and the anthers had not yet opened. One flower per EU was sampled, and the number of anthers per flower was recorded. Pollen was extracted into 5 mL of a 5 % glycerin solution, using one anther per flower in 2023 and two anthers per flower in 2024.

Tetrads were counted microscopically in 20 µL aliquots, one aliquot per anther in 2023 and two aliquots per anther in 2024. Pollen tetrads, rather than individual pollen grains, were counted as the pollen dispersal unit (Recalde et al., 2025), following the method of Shivanna & Tandon (2014) adapted for species with a high pollen load. Pollen production per anther (P) was estimated using Equation 1.

$$P = \frac{V_t \times N}{V_c} \quad (1)$$

Where P is pollen production per anther (tetrads per anther), V_t is the total volume of the pollen suspension, N is the number of tetrads counted in the aliquot, and V_c is the volume of the counted aliquot. Pollen production per

flower was calculated by multiplying P by the number of anthers per flower. Final values per EU were obtained by averaging across anthers and aliquots, where applicable.

In vitro pollen germination was assessed using pollen obtained from ten open flowers per EU collected at anthesis, when the corolla was fully expanded and the anthers were dehiscent. Pollen was obtained by gently rotating the flowers between the fingers following Dogterom et al. (2000). Samples were pooled to obtain a composite sample per EU.

Germination was assessed using the tetrad germination method adapted from Doi et al. (2021). Pollen was incubated in a medium containing 1 % agar, 20 % sucrose, and 0.01 % H_3BO_3 at 27 °C for 3 h. At least 200 tetrads per EU were evaluated under a light microscope. A tetrad was considered germinated when at least one pollen tube exceeded the diameter of the tetrad, and the percentage of *in vitro* pollen germination was then calculated.

Fruit set and number of well-developed seeds per fruit

Controlled pollinations were performed by hand on eight to twelve flowers per EU for each pollen source. Pollination treatments were defined as female cultivar × pollen donor cultivar combinations, including self-pollination ('Emerald' × 'Emerald'; 'Snowchaser' × 'Snowchaser') and cross-pollination ('Emerald' × 'Snowchaser'; 'Snowchaser' × 'Emerald'). Pollen from each cultivar and location was collected as described above and stored at −20 °C until use (Ren et al., 2022). Only pollen collected in the same year was used.

Pollinations were performed during full bloom, when open flowers were predominant across the canopy, as confirmed by field observations and previous phenological records for these cultivars under local conditions (Pannunzio et al., 2023). Flowers at pre-anthesis were emasculated using fine-tipped forceps, and the corresponding pollen was applied to the stigma using a fine-tipped brush. Pollinated inflorescences were labeled and covered with mesh bags to prevent fruit loss due to inadvertent harvesting, predation, or fruit drop (Campbell et al., 2018).

Fruits were harvested at maturity, approximately 90 days after pollination, consistent with the typical fruit development period of the cultivars under local conditions (Rivadeneira, 2022). Fruit set percentage was calculated as the proportion of pollinated flowers that developed into mature fruits. The number of well-developed seeds per fruit was then recorded. Seeds were considered well-developed when they exceeded 1 mm in length and had a dark brown testa, following Dogterom et al. (2000), who reported that only fully developed seeds were fertile and capable of producing new individuals.

Statistical analysis

The assumptions of normality and homogeneity of variances were evaluated using Shapiro–Wilk and Levene's tests, respectively. When necessary, data were transformed to meet analysis of variance (ANOVA) assumptions. Pollen production data were transformed using $\log_{10}(x + 1)$, pollen germination percentages were transformed using the logit function, and the number of well-developed seeds per fruit was transformed using a Box–Cox transformation ($\lambda = -0.3$). Fruit set data were analyzed without transformation. Factorial ANOVA models were fitted considering cultivar, location, and year, or pollination treatment, location, and year, as fixed effects, including all interaction terms. For unbalanced datasets, Type III sums of squares were used.

Results

Pollen production and *in vitro* pollen germination

Pollen production was significantly affected by year, and a significant cultivar $\times$ location $\times$ year interaction was detected, whereas cultivar and location effects, as well as the remaining interactions, were not significant (Table 1). *In vitro* pollen germination was significantly affected by cultivar, location, and year. Significant interactions were also detected for cultivar $\times$ location, cultivar $\times$ year, location $\times$ year, and cultivar $\times$ location $\times$ year.

Table 1. Summary of factorial analysis of variance (ANOVA) results for pollen production and *in vitro* pollen germination in southern highbush blueberry cultivars (*V. corymbosum*) grown at two locations in northeastern Argentina during 2023–2024.

