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Warm Bulb Storage Optimises Flowering Attributes and Foliage Characteristics in *Amaryllis belladonna* L.

Carolyn Margaret Wilmot [1], Muhali Olaide Jimoh [1,2] and Charles Petrus Laubscher [1,*]

[1] Department of Horticultural Sciences, Faculty of Applied Sciences, Cape Peninsula University of Technology, P.O. Box 1906, Bellville 7535, South Africa; wilmotc@cput.ac.za (C.M.W.); muhali.jimoh@oouagoiwoye.edu.ng (M.O.J.)
[2] Department of Plant Science, Olabisi Onabanjo University, P.O. Box 2002, Ago-Iwoye 120107, Nigeria
* Correspondence: laubscherc@cput.ac.za

Abstract: *Amaryllis belladonna* is an autumn-flowering bulbous geophyte endemic to the Western Cape, South Africa. The species' erratic flowering disposition and brief flowering period upon maturity limit its economic productivity and competitiveness within the traditional genera of cut flowers and potted plants. However, it can be an attractive, eco-friendly, seasonal addition to the specialty floriculture market. A 10-month study evaluated the effects of a warm storage period on *A. belladonna* bulbs' flowering yield, flowering time, quality characteristics, and foliage growth. The experiment comprised dormant flower-sized bulbs randomly assigned to one of six storage regimes of either a 0- (no storage control), 4-, 6-, 8-, 10-, or 12-week interval periods at a continuous warm temperature of 23 ± 1 °C before planting into pots between mid-November 2021 and mid-February 2022 in the greenhouse. The results showed that flowering production (64.3% flowering after the 12-week storage), flowering time (anthesis occurring 9 days after the 10- and 12-week storage), and quality attributes (number of florets in the inflorescence, scape diameter, inflorescence fullness ratio, and pot longevity) of *A. belladonna* scapes were significantly impacted by warm bulb storage, but not foliage growth. Irrespective of bulb storage, inflorescence abortion occurred. An extended bulb storage did not advance the flowering time despite a greater harvest and shorter cultivation periods after planting. This study established that a cumulative temperature range during bulb dormancy is crucial for supporting the *A. belladonna* inflorescence maturity's energetic demands and the opening of floret buds. Bulbs should be stored at elevated temperatures for at least 8–10 weeks to attain the best floret-quality attributes and longevity. However, for an economical and sustainable greenhouse and specialty cut flower production, 12-week warm bulb storage is recommended to achieve the optimal anthesis in the shortest interval for this seasonal single-harvest species after planting.

Keywords: Amaryllidaceae; anthesis; dormancy; specialty cut flower; temperature duration; traditional cut flower

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1. Introduction

Cut flowers and potted plants are among the most extensively produced and marketed ornamentals in the leading and competitive traditional floriculture sector and a multibillion-dollar international export-oriented industry [1,2]. Successful cultivation and production of these ornamental crops have generally emphasised the species appeal, aesthetic traits, and flowering time variation, with significant efforts to attain these targets to meet timeous demands [3,4]. However, a recent awareness of ornamental horticulture has rekindled the interest in features of production sustainability as a selection criterion [5,6]. This movement has been propelled by the realisation of the high levels of resource consumption, energy-intensive production techniques, rapid distribution channels, and profitability to preserve and maintain the traditional standards of ornamental crops at the expense of biodiversity and contribution to the values of the local ecosystems, culture, and societal well-being [5–7].

Due to the significant sustainability issues associated with ornamental plants, producers, and sellers must analyse and mitigate the species' life cycle assessment (LCA) through sustainable and integrated production techniques for future cultivation [5,6]. Among them, given the high cost of greenhouse production and maintenance, spending less time in the greenhouse would alleviate the load on the LCA and minimise production costs [5,8,9]. As a result, speciality cut flower (SCF) production and sales have increased over the last 15 years, drawing attention to the critical role they serve in the worldwide floriculture industry as a viable and sustainable substitute to traditional cut flower (TCF) crops [4]. The SCF market objectives promote various aesthetic features and are strengthened by the preservation of indigenous and underutilised flora grown locally, seasonally, and sustainably produced [4,6,10].

