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Floral Foraging Activity of *Amegilla calens* on *Solanum scabrum* Mill. (Solanaceae) and its Impact on Fruit Yield in Bambili, Cameroon

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Abstract

Solanum scabrum Mill. (Solanaceae) is a traditional leafy vegetable of major nutritional and socioeconomic value in Sub-Saharan Africa. Although capable of autonomous self-pollination, the precise contribution of native anthophilous insects—particularly buzz-pollinating bees—remains insufficiently quantified in Afromontane agroecosystems. This study evaluated the floral visitor complex, foraging behavior of *Amegilla calens* (Hymenoptera: Apidae), and insect-mediated yield enhancement in Bambili (North-West Cameroon) across two consecutive cropping seasons (2024/2025 and 2025/2026). Four experimental pollination treatments were established: open pollination (Treatment 1/1′), autonomous self-pollination in bagged flowers (Treatment 2/2′), single visit by *A. calens* on bagged flowers (Treatment 3/3′), and bagged control without insect visits (Treatment 4/4′). Data were analyzed using Generalized Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs), accounting for nested spatial and individual plant random effects. *Amegilla calens* was the predominant visitor, accounting for over 70% of total visits in both years. By vibrating its thoracic muscles (buzz pollination), *A. calens* efficiently extracted pollen from poricidal anthers. Open pollination significantly increased the mean number of seeds per fruit (69.10 ± 14.56 vs. 54.03 ± 10.71 seeds; $p < 0.001$) and seed normality (98.44% vs. 75.86%; $p < 0.001$) compared to autonomous selfing. A single visit by *A. calens* significantly increased seed number per fruit (+4.43 seeds) and normal seed percentage (+11.15%) in both study cycles. However, its effect on fruit set and mean fruit weight exhibited inter-annual variation, showing significant gains in 2024/2025 but non-significant differences in 2025/2026 ($p > 0.05$). *Solanum scabrum* possesses a mixed-mating system where specialized buzz pollinators provide essential pollination services that optimize seed set and seed vigor. Conserving wild bee nesting

sites and pollinator-friendly agricultural management are strongly recommended for regional smallholder farming systems.

Keywords

Amegilla calens, Buzz Pollination, Pollination Efficiency, *Solanum scabrum*, Yield Components

1. Introduction

Pollination is a fundamental process in the reproductive life cycle of angiosperms, facilitating the transfer of pollen grains from the male anthers to the receptive female stigma to ensure fertilization and fruit set [1]. This process occurs either within a single flower or between flowers of the same plant (self-pollination), or between different individuals of the same species (cross-pollination), thereby promoting genetic diversity [2]. Globally, animal vectors mediate approximately 80%-85% of biotic pollination in flowering plants [1]. According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) [3], animal pollination is critical to global food security, affecting a substantial proportion of world crop production. Beyond agricultural systems, pollinators sustain terrestrial biodiversity, supporting over 85% of wild flowering plant species [4] [5] and maintaining ecosystem stability [6].

Effective insect pollination relies heavily on functional diversity; higher pollinator diversity generally increases flower visitation frequencies and efficiency [4]. Among insect pollinators, bees (Hymenoptera: Apoidea) are widely recognized as highly efficient due to their specialized morphological adaptations for pollen collection and high flower constancy [7]. Despite their ecological and economic importance, beneficial insect populations are declining at an alarming rate due to anthropogenic pressures [6] [8]. This worldwide decline is predicted to trigger severe pollination deficits, threatening global agricultural yields and ecosystem resilience [9]. Consequently, assessing and conserving local pollinator biodiversity has become an urgent research priority.

In the western highlands of Cameroon, *Solanum scabrum* Mill. (Solanaceae), locally known as huckleberry or "Njama-Njama", stands out as a primary horticultural crop for smallholders, particularly rural women who dominate its production and retail sectors [10] [11]. This erect herbaceous plant reaches heights of 1.0 to 1.5 meters and is characterized by robust stems, large ovate deep-green leaves, and star-shaped white or light-purple flowers with prominent yellow-to-brown anthers [12] [13]. The fruits are broadly ovoid berries (12 - 17 mm in diameter) that transition from green to a deep purplish-black at maturity [12]. Highly valued for its rapid growth cycle and nutritional profile—being rich in essential micronutrients, vitamins, and minerals—*S. scabrum* is a traditional staple vital to regional food security [10] [14]. While historically grown for subsistence,

urbanization in major urban hubs has driven an increase in market demand, shifting its production toward intensive commercial farming systems [11] [15].

Despite the growing socioeconomic and nutritional importance of *S. scabrum* in Cameroon, most agronomic research has focused heavily on pathological constraints, soil fertility requirements, and vegetative yield optimization. Very little attention has been paid to its reproductive biology, particularly the functional role of floral entomofauna in fruit and seed development. Although many Solanaceae species benefit from buzz-pollination mediated by wild bees, the specific contribution of native species such as *Amegilla calens* to the yield parameters of *S. scabrum* remains insufficiently documented in the western highlands. Understanding these interactions is critical, as native pollinator populations face increasing pressures from habitat fragmentation and agrochemical use in peri-urban farming systems. To address these gaps, the present study was designed to clarify the functional relationship between *S. scabrum* and *A. calens* for improved crop and pollinator management in Bambili, Cameroon. Specifically, the objectives were to: (1) determine the relative abundance and composition of *A. calens* within the broader *S. scabrum* floral visitor assemblage; (2) characterize the specific foraging behavior and temporal dynamics of *A. calens* on *S. scabrum* flowers; and (3) evaluate the effect of insect access (comparing open exposure versus insect exclusion) alongside the specific yield contribution of single flower visits by *A. calens* on fruit set, fruit weight, and seed production. These findings aim to provide reliable baseline data for eco-friendly agricultural practices and pollinator conservation strategies tailored to smallholder agroecosystems in the region.

2. Materials and Methods

2.1. Study Site and Climate

The experiment was conducted during two consecutive cropping seasons (October-March 2024/2025 and October-March 2025/2026) in Bambili, Tubah Sub-Division, Mezam Division, North-West Region, Cameroon. Located along the Ring Road northeast of Bamenda, Bambili lies at 5˚56' N, a longitude of 10˚14' E, and an average elevation of 2,273 m above sea level [16]. The topography is undulating, featuring calderas, volcanic dykes, escarpments, plateaus, and valleys with elevations ranging between 900 m and 2,270 m [17]. The soils are predominantly lateritic and characterized by a distinctive red coloration [18]. The regional climate is tropical monsoonal, characterized by an average annual temperature of 22.5˚C and approximately 244 rainy days per year. It exhibits two distinct seasons: a rainy season extending from April to October and a dry season from November to March [19]. This rainfall regime supports both native vegetation and intensive subsistence farming, dominated by vegetable, tuber, and grain production.