Cuadro 1. Resumen de los resultados del análisis de varianza (ANDEVA) factorial para la producción de polen y la germinación de polen *in vitro* en cultivares de arándano *southern highbush* (*V. corymbosum*) cultivados en dos localidades del nordeste argentino durante los años 2023-2024.

Variable	Y	L	C	Y $\times$ L	Y $\times$ C	L $\times$ C	Y $\times$ L $\times$ C
Pollen production	***	NS	NS	NS	NS	NS	*
<i>In vitro</i> pollen germination	***	***	***	*	***	*	***

Y: Year. **L:** Location. **C:** Cultivar. **NS:** Not significant. * significant at $p \leq 0.05$. *** significant at $p \leq 0.001$. Factorial ANOVA models were fitted using transformed data when required to meet model assumptions: pollen production was analyzed after $\log_{10}(x + 1)$ transformation and *in vitro* pollen germination after logit transformation. / **Y:** Año. **L:** Localidad. **C:** Cultivar. **NS:** No significativo. * significativo a $p \leq 0,05$. *** significativo a $p \leq 0,001$. Los modelos de ANDEVA factorial fueron ajustados utilizando transformaciones de los datos cuando fue necesario para cumplir los supuestos del modelo: la producción de polen fue analizada después de la transformación $\log_{10}(x + 1)$ y la germinación de polen *in vitro* después de la transformación logit.

Pollen production ranged from 8,638.89 to 26,194.44 tetrads per flower, with significant effects of year and the cultivar $\times$ location $\times$ year interaction (Table 2). Tukey's test identified differences among some year $\times$ location $\times$ cultivar combinations, with higher values observed mainly in 2024. *In vitro* pollen germination ranged from 2.42 % to 63.93 % and differed significantly among year $\times$ location $\times$ cultivar combinations, with the lowest values recorded for 'Emerald' in Bella Vista and 'Snowchaser' in Concordia in 2024.

Fruit set and number of well-developed seeds per fruit

Fruit set varied significantly with year, location, and pollination treatment, and significant year $\times$ location, year $\times$ pollination treatment, location $\times$ pollination treatment, and year $\times$ location $\times$ pollination treatment interactions were detected (Table 3). The number of well-developed seeds per fruit was significantly affected by location and pollination treatment, and a significant year $\times$ pollination treatment interaction was detected, whereas year, year $\times$ location, location $\times$ pollination treatment, and year $\times$ location $\times$ pollination treatment interactions were not significant.

Table 2. Pollen production and *in vitro* pollen germination in southern highbush blueberry cultivars in Concordia (Entre Ríos) and Bella Vista (Corrientes), Argentina, during 2023–2024.**Cuadro 2.** Producción de polen y germinación *in vitro* del polen en cultivares de arándano *southern highbush* en Concordia (Entre Ríos) y Bella Vista (Corrientes), Argentina, durante 2023–2024.

Year	Location	Cultivar	Pollen production (tetrads per flower)		<i>In vitro</i> pollen germination (%)	
			Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
2023	Bella Vista	‘Emerald’	12,555.56 $\pm$ 5,298.55 ab	5,500–20,000	6.07 $\pm$ 3.50 b	3.02–12.45
2023	Bella Vista	‘Snowchaser’	9,166.67 $\pm$ 4,841.23 ab	5,000–17,500	52.23 $\pm$ 18.37 c	25.44–82.61
2023	Concordia	‘Emerald’	8,638.89 $\pm$ 4,505.40 a	2,500–13,750	52.02 $\pm$ 11.76 c	35.59–73.81
2023	Concordia	‘Snowchaser’	15,833.33 $\pm$ 6,731.46 ab	7,500–25,000	63.93 $\pm$ 11.26 c	51.40–79.58
2024	Bella Vista	‘Emerald’	12,888.89 $\pm$ 6,004.05 ab	2,500–25,000	2.42 $\pm$ 1.49 a	0.40–5.00
2024	Bella Vista	‘Snowchaser’	24,722.22 $\pm$ 17,916.67 b	7,500–57,500	56.31 $\pm$ 11.72 c	43.08–75.42
2024	Concordia	‘Emerald’	26,194.44 $\pm$ 27,461.27 ab	5,000–95,000	62.02 $\pm$ 6.49 c	50.49–69.55
2024	Concordia	‘Snowchaser’	24,333.33 $\pm$ 15,235.65 b	7,500–55,000	11.54 $\pm$ 4.91 b	7.12–21.38

Values are expressed as mean $\pm$ standard deviation (SD) and range (minimum–maximum). Different letters indicate significant differences among year $\times$ location $\times$ cultivar combinations according to Tukey’s test ($p \leq 0.05$). / Los valores se expresan como media $\pm$ desviación estándar (DE) y rango (mínimo–máximo). Las letras diferentes indican diferencias significativas entre las combinaciones año $\times$ localidad $\times$ cultivar según la prueba de Tukey ($p \leq 0,05$).