Amaryllis belladonna L. is an inimitable autumn-flowering bulbous geophyte endemic to the botanically diverse fynbos biome of South Africa's Cape Floristic Region [11–14]. Formerly, *A. belladonna* was classified as a monotypic genus of the Amaryllidaceae family [15]. The species is cultivated and naturalised in Mediterranean regions worldwide, where hot, dry summers alternate with mild, wet winters [11,13,14]. *Amaryllis belladonna* owes its numerous vernacular names, "Belladonna Lily", "March Lily", and "Naked Lady", to its hysteranthous habit, which displays a solitary inflorescence on a naked stem in late summer to early autumn. The umbellate floral arrangement consists of fragrant, trumpet-shaped florets that open in coordinated succession to exhibit a range of iridescent pale ivory to deep pink-shaded tepals (Figure 1A). Its strap-shaped leaves unfurl actively at the onset of winter rains and cooler autumn temperatures. When late spring transcends and seasonal temperatures rise, the leaves wither, initiating the bulb's summer dormancy [11–14].

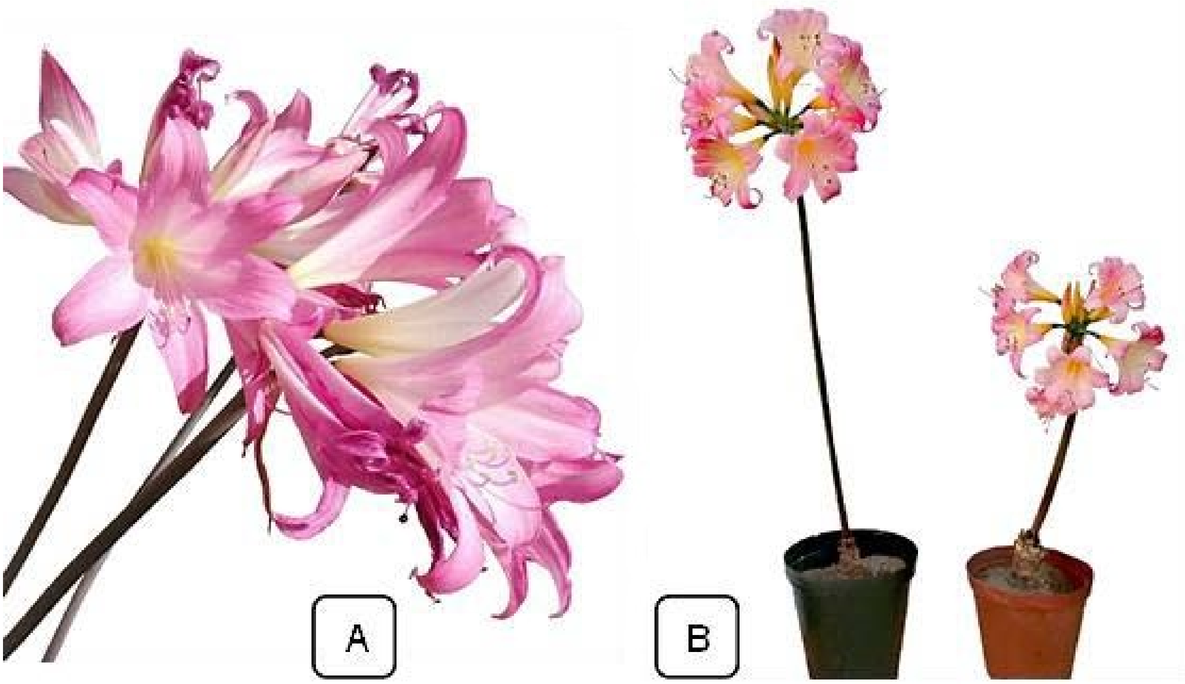

Figure 1. *Amaryllis belladonna* in full anthesis as a cut flower (**A**) or potted plant (**B**) (photos: C. Wilmot).