2.2. Biological Materials

The plant material consisted of *Solanum scabrum* Mill., established using stem cuttings sourced from local farms in Bambili. The entomological material focused

on the wild bee *Amegilla calens* (Lepeletier, 1841) (Hymenoptera: Apidae), alongside the broader community of anthophilous insects naturally present on the experimental plot. The surrounding natural vegetation provided alternative floral resources for the local insect fauna.

2.3. Crop Management and Experimental Design

On 2 October 2024 and 15 November 2025, experimental plots were tilled and partitioned into 24 subplots (4 m × 2 m × 0.3 m). Subplots were separated by a 50 cm buffer zone. *Solanum scabrum* stem cuttings (5 - 7 cm height) were planted in four rows per subplot (50 cm between rows, 30 cm between plants within rows; total density of 24 plants per subplot). Manual irrigation was applied during establishment, and failed cuttings were promptly replaced. Manual weeding was conducted regularly. No chemical fertilizers or synthetic pesticides were applied to prevent disruption to native insect communities.

2.4. Assessment of Insect Contribution to Yield

To assess the breeding system and the degree to which crop yield depends on insect flower access, a Randomized Complete Block Design (RCBD) was implemented across four blocks per experimental season (2024/2025 and 2025/2026), with two subplots per block assigned to each core treatment. Two primary treatments were established at the balloon stage (immediately prior to anthesis) on labeled flower buds across 192 plants per year (n = 240 labeled buds per treatment per year):

Treatment 1 (2024/2025)/Treatment 1′ (2025/2026) (Unprotected Flowers, UF): 120 flower buds per year were left uncovered and fully exposed to open pollination throughout their lifespan.

Treatment 2 (2024/2025)/Treatment 2′ (2025/2026) (Protected Flowers, PF): 120 flower buds per year were enclosed in fine gauze mesh bags (mesh size 0.2 mm) to prevent all insect access, evaluating autonomous self-pollination.

Four weeks after the senescence of the last flower, the number of developed fruits was recorded for each treatment. The fruiting index (*Fi*) was calculated following Tchuenguem *et al.* [20] as follows:

$$F_i = F_a / F_b$$

where F_a is the number of fruits formed and F_b is the number of viable flower buds initially labeled. The allogamy rate (*Alr*) and the derived autogamy rate (*Atr*) were calculated according to Demarly [21]:

$$Alr = \left[\left(Fi_x - Fi_y\right)/Fi_x\right] \times 100$$

where Fi_x and Fi_y represent the mean fruiting indexes of the open-pollinated (Treatment 1 and Treatment 1') and bagged flowers (Treatment 2 and Treatment 2'), respectively. The autogamy rate (*Atr*) was deduced as:

$$Atr = 100 - Alr$$

2.5. Flower Visitor Composition and Voucher Specimens

Observations were conducted on open-pollinated flowers (n = 120 labeled flowers daily across Treatment 1 and 1' subplots) from 26 February to 3 March in 2025 and 2026. Daily counts of total open flowers per subplot were recorded prior to survey sessions. Field observations were structured across six daily time intervals: 06:00 - 07:00 h, 08:00 - 09:00 h, 10:00 - 11:00 h, 12:00 - 13:00 h, 14:00 - 15:00 h, and 17:00 - 18:00 h. During each interval, transect walks were conducted at a slow, standardized pace along the subplots of Treatments 1 and 1'. All anthophilous insects encountered on the labeled flowers were recorded following the method described by Tchuenguem [22]. Cumulative observation data were expressed as the total number of visits to establish the relative abundance and composition of the flower-visiting entomofauna of *S. scabrum* [23]. To evaluate the relative importance of each insect species, the visiting frequency (*Vf*) was calculated for each study period using the following formula adapted from Tchuenguem *et al.* [20]:

$$Vf = \left[\left(V_i / V_t\right) * 100\right]$$

where V_i represents the number of visits registered for a specific insect species on open-pollinated flowers, and V_t is the cumulative number of floral visits recorded across all insect species on those same flowers. Representative insect specimens were collected on adjacent, non-experimental *S. scabrum* plants using an insect net. Lepidoptera were stored dry in glassine envelopes; all other taxa were preserved in 70% ethanol. Taxa were identified to the lowest possible taxonomic rank using regional identification keys and taxonomic literature [24]-[26]. *Amegilla calens* (Lepeletier, 1841) was confirmed using diagnostic morphological keys for Afrotropical Anthophorini. Reference voucher specimens were deposited in the collection of the Laboratory of Zoology, Department of Biological Sciences, The University of Bamenda, Cameroon.

2.6. Foraging Behavior and Abundance of *Amegilla calens*

2.6.1. Floral Resources Harvested

In addition to assessing insect visitation frequencies, the specific foraging behavior of *A. calens* was directly monitored in the field to identify the floral resources collected (nectar, pollen, or both). Resource identification was based on characterization of foraging maneuvers: Nectar-foraging bees were identified by the extension of their proboscis towards the base of the corolla. Given the poricidal anthers of *S. scabrum*, pollen gatherers were identified by their characteristic floral vibrations (buzz pollination or sonication) to release pollen from the anthers, occasionally accompanied by active grooming of the anthers using their mandibles and legs [27].

These behavioral observations were carried out concurrently with the entomofauna surveys.

2.6.2. Duration of Floral Visits

The duration of a floral visit—defined as the total time spent by an individual bee

on a single flower to harvest nectar and/or pollen [22]—was recorded separately for both resource types. Timings were measured to the nearest second using a digital stopwatch, initiated immediately as the bee landed on a flower and stopped upon its departure. Measurements were taken across the same observation dates during six daily time frames designed to alternate with the faunistic surveys (07:00 - 08:00 h, 09:00 - 10:00 h, 11:00 - 12:00 h, 13:00 - 14:00 h, 15:00 - 16:00 h, 17:00 - 18:00 h), with a minimum of five distinct observations completed per time slot. Concurrently, we recorded whether the foraging bee made physical contact with the flower's stigma [28], serving as an indicator of pollination efficacy.

2.6.3. Foraging Speed

Foraging speed (*Fs*), defined as the number of flowers visited by an individual bee per minute [28], was evaluated during the same periods and time slots designated for visit duration. The digital stopwatch was started as soon as a focal bee landed on an initial flower, and the number of subsequent flowers visited was counted. The timer was stopped when the individual flew out of sight or transitioned to another plant species.