Table 3. Summary of factorial analysis of variance (ANOVA) results for fruit set and number of well-developed seeds per fruit in controlled crosses of southern highbush blueberry cultivars (*V. corymbosum*) performed in northeastern Argentina during 2023–2024.**Cuadro 3.** Resumen de los resultados del análisis de varianza (ANDEVA) factorial para el cuajado de frutos y el número de semillas bien desarrolladas por fruto en cruzamientos controlados de cultivares de arándano *southern highbush* (*V. corymbosum*) realizados en el nordeste argentino durante 2023–2024.

Variable	Y	L	C	Y $\times$ L	Y $\times$ C	L $\times$ C	Y $\times$ L $\times$ C
Fruit set	***	**	***	*	**	*	**
Number of well-developed seeds per fruit	NS	*	***	NS	*	NS	NS

Y: Year. **L:** Location. **C:** Pollination treatment. **NS:** Not significant. * significant at $p \leq 0.05$. ** significant at $p \leq 0.01$. *** significant at $p \leq 0.001$. Factorial ANOVA models were fitted using transformed data when required to meet model assumptions: the number of well-developed seeds per fruit was analyzed after Box–Cox transformation ($\lambda = -0.3$). / **Y:** Año. **L:** Localidad. **C:** Tratamiento de polinización. **NS:** No significativo. * significativo a $p \leq 0,05$. ** significativo a $p \leq 0,01$. *** significativo a $p \leq 0,001$. Los modelos de análisis de varianza factorial (ANDEVA) se ajustaron utilizando datos transformados cuando fue necesario para cumplir los supuestos del modelo: el número de semillas bien desarrolladas por fruto se analizó después de la transformación Box–Cox ($\lambda = -0,3$).

Fruit set ranged from 15.0 % to 77.86 % among year $\times$ location $\times$ pollination treatment combinations (Table 4). The lowest fruit set values were observed in ‘Emerald’ $\times$ ‘Emerald’ and in combinations using ‘Snowchaser’ as the female parent in Concordia in 2024. The number of well-developed seeds per fruit ranged from 1.45 to 25.53, with the highest values recorded in ‘Snowchaser’ $\times$ ‘Snowchaser’ in Concordia in 2024.

Table 4. Fruit set and number of well-developed seeds per fruit under pollination treatments in southern highbush blueberry cultivars in Concordia and Bella Vista, Argentina (2023–2024).

Cuadro 4. Cuajado de frutos y número de semillas bien desarrolladas por fruto bajo tratamientos de polinización en cultivares de arándano *southern highbush* en Concordia y Bella Vista, Argentina (2023–2024).

Year	Location	Pollination treatment	Fruit set (%) Mean $\pm$ SD	Number of well-developed seeds per fruit	
				Mean $\pm$ SD	Range
2023	Bella Vista	'EM' $\times$ 'EM'	38.54 $\pm$ 20.80 abc	3.08 $\pm$ 3.75 abc	0–8
2023	Bella Vista	'EM' $\times$ 'SN'	69.71 $\pm$ 17.43 c	4.72 $\pm$ 2.79 abcd	1.67–10.20
2023	Bella Vista	'SN' $\times$ 'EM'	64.41 $\pm$ 28.09 c	1.45 $\pm$ 0.81 ab	0.50–2.75
2023	Bella Vista	'SN' $\times$ 'SN'	70.64 $\pm$ 15.66 c	4.37 $\pm$ 3.01 abcd	2–11.83
2023	Concordia	'EM' $\times$ 'EM'	15.00 $\pm$ 18.32 a	1.67 $\pm$ 2.89 a	0–5
2023	Concordia	'EM' $\times$ 'SN'	56.19 $\pm$ 24.90 bc	5.63 $\pm$ 3.90 abcd	2–13.67
2023	Concordia	'SN' $\times$ 'EM'	74.40 $\pm$ 30.55 c	8.30 $\pm$ 4.79 cd	3.20–17.75
2023	Concordia	'SN' $\times$ 'SN'	77.86 $\pm$ 25.04 c	6.36 $\pm$ 3.33 bcd	1.60–10.71
2024	Bella Vista	'EM' $\times$ 'EM'	45.56 $\pm$ 20.81 abc	2.38 $\pm$ 1.72 abc	1–6.67
2024	Bella Vista	'EM' $\times$ 'SN'	45.94 $\pm$ 20.68 abc	2.13 $\pm$ 1.83 abc	1–6.33
2024	Bella Vista	'SN' $\times$ 'EM'	44.41 $\pm$ 25.98 abc	6.34 $\pm$ 3.43 abcd	1.33–12
2024	Bella Vista	'SN' $\times$ 'SN'	66.78 $\pm$ 25.22 c	7.90 $\pm$ 8.23 abcd	1–25
2024	Concordia	'EM' $\times$ 'EM'	21.66 $\pm$ 28.32 ab	2.27 $\pm$ 1.63 abcd	0.83–4.50
2024	Concordia	'EM' $\times$ 'SN'	56.13 $\pm$ 34.19 abc	3.93 $\pm$ 0.69 abcd	2.86–4.88
2024	Concordia	'SN' $\times$ 'EM'	18.41 $\pm$ 16.18 ab	19.63 $\pm$ 19.62 bcd	1–48
2024	Concordia	'SN' $\times$ 'SN'	16.39 $\pm$ 15.02 a	25.53 $\pm$ 23.01 d	1–58