In a variety of floriculture, landscape, and ornamental industry settings, the perennial bulb's seasonal adaptability, aesthetic splendour, drought tolerance, and minimal maintenance needs, along with its closely related and well-known species, *Clivia*, *Narcissus*, and *Nerine*, have brought conscious recognition to their valuable and desirable commodities [3,4,16–18]. The comparatively short flowering period of *A. belladonna*, which predictably lasts between six and nine weeks, is a significant shortcoming despite the species' promising allure. In addition, once a critical bulb size is attained, each bulb produces only a single inflorescence per season and often encounters a capricious flowering disposition [12,14,19], limiting its marketable application as an influential cut flower and potted plant under the tight parameters of the traditional floriculture trade (Figure 1A,B).

Flowering is a multifaceted complexity of sequential events governed by endogenous mechanisms and extrinsic environmental signals [20–22]. According to several authors, temperature is a critical factor influencing the numerous physiological and morphological processes involved in the induction and differentiation of floral organs and flowering time [21,23–28]. Temperature regulation during dormancy is crucial to regulate bulbs' reproductive forcing, qualities and timing intended to produce timely high-quality flowers [5,29,30]. Although organogenesis of bulb dormancy is an ecological adaptation that allows plant species to survive unfavourable climatic conditions below the soil surface, it provides a favourable stage for handling, treatment, and shipping [31]. Depending on their natural phenological growth conditions, different taxa require different successive temperature regimes to pass through certain developmental stages to flowering [12,25,32]. Mediterranean geophytes' annual rhythmic cycles typically follow a warm–cold–warm cycle.

According to [33], there are many possibilities to increase flowering in *A. belladonna* bulbs, including physical bulb traits (age, size, and dormancy), bulb disturbance and replanting establishment, and environmental factors, such as temperature, to stimulate flower initiation. Exposure to greater temperatures during summer dormancy encourages flowering in the bulbs [13]. Warm storage treatments during dormancy are well-established in the floriculture industry, and in addition to their ability to accelerate or delay flowering, they increase quality attributes and yield percentages. Warm storage (between 25 °C and 30 °C) resulted in later flowering or vernalisation in several *Ornithogalum* bulb species, leading to higher percentage yields and earlier flowering [24]. Similarly, when subjected to consistently higher storage temperatures immediately after leaf wilting, saffron (*Crocus sativus* L.) bulbs flowered earlier [34]. Storage temperatures up to 25 °C promoted healthy vegetative development, inflorescence maturity and flower bud opening in *Watsonia* corms [35]. Storage significantly impacted the flower diameter and number of days before flowering in *Hippeastrum* [36] and accelerated flowering in *Eucomis* species [37]. Other Amaryllidaceae genera that flourish in hot, dry summer areas and respond to warm storage techniques include *Narcissus* species, *Nerine flexuosa*, and *N. sarniensis* [38]. According to [24], standardised forcing protocols make an analysis and comparison extremely challenging; therefore, clarifying the processes that modify these factors in floricultural crops is essential to achieve sustainable production and increased product quality.

There is a pressing need to advance specialized cultivation technologies and adaptations to overcome obstacles in furthering our understanding of indigenous and underutilised plant species [10,16,39]. Progress cannot advance without thorough scientific investigation, and the awareness that ornamental geophytes' intrinsic genetic variation and composition are increasingly valued [16,40,41], and research is needed to encourage growers to cultivate and reintroduce these species to the industry [42,43]. Furthermore, geophytes are a broad group of plants that impact agricultural production and as a result, each novel insight into a species's behavioural characteristics is crucial to its development [31,44,45]. The floriculture industry may implement strategies in contrast to the conventional mainstream that explore and establish alternative approaches to encourage producers to cultivate and reintroduce more sustainable and resilient indigenous and underutilised species for the SCF market, particularly in hot, dry climates with limited water availability. Although extending *A. belladonna's* flowering time would improve the seasonal period of successful SCF production, the competent number of flower stems grown could facilitate and regulate the expansion. These developments would enable greater financial returns through increased market penetration and the ability to manage a larger, more efficient single-harvest crop under sustainable growing methods at the same or lower cost per unit value within the growing season [33]. The most effective approach for inducing optimal flowering during *A. belladonna's* dormancy has not been clearly defined, and there is a scarcity of published scientific research assessing the precise duration of simulating warm temperatures and subsequent planting for these purposes. Therefore, to disseminate a better understanding of the species complex LCA and facilitate the efficiency and expansion of flower production as a sustainable niche crop for the SCF sector of the floricultural network, *Amaryllis belladonna* bulbs were evaluated to establish the most effective warm storage duration for the optimal flowering production, flowering time, visual quality, and foliage characteristics after planting in the greenhouse.