The foraging speed (*Fs*, in flowers per minute) was calculated as:

$$F_s = \left(N_f / d_v\right) * 60$$

where N_f is the number of flowers visited during the observation period, and d_v is the active foraging duration in seconds. If a bee returned to a previously visited flower during a single sequence, it was counted as two distinct floral visits [22].

2.6.4. Abundance of *Amegilla calens*

The abundance of *A. calens* was assessed using two metrics: the number of active foragers per flower and the abundance per 1,000 flowers (A_{1000}). Observations were synchronized with the dates and time slots of the visit duration monitoring. While the number of foragers per flower was determined by direct count, the abundance per 1,000 flowers was calculated following Tchuenguem Fohouo [22]:

$$A_{1000} = \left[\left(A_x / F_x\right) * 1000\right]$$

where A_x is the number of *A. calens* individuals actively foraging at time x, and F_x is the total number of open flowers counted on the surveyed subplots at the same time. At least three independent replicates of these counts were conducted per daily observation slot.

2.6.5. Foraging Ecology and Environmental Parameters

To assess the ecological context of the foraging activity, we monitored the disruption of *A. calens* visits by competitors or predators via direct observation. Additionally, the attractive pull of competing co-flowering plant species was evaluated by recording the number of times individual bees transitioned directly from *S. scabrum* to neighboring flora and vice versa. To correlate foraging dynamics with microclimate, ambient temperature (˚C) and relative humidity (%) were monitored at 30-minute intervals within the experimental station using a portable dig-

ital thermo-hygrometer positioned in the shade [22].

2.7. Single-Visit Efficiency Protocol for *Amegilla calens* and Handling Controls

To evaluate the single-visit efficiency of *A. calens*, a dedicated cohort of flower buds (n = 240 per year, out of the total N = 480 monitored flowers per year across all four treatments) was protected prior to anthesis using fine gauze mesh bags (0.2 mm mesh size). Upon anthesis, individual flowers were unbagged and monitored continuously:

Treatment 3 (2024/2025)/Treatment 3' (2025/2026) (Single Visit by *A. calens*, Fpvx): Flower buds were bagged prior to anthesis. At flower opening, bags were temporarily removed and monitored for up to 10 minutes. Once an individual flower received exactly one foraging visit by *A. calens* involving active thoracic vibrations (buzz pollination), it was immediately re-bagged until fruit maturity (n = 120 flowers in 2024/2025; n = 120 flowers selected from 145 monitored flowers in 2025/2026).

Treatment 4 (2024/2025)/Treatment 4' (2025/2026) (Handling Control without Insect Visit, Fpwv): 120 bagged flower buds per year were unbagged for up to 10 minutes while being strictly guarded against insect visits, and then re-bagged. This controlled for potential microclimatic alterations and mechanical handling artifacts associated with Treatment 3/3'.

At harvest maturity, all developed fruits across Treatments 1 through 4 (and 1' through 4') were harvested individually. The evaluated reproductive parameters included: Fruit set (fruiting rate, %); Mean fruit weight (g); Total seed count per fruit; Percentage of normal seeds (% fully developed, well-filled, viable seeds; [29]). Flat, shriveled, or aborted seeds were classified as abnormal.

2.8. Calculation of Specific Yield Contributions

The overall contribution of the open floral insect visitor community (Pr_i, %) to fruit set, fruit weight, seed count per fruit, and percentage of normal seeds was evaluated by comparing open exposure (T1/T1'), bagged control (T2/T2'), and handling control (T4/T4'):

$$P_{ri} = \left\{ \left[\left(P_{r1} - P_{r4} \right) / \left(P_{r1} + P_{r2} - P_{r4} \right) \right] * 100 \right\}$$

where P_{r1}, P_{r2}, and P_{r4} represent the fruiting rates obtained in Treatment 1 (open pollination), Treatment 2 (autonomous self-pollination), and Treatment 4 (bagged control), respectively.

The specific net contribution of a single visit by *A. calens* (P_{rAc}, %) was calculated relative to the unvisited handling control.

$$P_{rAc} = \left\{ \left[\left(P_{r3} - P_{r4} \right) / \left(P_{r3} \right) \right] * 100 \right\}$$

where P_{r3} is the mean yield parameter recorded in Treatment 3 (single visit by *A. calens*), and P_{r4} is the mean yield parameter recorded in Treatment 4 (unvisited handling control).

2.9. Statistical Analysis

Data were analyzed using mixed-effects models in R (v4.3.2) to account for the hierarchical experimental design (flowers and fruits nested within plants, subplots, blocks, and seasons). Treatment (T1 - T4/T1' - T4') and season (2024-2025 vs. 2025-2026) were defined as fixed factors, while block, subplot, and plant identity were included as random intercepts. Binary outcomes (fruit set) and proportions (% normal seeds) were analyzed using Generalized Linear Mixed Models (GLMM, lme4 package) with a binomial distribution and logit link function. Continuous variables (fruit weight, seed count, visit duration, foraging speed) were tested using Linear Mixed Models (LMM). Normality and homoscedasticity were verified via Shapiro-Wilk and Levene's tests, with log transformations applied when necessary. Visitor frequencies and counts were compared using Pearson's Chi-square (χ^2) or Fisher's exact tests. Relationships between microclimate (temperature, humidity) and foraging metrics (A_{1000}, duration) were assessed using Pearson correlation coefficients (r).

Post-hoc pairwise comparisons were conducted using Tukey's HSD test for LMMs and Bonferroni-adjusted z-tests for GLMMs via the emmeans package. Statistical significance was set at $\alpha = 0.05$.

3. Results

3.1. Floral Visitor Composition and Abundance

Table 1. Insect species recorded on *Solanum scabrum* flowers, with their visit numbers and relative frequencies (%) during the 2024/2025 and 2025/2026 cropping seasons.

Insects			2024/2025		2025/2026		Total	
Order	Family	Genus, species	n_1	p_1(%)	n_2	p_2 (%)	n_t	p_t (%)
Hymenoptera	Apidae	*Amegilla calens*[N, P]	693	94.67	713	66.08	1406	77.64
		Amegilla sp.[P]	-	-	128	11.86	128	7.07
		Apis mellifera[N, P]	24	3.28	48	4.45	72	3.98
	Halictidae	*Lasioglossum* sp.[P]	15	2.05	190	17.61	205	11.31
			732	100	1079	100	1811	100

Note: N: nectar foraging; P: pollen foraging; n_1: number of visits to 120 flowers in 7 days during the 2024/2025 season; n_2: number of visits to 120 flowers in 7 days during the 2025/2026 season; n_t: total number of visits across both seasons ($n_t = n_1 + n_2$); p_1, p_2 and p_t: percentages of visits for 2024/2025 [$p_1 = (n_1/732) \times 100$], 2025/2026 [$p_2 = (n_2/1079) \times 100$], and total visits [$p_t = (n_t/1811) \times 100$], respectively.