EM: 'Emerald'. **SN:** 'Snowchaser'. Pollination treatments are expressed as female cultivar $\times$ pollen donor cultivar. Values are expressed as mean $\pm$ standard deviation (SD). Different letters indicate significant differences among year $\times$ location $\times$ pollination treatment combinations according to Tukey's test ($p \leq 0.05$). / **EM:** 'Emerald'. **SN:** 'Snowchaser'. Los tratamientos de polinización se expresan como cultivar femenino $\times$ cultivar donante de polen. Los valores se expresan como media $\pm$ desviación estándar (DE). Las letras diferentes indican diferencias significativas entre las combinaciones año $\times$ localidad $\times$ tratamiento de polinización según la prueba de Tukey ($p \leq 0.05$).

Discussion

Northeastern Argentina represents an important production area for SHB, including locations with contrasting environmental conditions during the reproductive period. Bella Vista and Concordia have historically differed in climatic characteristics, with higher mean temperatures in Bella Vista (15.3–18.4 °C) than in Concordia (12.5–15.8 °C) (available data: 1967–2022), and lower relative humidity values in Bella Vista (68.6–77.3 %) than in Concordia (73.7–83.6 %) during June–September (available data: 1994–2022) (M. A. Almiron, personal communication, March 10, 2025; S. O. Ramos, personal communication, May 21, 2025). These differences provide the environmental context for interpreting reproductive responses among cultivars.

Pollen production was more strongly influenced by variation among growing seasons than by location or cultivar. Environmental effects on pollen production have been associated with alterations in reproductive developmental processes (Lohani et al., 2025; Stokes & Geitmann, 2025). Accordingly, the variation observed among year $\times$ location $\times$ cultivar combinations suggests that environmental conditions during each growing season may have contributed to the observed variation in pollen production among specific combinations.

In *Vaccinium* species, pollen production ranges from 2,400–30,000 tetrads per flower. Lower values (approximately 5,600–8,300 tetrads per flower) have been reported in *V. ashei* Reade, *V. boreale* Hall & Aalders, and *V. macrocarpon* Aiton, whereas values exceeding 20,000 tetrads per flower have been observed in *V. myrtillus* L., *V. vitis-idaea* L., and *V. cylindraceum* Sm. (Brevis et al., 2006; Cane et al., 1996; Jacquemart & Thompson, 1996; Pereira, 2008; Stephens et al., 2012). The values obtained for ‘Emerald’ and ‘Snowchaser’ in northeastern Argentina fall within the intermediate to upper portion of those reported for *Vaccinium*. However, pollen production alone does not necessarily indicate whether reproductive performance is limited, particularly given the variation observed in pollen germination.

Unlike pollen production, pollen germination exhibited a strong dependence on genotype, location, growing season, and their interactions, indicating that pollen functionality was highly responsive to the environmental conditions associated with each production environment. Because pollen germination reflects the physiological status acquired during pollen maturation, these results suggest that environmental conditions during reproductive development may have differentially affected pollen performance depending on the cultivar and production environment.

Pollen germination in *Vaccinium* varies widely among species and cultivars, ranging from 23–72 % in blueberry varieties (Brewer & Dobson, 1969) and 26–45 % in stored northern highbush pollen (Doi et al., 2021). In southern highbush blueberry, fresh and stored pollen can exceed 80–90 % germination in some cultivars, with strong genotypic differences (Huang & Johnson, 1996; Lang & Parrie, 1992). Pollen viability, assessed by fluorescein diacetate (FDA) staining, varies among *Vaccinium* species, with values of 51–97 % in *V. myrtilloides* Michx. and *V. vitis-idaea* (Stephens et al., 2012). Germination in the present study ranged from very low values to 63.93 %, which is consistent with the observed effects of genotype, environmental conditions, and their interaction on pollen functionality.