2. Materials and Methods

2.1. Experimental Location

A 10-month study was conducted from mid-November 2021 to the end of September 2022 in the research greenhouse facility of the Department of Horticultural Sciences at the Cape Peninsula University of Technology in Bellville, Cape Town, South Africa, 33°55′45″ S, 18°38′31″ E. The ventilated greenhouse includes a thermostatically regulated system and a transparent polycarbonate roof sheet (Envirowatch, Envirowatch Solutions, Estcourt, South Africa). Evaporative cooling walls, extractor fans, and heaters kept air temperatures in the greenhouse between 21 °C and 26 °C during the day and 14 °C and 18 °C at night. The relative humidity (RH) averaged 60%. Under natural light conditions, the daily average photosynthetic photon flux density (PPFD) was 420 µmol/m^2/s, with the intensity peaking at 1020 µmol/m^2/s. The photoperiod corresponded to the prevailing conditions between late spring and early winter (9–12 h).

2.2. Plant Material and Preparation

Eighty-four dormant, flower-sized *A. belladonna* bulbs (30–33 cm circumference, corresponding to a diameter of 9.5–11 cm) were obtained from Assegaaibosch Farm on the Agulhas Plain in the Western Cape, South Africa, in mid-November 2021 (mid–late spring in the southern hemisphere) at the commencement of their dormancy period. Two weeks prior, the contractile bulb roots were undercut deep beneath the soil to accelerate the progression rate of late leaf senescence. After two weeks, the bulbs were uprooted while preserving as many roots as possible and minimising damage, utilising traditional cultural practices and those particular to the Amaryllidaceae species, as [46] outlined. The bulbs were rinsed to remove any unwanted surface soil debris, stripped of senescent leaves, and sorted to ensure sample homogeneity. Selected bulbs were later dipped in Sporekill™ (ICA International Chemicals (Pty) Ltd., Stellenbosch, South Africa), a biocidal solution with didecyldimethylammonium chloride as the active ingredient, at a dilution rate of 0.1% for 5 min, removed, air dried, and placed in warm storage.

2.3. Experimental Design and Treatment Set-Up

Experimental treatments included bulbs randomly assigned to one of six storage regimes with intervals of 0 (no storage, control), 4, 6, 8, 10, or 12 weeks (Table 1). Storage-treated bulbs were conditioned in breathable containers at a constant temperature of 23 ± 1 °C and 60% relative humidity in a ventilated and darkened room in mid-November 2021. The continuous warm storage temperature was derivative of the relative mean ambient temperature of the bulb's endemic phenological region during the height of summer. After the prescribed storage intervals, the bulbs were planted individually into standard round plastic pots (20 cm diameter and 3 L volume) in mid-November (0-control), mid-December (4 weeks), end-December (6 weeks), mid-January (8 weeks), end-January (10 weeks), and mid-February (12 weeks) and placed in the greenhouse for further development, differentiation, and flowering (Table 1). The pots were filled with a growing substrate consisting of sieved compost, fine river sand, and pre-rinsed silica sand (Consol®, grade 6/17) at a ratio of 1:1:1 (*v*/*v*/*v*), ensuring that the neck of each bulb was visible on the surface [46]. A weekly soil drench with tap water (of equal quantities) was applied manually to maintain moisture levels in all planted bulb treatments. Experimental pots were placed on the greenhouse floor in a complete randomised block design (CRBD) with 14 sample replicates per storage interval (n = 14).