During the flowering periods of 2024/2025 and 2025/2026, four anthophilous insect species belonging to two families (Apidae and Halictidae) in the order Hymenoptera were recorded on *Solanum scabrum* flowers (Table 1). A total of 1,811 visits were observed across all species, with 732 visits recorded during the 2024/2025 season and 1,079 in the 2025/2026 season. *Amegilla calens* was by far the most abundant floral visitor, accounting for 94.67% ($n = 693$) of total visits in 2024/2025 and 66.08% ($n = 713$) in 2025/2026 (Table 1). Overall, *A. calens* represented

77.64% (n = 1,406) of all floral visits combined across both seasons. The proportion of *A. calens* visits differed significantly between the two experimental seasons (χ^2 = 217.10, df = 1, p < 0.001). Other recorded visitors included *Apis mellifera* (3.28% in 2024/2025; 4.45% in 2025/2026), *Lasioglossum cameroseliatus* (2.05% in 2024/2025; 17.61% in 2025/2026), and an undetermined congeneric species, *Amegilla* sp., which was exclusively recorded during the second season (11.86% in 2025/2026; Table 1).

3.2. Foraging Behavior and Activity Dynamics of *Amegilla calens*

3.2.1. Floral Resources Harvested by *Amegilla calens*

(a) (b)

Figure 1. *Amegilla calens*, (a) and *A. mellifera*; (b) collecting pollen from the flowers of *Solanum scabrum* at Bambili in 2025.

On *Solanum scabrum* flowers, *Amegilla calens* individuals actively harvested pollen (Figure 1(a)), whereas nectar collection was significantly less frequent. *Amegilla calens* exhibited specialized buzz-pollination behavior. Upon landing on the cone-like anther structure of *S. scabrum* (Figure 1(b)), the bee curled its body around the stamens, firmly grasped the filaments with its mandibles and legs, and rapidly contracted its thoracic flight muscles without moving its wings. This sonication resulted in an audible buzz that ejected a cloud of pollen grains through the apical pores onto the ventral abdominal and thoracic scopa of the bee, as well as onto the protruding receptive stigma. *Amegilla calens* exhibited high constancy regarding the type of floral reward harvested. In the 2024/2025 season, pollen harvesting accounted for 78.20% (n = 542) of total visits, while nectar collection represented 21.80% (n = 151). Similarly, in 2025/2026, the bees dedicated a significantly greater proportion of their visits to pollen collection (85.36%, n = 609) than to nectar harvesting (14.64%, n = 104). The difference between pollen and nectar harvesting frequencies was highly significant in both 2024/2025 (χ^2 = 219.60, df = 1, p < 0.001) and 2025/2026 (χ^2 = 355.80, df = 1, p < 0.001). Overall, across both crop-

ping seasons, pollen collection was overwhelmingly predominant over nectar foraging ($\chi^2 = 571.05$, $df = 1$, $p < 0.001$), with a significantly higher proportion of pollen-collecting visits observed during the second season ($\chi^2 = 12.45$, $df = 1$, $p < 0.001$).

3.2.2. Foraging Dynamics in Relation to Flowering Phenology

The foraging activity of *A. calens* was closely linked to the flowering phenology of *S. scabrum*. A strong positive and highly significant correlation was recorded between the daily number of *A. calens* floral visits and the number of open flowers in 2024/2025 ($r = 0.86$; $df = 4$; $p < 0.01$; Figure 2(A)) as well as in 2025/2026 ($r = 0.98$; $df = 5$; $p < 0.01$; Figure 2(B)).

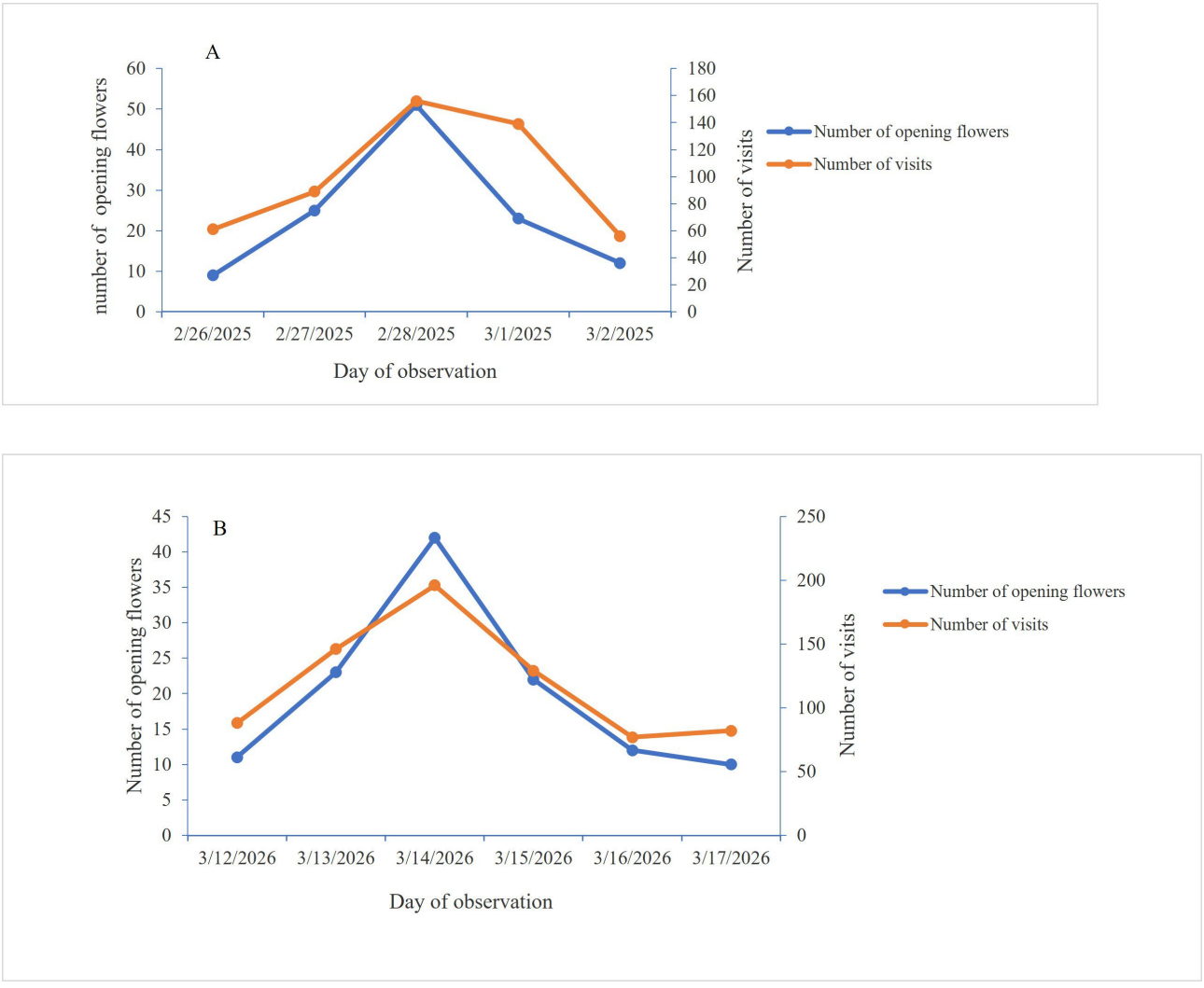
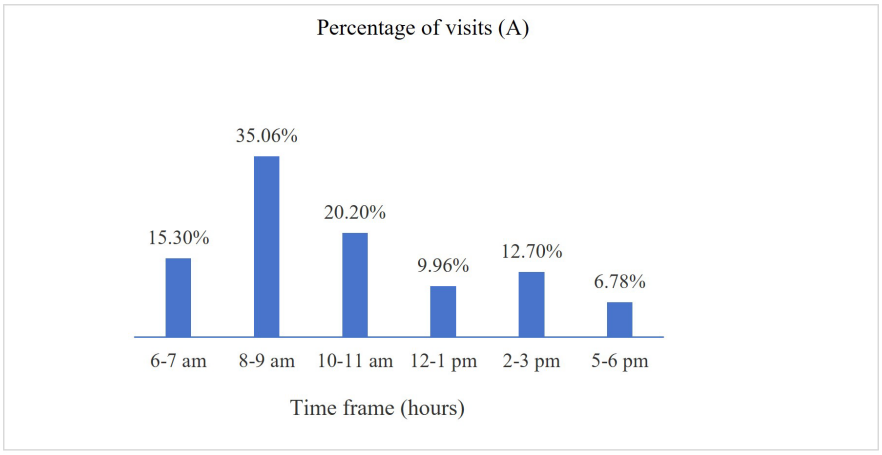