Pollen production and pollen germination represent complementary but distinct components of male reproductive performance in *Vaccinium*. While pollen production showed greater consistency among cultivars and locations, with variation mainly associated with growing season and specific year $\times$ location $\times$ cultivar combinations, pollen germination exhibited a stronger dependence on genotype and environmental conditions. Together, these results indicate that pollen quantity alone may not fully reflect reproductive potential, as pollen functionality represents an additional and potentially more environmentally responsive component of male reproductive performance under contrasting production environments.

Beyond pollen performance, reproductive success ultimately depends on the outcome of pollen–pistil interactions and subsequent seed development. The genus *Vaccinium* is generally considered self-compatible, as self-pollen is capable of germination, pollen tube growth, and ovule fertilization (DeVetter et al., 2022). However, reproductive success in *V. corymbosum* is strongly influenced by cultivar-specific responses and by the interaction between pollen source and female genotype, which can modulate fertilization efficiency and subsequent seed development (Leposavić et al., 2021; Liu et al., 2022; Martin et al., 2025). In addition, early-acting inbreeding depression has been reported in the genus, potentially leading to embryo abortion after self-fertilization and contributing to differences between fruit set and seed development (DeVetter et al., 2022).

Within this framework, cross-pollination has been associated with improved reproductive performance, although the magnitude of this response is genotype-dependent (Doi et al., 2018, 2021; Huang et al., 1997; Nagasaka et al., 2022; Noormets & Olson, 2006). In the present study, fruit set was influenced by the interaction among growing season, location, and pollination treatment, indicating that reproductive success depended not only on parental combination but also on the environmental conditions during each reproductive period. Similarly, the number of well-developed seeds per fruit was primarily affected by pollination treatment and location, with an additional influence of the year $\times$ pollination treatment interaction. These results suggest that fertilization success and seed development are influenced by the combined effects of genotype and environment.

Differences in the magnitude and direction of these responses are consistent with previous evidence indicating that reproductive outcomes in *Vaccinium* may depend on cultivar-specific genetic background and the expression of early-acting inbreeding depression (DeVetter et al., 2022; Krebs & Hancock, 1988). The observed dissociation between fruit set and the number of well-developed seeds per fruit indicates that these traits represent distinct components of reproductive success, with fruit set reflecting early reproductive processes and seed development involving subsequent stages of fertilization and embryo survival. However, the present study did not directly assess embryo abortion, inbreeding levels, or the physiological mechanisms underlying these responses, so interpretation is limited to phenotypic patterns.

Further studies integrating genetic, physiological, developmental, and environmental approaches may help elucidate the mechanisms responsible for reproductive variation in blueberry. A more detailed characterization of environmental conditions during critical reproductive stages, including temperature fluctuations and other microclimatic factors, would contribute to identifying the specific environmental drivers associated with variation among cultivars and locations. Such approaches would allow for a better understanding of genotype $\times$ environment interactions and their influence on pollen performance, fruit set, and seed development under contrasting production conditions.

Conclusions

This study provides the first characterization of the reproductive performance of southern highbush blueberry cultivars under the contrasting environmental conditions of northeastern Argentina. The differences between production locations and growing seasons, together with the contrasting responses observed among reproductive traits, indicate that pollen production, *in vitro* pollen germination, fruit set, and seed development should be considered jointly when evaluating reproductive performance. These findings contribute to understanding blueberry reproductive biology in this production region and provide a basis for cultivar evaluation and breeding programs. They also highlight the value of further characterizing environmental conditions across production locations and reproductive stages to better contextualize reproductive performance and guide future studies.

Acknowledgement

Grateful acknowledgment is extended to the Estaciones Experimentales Agropecuarias Bella Vista and Concordia, Instituto Nacional de Tecnología Agropecuaria (INTA), for their support during the study. Special thanks are extended to Víctor Manuel Beltrán for his technical assistance with fieldwork and phenology monitoring, and to Mario Alberto Almirón and Sergio Orlando Ramos for providing meteorological data from the Bella Vista and Concordia Experimental Stations, respectively. Appreciation is also extended to the commercial establishments “Fruitcrop S.A. – Quinta Palma Sola”, Concordia Department, and “El Panqueque S.R.L.”, Bella Vista Department, for providing access to their blueberry orchards and facilitating sample collection and experimental activities.

Interests conflict

The authors declare that there are no conflicts of interest related to this study.

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