Table 1. Warm bulb storage duration of a continuous 23 ± 1 °C at 60% RH in a ventilated, darkened room and the subsequent planting time after storage in the greenhouse.

S/N	Code	Storage Duration Description	Subsequent Planting Time after Storage
1	D1	0-week bulb storage (c) (0 days)	(mid-November 2021)
2	D2	4-week bulb storage (28 days)	(mid-December 2021)
3	D3	6-week bulb storage (42 days)	(end-December 2021)
4	D4	8-week bulb storage (56 days)	(mid-January 2022)
5	D5	10-week bulb storage (70 days)	(end-January 2022)
6	D6	12-week bulb storage (94 days)	(mid-February 2022)

D = storage duration; (c) = control.

2.4. Data Collection

2.4.1. Determination of Inflorescence Morphological Development

Morphological data were recorded as markers of inflorescence growth and development (that remained attached to the potted bulb) using a standard soft cloth metric tape measure (Empisal EMT-001, Builders Warehouse, Boksburg, South Africa), a stainless-steel ruler (Sealy, Leroy Merlin, Boksburg, South Africa) with readability of 1500 × 12 mm and 450 × 25 mm, respectively, and a steel vernier calliper (Grip GV9370, Leroy Merlin, South Africa) with a readability of 0.02 mm.

The following parameters were used to assess inflorescence characteristics: percentage of bulbs that produced a flowering inflorescence, length and diameter of the stem (scape) (mean relative value determined both at the widest point and when rotated horizontally through 90°), number of florets per inflorescence, and length and diameter of a single floret (the first floret to develop). The diameter of the inflorescence crown, fullness ratio, and potted longevity were evaluated to assess the marketability of the potted bulb inflorescence. The diameter of the inflorescence crown was determined using the mean relative value of the distance measured from one side of the circumferential edge through the centre of the umbel arrangement to the outermost edge and at a horizontal rotation of 90° (Figure 2). The fullness ratio was calculated as the ratio of florets to crown diameter, and inflorescence longevity was characterised as the time interval between the opening of the first and the wilting of the last floret on a potted inflorescence scape.

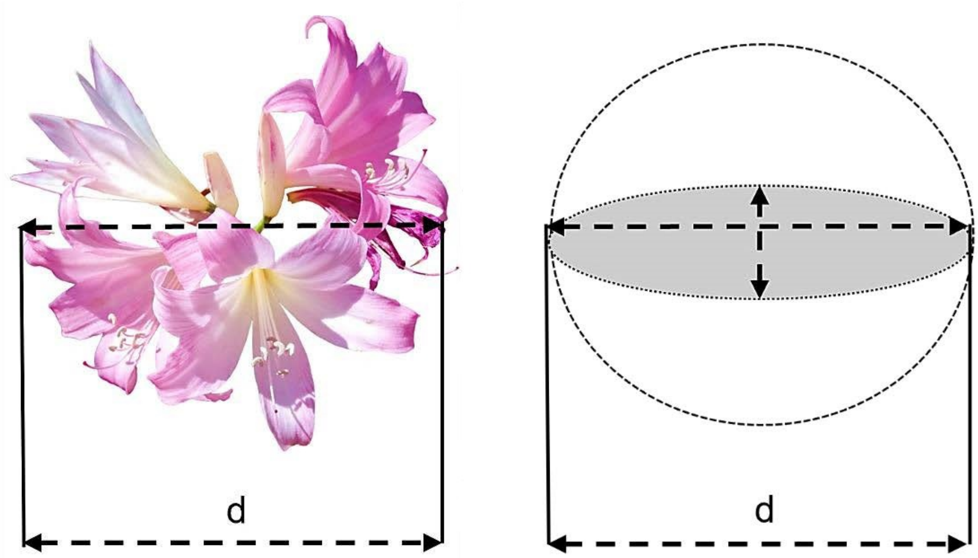

Figure 2. Determination of the relative average inflorescence crown diameter (d) of *Amaryllis belladonna*; measured from one side of the circumferential edge through the centre of the umbel arrangement to the other side and at a 90° horizontal rotation. (photo and diagram: C. Wilmot).