Figure 2. Daily variation of the number of *Solanum scabrum* open flowers and the number of *Amegilla calens* visits on these organs in the 2024/2025 (A) and 2025/2026 (B) cropping seasons at Bambili.

3.2.3. Daily Foraging Rhythm

Daily observations revealed that *A. calens* foragers were active on *S. scabrum* flowers from 6 h to 18 h. A peak in visit frequency occurred between 8 h and 9 h in both 2024/2025 and 2025/2026 (Figure 3).



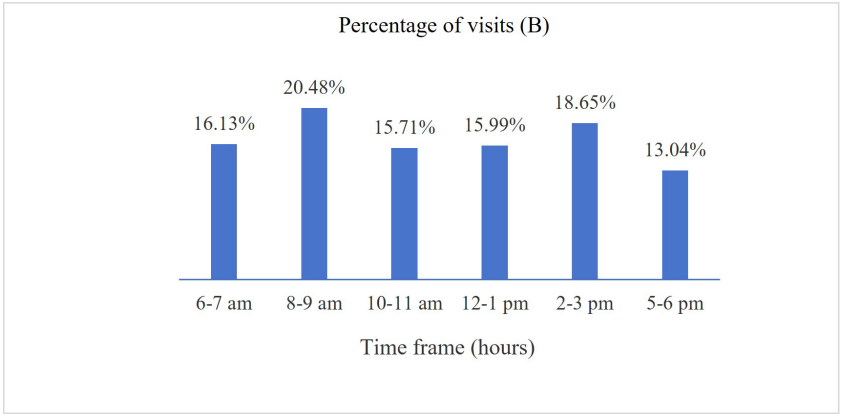


Figure 3. Diurnal foraging activity pattern of *Amegilla calens* on *Solanum scabrum* flowers by hour during the 2024/2025 (A) and 2025/2026 (B) cropping seasons.

Table 2. Mean ambient temperature (˚C) and relative humidity (%) across daily time intervals during the 2024/2025 and 2025/2026 cropping seasons.

Year	Parameters	Daily period (hours)					
		7 - 8	9 - 10	11 - 12	13 - 14	15 - 16	17 - 18
2024/2025	Number of visits	106	243	142	69	86	47
	Temperature (˚C)	27.46	36.32	36.77	39.92	36.86	31.85
	Hygrometry (%)	64.67	66.67	51.13	46.53	47.13	46.8
2025/2026	Number of visits	115	146	112	114	133	93
	Temperature (˚C)	18.8	20.41	24.72	26.16	23.97	22.70
	Hygrometry (%)	55.94	52.89	54.94	55.89	58.22	55.63

The relationship between environmental variables (ambient temperature and relative humidity) and the daily visitation activity of *A. calens* on *S. scabrum* flowers varied across the study period (Table 2). No significant correlation was detected between the number of *A. calens* visits and ambient temperature in 2024/2025 ($r = -0.14$, $df = 4$, $p = 0.787$) or in 2025/2026 ($r = -0.40$, $df = 4$, $p = 0.434$). Similarly, relative humidity showed a positive, non-significant correlation with visita-

tion frequency in both 2024/2025 ($r = 0.75$, $df = 4$, $p = 0.085$) and 2025/2026 ($r = 0.22$, $df = 4$, $p = 0.671$; Table 2).

3.2.4. Abundance of *Amegilla calens*

The maximum number of *A. calens* individuals observed active simultaneously on a single *Solanum scabrum* flower was one in both study years, indicating a solitary foraging behavior per flower. However, total forager density on the crop field differed significantly between experimental seasons: the mean number of foragers per 1,000 open flowers was significantly higher in 2024/2025 (369 ± 127; $n = 72$) than in 2025/2026 (276 ± 161; $n = 75$; $t = 3.86$, $df = 145$, $p < 0.001$). A peak density of 500 foragers per 1,000 open flowers was recorded in both experimental seasons.

3.2.5. Visit Duration of *Amegilla calens* according to Resource Type

Table 3. Duration of *Amegilla calens* visits on *Solanum scabrum* flowers during the 2024/2025 and 2025/2026 cropping seasons in Bambili, Cameroon.