2.4.2. Determination of Inflorescence Flowering Time Course

Observations made up to five times per week were evaluated to determine different transition events during the flowering phase. Days to flowering were observed as the date of appearance of the visible flower buds, the opening of the first floret (anthesis), the opening of 50% of florets per inflorescence, and complete floral senescence (the wilting of the last floret on the inflorescence stem) and recorded as the number of days after planting (DAP) in the greenhouse.

2.4.3. Determination of Leaf Morphological Growth

During the resumptive vegetative leaf phase, morphological data were collected using the precision measuring devices described above to assess leaf growth and development. The number of leaves produced by each bulb, leaf length, leaf width, and leaf area were recorded. The number of leaves was determined manually, and leaf length was determined as the distance between the base of the longest leaf (where it first emerged from the bulb) and its apex, while leaf width was measured at the widest point of the leaf. The Montgomery equation (ME) described by [47,48] was used to calculate leaf area.

$$A_{leaf} \propto L_{leaf} \times W_{leaf}$$

where A = area; L = length; W = width; and α = Montgomery parameter.

2.5. Statistical Analysis

Morphological data were calculated and analysed using statistical data analysis software (Minitab 17, Minitab LLC, Pennsylvania State University, USA). Data were subjected to one-way analysis of variance (ANOVA) for the factor bulb storage duration (6 levels) and presented as means with standard errors (S.E.s). Fisher's least significant difference (LSD) was used to further separate the means at a significance level of $p \leq 0.05$. Means with a different letter(s) differed significantly at the 95% confidence level.

3. Results

3.1. Effect of Warm Bulb Storage Period on Inflorescence Morphological Development

3.1.1. Percentage Flowering Yield

This study showed that bulb storage treatments significantly affected the number of bulbs that flowered in the greenhouse in a storage-dependent manner ($p \leq 0.05$). As shown in Figure 3, between 14.3% and 64.3% of the *A. belladonna* bulbs produced an emergent inflorescence and flowered, while the remaining bulbs persisted in a vegetative state. The practical flowering potential of the bulbs increased dramatically after 12 weeks of storage and planting in mid-February 2022, with the maximum proportion of emerging flower buds (64.3%). However, the variance was statistically marginal compared with the control without storage and immediate planting (50%). The percentage of flowering bulbs declined within the 4- and 10-week storage range, with the shorter storage durations and subsequent planting showing the most significant reduction (14.3%).

3.1.2. Inflorescence Stem Length and Stem Diameter

Inflorescence stem length was not affected by the storage duration ($p > 0.05$); however, there were significant visual differences (37.0–56.7 cm) between treatments (Figure 1B). In contrast, the stem diameter responded differently, and the bulb storage had a significantly positive effect ($p \leq 0.05$) on the inflorescence stem thickness (Table 2). Compared to the no-storage control (8.9 mm), the stem diameter was thicker in all storage-treated bulbs (9.6–12.7 mm) (Table 2). The bulbs stored for 8 weeks had the longest (56.7 cm) and thickest (12.7 mm) inflorescence stems.