Years	Visit for nectar harvesting			Visit for pollen harvesting		
	n	*m*	*sd*	*n*	*m*	*sd*
2024/2025	34	7.18	5.42	78	4.99	5.70
2025/2026	35	8.54	5.54	73	6.27	4.00
Total	69	7.87	5.48	151	5.61	4.98
	t = −1.03, *df* = 67, p = 0.308			t = −1.60, *df* = 149, p = 0.112		

Note: According to floral reward (nectar or pollen): *n*: number of visits; *m*: mean duration in seconds (s); *sd*: standard deviation.

The mean duration of *A. calens* visits on *S. scabrum* flowers depended on the type of reward collected (Table 3). During the 2024/2025 season, the mean visit duration was 7.18 ± 5.42 s ($n = 34$, maximum = 32 s) for nectar harvesting and 4.99 ± 5.70 s ($n = 78$, maximum = 46 s) for pollen harvesting. In 2025/2026, the mean visit durations were 8.54 ± 5.54 s ($n = 35$, maximum = 22 s) and 6.27 ± 4.00 s ($n = 73$, maximum = 15 s) for nectar and pollen, respectively. Between-year differences in mean visit duration were not statistically significant for either nectar ($t = -1.03$, $df = 67$, $p = 0.308$) or pollen ($t = -1.60$, $df = 149$, $p = 0.112$). Across both study seasons combined, the overall mean visit duration per flower was 6.31 ± 5.17 s ($n = 220$), with nectar visits (7.87 ± 5.48 s, n = 69) being noticeably longer than pollen-collecting visits (5.61 ± 4.98 s, n = 151).

3.2.6. Foraging Speed of *Amegilla calens* on *Solanum scabrum* Flowers

On *S. scabrum* flowers, the foraging speed of *A. calens* ranged from 5 to 15 flowers/min during the 2024/2025 cropping season and from 2 to 19 flowers/min during the 2025/2026 cropping season. The mean foraging speed was 6.69 flowers/min ($n = 64$; $sd = 3.94$) in 2024/2025 and 6.85 flowers/min ($n = 71$; $sd = 4.12$) in 2025-2026. The difference between these two annual means was not statistically significant ($t = -0.15$; $df = 133$; $p = 0.881$).

3.2.7. Influence of Floral Arthropod Presence on Foraging Behavior

The visit duration of *A. calens* was occasionally reduced by physical obstructions or behavioural disruptions caused by other arthropods present on *S. scabrum* flowers (Table 4). During the 2024/2025 cropping season, out of 693 recorded visits, 8 (1.15%) were interrupted by three insect species occupying the floral parts: *Aphis fabae solanella* (n = 4; p = 0.58%), *Camponotus* sp. ($n = 2$; $p = 0.29\%$), and *Coccinella* sp. ($n = 2$; $p = 0.29\%$). During the 2025/2026 cropping season, out of 713 recorded visits, 12 (1.68%) were interrupted by five insect species: *Aphis fabae solanella* ($n = 4$; $p = 0.56\%$), *Apis mellifera* ($n = 1$; $p = 0.14\%$), *Belonogaster* sp. ($n = 1$; $p = 0.14\%$), *Camponotus* sp. ($n = 2$; $p = 0.28\%$), and *Coccinella* sp. ($n = 4$; $p = 0.56\%$). The overall interruption rate did not differ significantly between cropping seasons ($\chi^2 = 0.74$, $df = 1$, $p = 0.389$).

Table 4. Interruption frequency of *Amegilla calens* visits on *Solanum scabrum* flowers during the 2024/2025 and 2025/2026 cropping seasons in Bambili, Cameroon.

Interrupter species	2024/2025 ($N = 693$)		2025/2026 ($N = 713$)	
	n	p (%)	n	p (%)
Aphis fabae solanella	4	0.58	4	0.56
Coccinella sp.	2	0.29	4	0.56
Camponotus sp.	2	0.29	2	0.28
Belonogaster sp.	0	0.00	1	0.14
Apis mellifera	0	0.00	1	0.14
Total interrupted visits	8	1.15	12	1.68

Note: N = total number of recorded visits by *Amegilla calens* per cropping season; n = number of interrupted visits; p = percentage of interrupted visits [$p = (n/N) \times 100$].

3.2.8. Influence of Neighboring Flora

During the study period, several co-flowering plant species competed with *Solanum scabrum* for *A. calens* visits for either pollen or nectar. These co-flowering species included *Callistemon rigidus* (Myrtaceae), *Talinum fruticosum* (Talinaceae), *Bidens pilosa* (Asteraceae), and *Vernonia amygdalina* (Asteraceae). During the 2024/2025 flowering period of *S. scabrum*, *A. calens* individuals exhibited strict flower constancy, with no individuals observed switching between *S. scabrum* and neighbouring flowers during a foraging bout. During 2025/2026, high floral fidelity was maintained, with only a single instance of a bee switching from *S. scabrum* to *T. fruticosum* to harvest nectar.

3.3. Reproduction Mode of *Solanum scabrum*

The fruit set of *S. scabrum* reached 0.98 (97.50%), 0.83 (82.50%), 0.93 (93.33%), and 0.78 (78.33%) for Treatments 1, 2, 1', and 2', respectively. During the 2024/2025 cropping season, the autonomous self-pollination rate was estimated at 84.69%, with insect-mediated pollination contributing an index of 15.31%. Sim-

ilar trends were observed in 2025/2026, with an autonomous selfing contribution of 83.93% and an insect-mediated contribution index of 16.07%. Across both cropping seasons combined, *S. scabrum* exhibited a mixed mating system predominantly supported by autonomous self-pollination (84.31%), complemented by an insect-mediated contribution index of 15.69%. The estimated insect contribution index did not differ significantly between the two cropping seasons (χ^2 = 0.01, df = 1, p = 0.922).