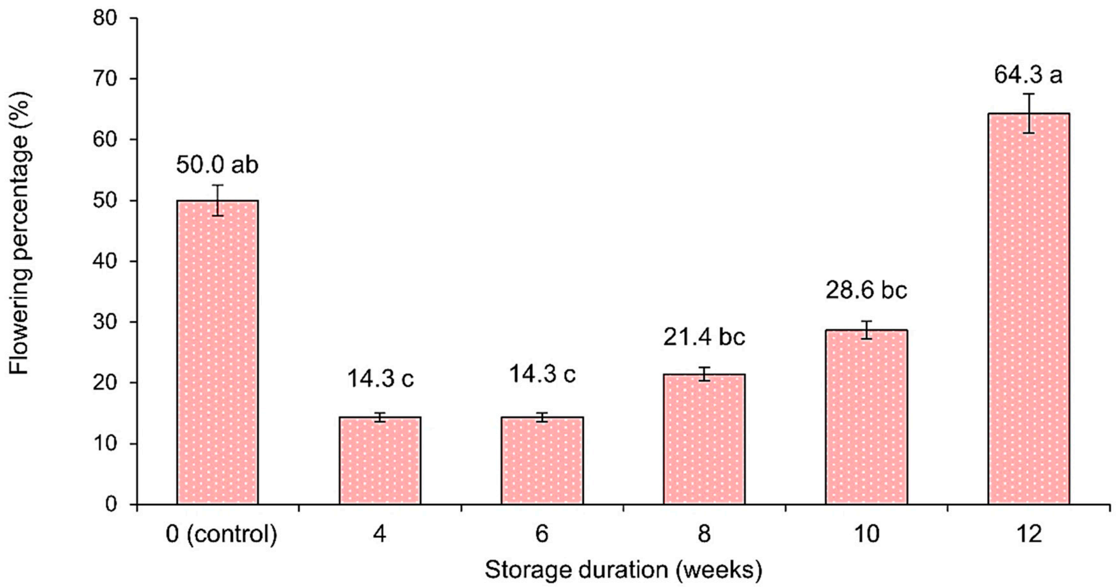

Figure 3. The effect of warm bulb storage duration and subsequent planting on flowering percentage, as defined by successful potted inflorescence maturation of *Amaryllis belladonna* bulbs. Bars represented by mean values followed by a different letter(s) are significantly different at $p \leq 0.05$, according to Fisher's least significant difference (L.S.D).

Table 2. Effects of warm bulb storage period over 12 weeks on inflorescence characteristics of stem length, stem diameter, number of florets, floret length, floret diameter, crown diameter, and fullness ratio of *Amaryllis belladonna* bulbs under greenhouse conditions.

Bulb Storage (Weeks)	Inflorescence Characteristics						
	Inflorescence Stem Length (cm)	Inflorescence Stem Diameter (mm)	Number of Florets (n)	Floret Length (cm)	Floret Diameter (cm)	Inflorescence Crown Diameter (cm)	Inflorescence Fullness Ratio
0 (control)	45.1 ± 2.89 b	8.9 ± 0.39 d	9.6 ± 0.90 b	12.0 ± 0.36 a	9.8 ± 0.21 a	22.7 ± 0.64 a	0.4 ± 0.04 b
4	39.2 ± 6.00 b	9.6 ± 0.66 cd	8.0 ± 4.00 b	11.4 ± 0.75 a	9.2 ± 0.55 a	21.6 ± 1.35 a	0.4 ± 0.21 b
6	37.0 ± 6.55 b	10.5 ± 0.09 bcd	12.5 ± 4.50 ab	11.8 ± 0.85 a	9.5 ± 0.70 a	22.4 ± 1.46 a	0.6 ± 0.24 ab
8	56.7 ± 6.08 a	12.7 ± 0.02 a	17.0 ± 5.78 a	11.5 ± 0.10 a	9.6 ± 0.07 a	21.9 ± 0.17 a	0.8 ± 0.03 a
10	43.2 ± 5.72 b	11.7 ± 0.75 ab	16.5 ± 1.50 a	10.8 ± 0.53 a	8.9 ± 0.42 a	21.0 ± 0.87 a	0.8 ± 0.09 a
12	44.0 ± 1.23 b	10.2 ± 0.36 c	10.2 ± 0.97 b	11.6 ± 0.39 a	9.5 ± 0.36 a	22.0 ± 0.72 a	0.5 ± 0.05 b
			One-way ANOVA F-statistic				
Bulb storage	2.15 ns	7.16 *	5.31 *	0.74 ns	0.67 ns	0.50 ns	4.51 *

Mean values ± standard error (S.E.) in the same column with a different letter(s) are significantly different at $p \leq 0.05$ (*) based on Fisher's least significant difference (L.S.D); ns = not significant.