3.4. Impact of Insect Access on *Solanum scabrum* Yield Components

During nectar or pollen harvest on *S. scabrum* flowers, foraging insects systematically vibrated the flowers and regularly contacted both anthers and stigma, thereby increasing opportunities for self- and/or cross-pollination. Table 5 presents the fruiting rate, mean number of seeds per fruit, and percentage of normal seeds across the different pollination treatments.

a. Fruiting Rate (Fruit Set)

During the 2024/2025 cropping season, fruit set rates were 97.50% (T1), 82.50% (T2), 89.17% (T3), and 80.83% (T4). During the 2025/2026 cropping season, corresponding values were 93.33% (T1'), 78.33% (T2'), 75.00% (T3'), and 76.67% (T4'). Overall, differences among these eight treatment groups were highly significant (χ^2 = 42.77, df = 7, p < 0.0001). GLMM analysis revealed a highly significant effect of treatment on fruit set (χ^2 = 28.45, df = 3, p < 0.001). Pairwise contrasts showed that open-pollinated flowers (T1/T1') achieved a significantly higher fruit set than continuously bagged flowers (T2/T2') across both cropping seasons (p < 0.001), representing an overall insect-mediated fruit set increase of 15.00%. However, during the 2024/2025 cropping season, a single visit by *A. calens* resulted in a non-significant trend toward a higher fruit set compared to handling controls (89.17% vs. 80.83%; GLMM z = 1.83, p = 0.067). During the 2025/2026 cropping season, no significant difference was observed between T3' and T4' (75.00% vs. 76.67%; GLMM z = −0.31, p = 0.750). Across both years combined, a single visit by *A. calens* (T3/T3') did not significantly increase fruit set compared to unvisited bagged control flowers (T4/T4') (p = 0.182).

b. Mean Number of Seeds per Fruit

During the 2024/2025 cropping season, mean seed counts per fruit were 69.79 ± 14.31 (T1), 57.85 ± 10.22 (T2), 61.60 ± 17.81 (T3), and 57.76 ± 15.22 (T4). During the 2025/2026 cropping season, corresponding values for Treatments 1' to 4' were 68.40 ± 14.80 (T1'), 50.20 ± 11.20 (T2'), 56.70 ± 13.50 (T3'), and 53.10 ± 14.10 (T4'). Overall, differences among these eight treatment groups were highly significant ($F_{7, 800}$ = 24.78, p < 0.0001). Linear Mixed Model (LMM) analysis (accounting for plant and subplot random effects) confirmed a highly significant main effect of pollination treatment on the number of seeds per fruit ($F_{3, 796}$ = 31.42, p < 0.001). Post-hoc pairwise contrasts indicated that open-pollinated flowers (T1/T1') produced significantly more seeds per fruit than continuously bagged

flowers (T2/T2') across both cropping seasons ($p < 0.001$), representing an overall mean increase of 15.07 seeds per fruit (+27.89% relative to bagged self-pollinated flowers).

In both cropping seasons, a single visit by *A. calens* significantly increased seed count over control flowers ($p < 0.001$ in 2024/2025; $p = 0.004$ in 2025/2026). Across both years combined, a single foraging visit (T3/T3') added an average of +4.43 normal seeds per fruit (p=0.024 compared to T4/T4'), demonstrating that even a single foraging visit significantly enhances seed set in *S. scabrum*.

c. Percentage of Normal Seeds

Seed normality was 98.80% (T1), 58.01% (T2), 94.52% (T3), and 82.83% (T4) during the 2024/2025 cropping season, compared to 98.08% (T1'), 93.70% (T2'), 95.21% (T3'), and 84.59% (T4') during the 2025/2026 cropping season. Overall, differences among these eight treatment groups were highly significant ($\chi^2 = 79.99$, $df = 7$, $p < 0.0001$). The Generalized Linear Mixed Model (GLMM with binomial error distribution, accounting for plant and subplot random effects) confirmed a highly significant main effect of pollination treatment on seed normality ($\chi^2 = 56.34$, $df = 3$, $p < 0.001$). Overall, open pollination (T1/T1') significantly improved seed normality compared to autonomous self-pollination (T2/T2') ($\chi^2 = 54.18$, $df = 1$, $p < 0.001$), yielding a two-year average boost in seed normality of 22.58 percentage points. Post-hoc pairwise contrasts indicated that this enhancement was highly significant during the 2024/2025 cropping season ($p < 0.001$), whereas the difference was not statistically significant in 2025/2026 ($p = 0.390$).

Furthermore, a single visit by *A. calens* (T3/T3') significantly increased the percentage of normal seeds in both 2024/2025 (94.52% vs. 82.83%; $p < 0.001$) and 2025/2026 (95.21% vs. 84.59%; $p < 0.001$), representing a two-year mean gain in seed normality of +15.15% ($p < 0.01$ compared to T4/T4') and demonstrating that *A. calens* foraging visits substantially contribute to seed quality in *S. scabrum*.

d. Mean Fruit Weight

Mean fruit weights during the 2024/2025 cropping season were 0.072 ± 0.017 g (T1), 0.075 ± 0.021 g (T2), 0.065 ± 0.016 g (T3), and 0.057 ± 0.018 g (T4) ($F_{3, 210} = 9.209$, $p < 0.001$). During the 2025/2026 cropping season, values were 0.053 ± 0.021 g (T1'), 0.039 ± 0.013 g (T2'), 0.045 ± 0.019 g (T3'), and 0.050 ± 0.019 g (T4') ($F_{3, 171} = 14.906$, $p < 0.001$). Across both cropping seasons combined, the overall difference among these eight treatment means was highly significant ($F_{7, 520} = 27.02$, $p < 0.0001$).

Linear Mixed Model (LMM) analysis (accounting for plant and subplot random effects) confirmed a highly significant main effect of pollination treatment on fruit weight ($F_{3, 516} = 22.18$, $p < 0.001$). Post-hoc pairwise contrasts revealed that open pollination significantly increased fruit weight compared to bagged self-pollination during the 2025/2026 cropping season (T1' vs. T2': 0.053g vs. 0.039g; $p < 0.001$), whereas this effect was not statistically significant in 2024/2025 (T1 vs. T2: 0.072g vs. 0.075g; $p = 0.420$). Regarding single-visit efficiency, a single visit by *A. calens* significantly

enhanced fruit weight relative to unvisited bagged flowers during the 2024/2025 cropping season (T3 vs. T4: 0.065g vs. 0.057g; p = 0.018), whereas no significant difference was detected in 2025/2026 (T3' vs. T4': 0.045 g vs. 0.050 g; $p = 0.210$), highlighting inter-annual variation in single-visit effectiveness on fruit biomass.

e. Mean Seed Weight per Fruit

Linear Mixed Model (LMM) analysis (accounting for plant and subplot random effects) confirmed that across both cropping seasons, open-pollinated flowers (T1/T1') produced a significantly higher mean seed weight per fruit than continuously bagged self-pollinated flowers (T2/T2') ($F_{1, 381} = 21.69$, $p < 0.001$). Post-hoc pairwise comparisons showed that this difference was statistically significant during both the 2024/2025 cropping season (T1 vs. T2: $t = 20.86$, $df = 210$, $p < 0.001$) and the 2025/2026 cropping season (T1' vs. T2': $t = 14.20$, $df = 171$, $p < 0.001$).

Table 5. Fruit set rate, mean fruit weight, mean number of seeds per berry, and percentage of normal seeds across different pollination treatments of *Solanum scabrum* during the 2024/2025 and 2025/2026 cropping seasons in Bambili, Cameroon.

Year	Treatment	NF	NFr	FrR (%)	Seeds/fruit ($m \pm sd$)	Weight(g) ($m \pm sd$)	TNS	NNS	% NS
2025	1 (UF)	120	117	97.50	69.79 ± 14.31	0.072 ± 0.017	5095	5034	98.80
	2 (PF)	120	99	82.50	57.85 ± 10.22	0.075 ± 0.021	1967	1141	58.01
	3 (Fpvx)	120	107	89.17	61.60 ± 17.81	0.065 ± 0.016	4127	3901	94.52
	4 (Fpwv)	120	97	80.83	57.76 ± 15.22	0.057 ± 0.018	2429	2012	82.83
2026	1' (UF)	120	112	93.33	68.40 ± 14.80	0.053 ± 0.021	6841	6710	98.08
	2' (PF)	120	94	78.33	50.20 ± 11.20	0.039 ± 0.013	4258	3990	93.70
	3' (Fpvx)	120	90	75.00	56.70 ± 13.50	0.045 ± 0.019	4680	4456	95.21
	4' (Fpwv)	120	92	76.67	53.10 ± 14.10	0.050 ± 0.019	4250	3595	84.59

Note: NF: number of flowers; NFr: number of fruits; FrR: fruiting rate; TNS: total number of seeds; NNS: number of normal seeds; % NS: percentage of normal seeds; UF: unprotected flowers; PF: protected flowers; Fpvx: flowers bagged, visited once by *Amegilla calens* and rebagged; Fpwv: flowers bagged, uncovered and recovered without any visit; *sd* = standard deviation; *m*: mean.

4. Discussion

4.1. Floral Visitor Composition and the Role of Buzz Pollination

Amegilla calens was identified as the overwhelmingly predominant floral visitor of *S. scabrum* in Bambili, performing over 70% of the total recorded visits. This finding contrasts with reports on other Solanaceae in lower-altitude regions of Cameroon—such as Pando *et al.* [30] on *Capsicum annuum* in West Cameroon and Hassana *et al.* [31] on *Solanum aethiopicum* in Dang—where *Apis mellifera* was reported as the primary visitor. These geographic variations reflect regional climate shifts, altitude-dependent bee distributions, and floral morphological constraints [1]. The morphological match between *A. calens* and *S. scabrum* explains this predominance. The poricidal anthers of *S. scabrum* restrict passive pollen discharge. While generalist honeybees (*A. mellifera*) lack the thoracic vibrating mechanism required for sonication, *A. calens* is a specialized anthophorid bee ca-

pable of high-frequency buzz pollination. By rapidly vibrating the stamens, *A. calens* triggers massiv pollen ejection, maximizing pollination efficiency per unit time [32].

4.2. Insect-Mediated Yield Contribution vs. Autonomous Selfing

Our results demonstrate that while *S. scabrum* achieves high baseline autogamy (78.33% - 82.50% fruit set in bagged flowers), open access to anthophilous insects significantly improves fruit set, seed quantity, and seed quality. Open pollination increased seed count per fruit by ~28% and seed normality by ~22% over autonomous selfing. This enhancement aligns with broader findings on Solanaceae crops. For instance, Saidou *et al.* [33] recorded a 35.65% increase in seed count on *Solanum melongena* following *A. calens* visits, while Djakbé *et al.* [34] and Mamoudou *et al.* [35] documented significant yield gains on *Physalis minima* and *Solanum nigrum*, respectively. Rather than replacing autogamy, insect visits complement self-pollination by increasing pollen deposition density on the stigma and introducing cross-pollen (geitonogamy and xenogamy), thereby boosting fertilization rates and reducing potential inbreeding depression [5] [36].

4.3. Efficiency of Single Visits and Interannual Variability

The single-visit experiment (Treatment 3/3' vs. handling control Treatment 4/4') isolates the functional capability of *A. calens*. A single sonication event deposited sufficient pollen to significantly increase seed count (+4.43 seeds/fruit across seasons) and seed normality (+11.15%) compared to unvisited open-flower controls in both study years. However, the impact of a single visit on overall fruit set and fruit weight showed inter-annual variation—yielding statistically significant gains in 2024/2025, but non-significant differences in 2025/2026. This variability emphasizes that single visits may not always supply threshold pollen quantities required to maximize fruit pericarp expansion, especially under fluctuating ambient temperatures, rainfall, or plant resource constraints [6]. Multiple visits under open conditions remain necessary to achieve full agronomic potential.

5. Conclusion

Solanum scabrum cultivated in the Afromontane agroecosystem of Bambili possesses a mixed-mating system dominated by autonomous self-pollination, which is substantially optimized by the activity of native anthophilous insects. *Amegilla calens* is the primary and most efficient floral visitor, utilizing specialized thoracic sonication (buzz pollination) to extract pollen from poricidal anthers and ensure effective stigmatic deposition. Although autonomous selfing provides a reliable baseline fruit set, open insect access—and single foraging visits by *A. calens*—significantly enhance fruit yield parameters, particularly seed count per fruit and seed normality. These findings highlight the functional necessity of native wild bees in optimizing indigenous leafy vegetable production. Integrating pollinator-friendly practices, such as preserving natural nesting habitats and minimizing

chemical pesticide use, is strongly recommended to sustain pollination ecosystem services and secure seed production for smallholder farmers in the region.

Limitations of the Study

This study has several limitations. Geographically restricted to a single site in Bambili, the findings may not fully apply across diverse agroecological zones with varying microclimates. Methodologically, the experimental bagging design distinguished open pollination from autonomous selfing but could not differentiate geitonogamous from xenogamous pollen transfer, nor completely rule out microarthropods (e.g., thrips). Furthermore, the nesting habitat ecology of A. calens remains unquantified in the surrounding landscape. Finally, yield enhancements were assessed purely biologically, without a socio-economic valuation of seed production for smallholders.

Recommendations

To preserve *A. calens* and optimize *S. scabrum* seed production, local farmers should minimize broad-spectrum insecticide applications during peak flowering and protect unplowed soil banks that serve as nesting sites near crop fields. Future research should extend to multi-site assessments across different agro-ecological zones to map wild bee nesting preferences and quantify the monetary value added by buzz pollination to smallholder farming systems.

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Author Contributions

OANE conceived, designed, and supervised the study. NMT and YW contributed to supervision. NA carried out the field collection and performed the laboratory analysis. OANE and NA analyzed the data and wrote the manuscript. NMT and YW contributed to the draft of the manuscript. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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