3.1.3. Number of Florets

The analysis showed that the storage treatments had a significant ($p < 0.05$) effect on the number of florets produced by each inflorescence, as shown in Table 2. Bulbs stored for 8 weeks had the most florets (17.0); however, there were no statistically significant differences between the 6- and 10-week treatments. Although statistically comparable to the control and 12-week treatments, the lowest number of florets (8.0) was observed in inflorescences after 4 weeks of storage.

3.1.4. Floret Length and Diameter

The storage period did not significantly affect treatment comparisons of floret length ($p \leq 0.05$). The floret diameter showed a similar tendency. Nevertheless, the control treatment (12.0 and 9.8 cm) had the highest and the 10-week storage (10.8 and 8.9 cm) the lowest values for the floret length and diameter characteristics for all treatments, as indicated in Table 2.

3.1.5. Inflorescence Crown Diameter

At the 95% confidence level, the storage interval had no discernible effect on the spherical-ovate crown diameter of the inflorescence arrangement. Table 2 shows that although there was no statistically significant difference between treatments, the control (22.7 cm) had the largest crown diameter, about 2 cm wider than the smallest diameter in the 10-week storage period (21.0 cm).

3.1.6. Inflorescence Fullness Ratio

The visual quality of the inflorescence was assessed by comparing the fullness ratio. Storage duration strongly influenced this characteristic reception, as shown in Table 2 ($p \leq 0.05$). The highest ratios (0.8:1) were observed in inflorescences stored for 8 and 10 weeks; however, the crowns were not significantly fuller than those stored for 6 weeks (Table 2). In addition, although not statistically different and less compact, a ratio of 0.4:1 was observed in the control and at 4 and 12 weeks of storage.

3.1.7. Inflorescence Longevity

The data presented in Figure 4 show a significant effect of storage treatment ($p \leq 0.05$) and subsequent planting on the potted inflorescence longevity of *A. belladonna* scapes. Apart from the shortest storage duration of 4 weeks (10 days), the bulb scapes in the 10-week storage had the longest flowering interval (17.5 days) but did not differ significantly from the control or any other treatments (14.6–16.7 days).

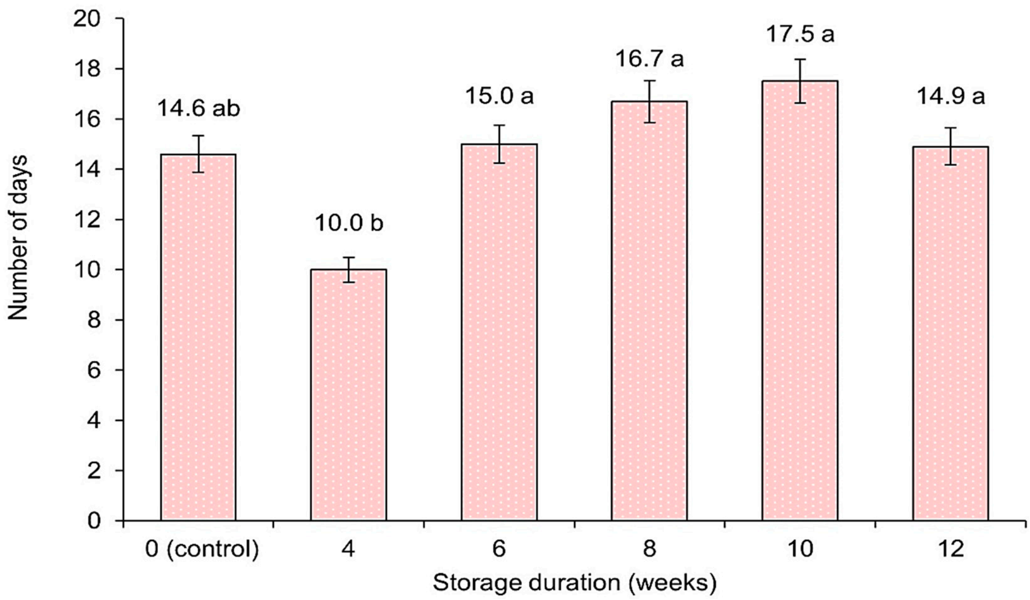

Figure 4. The effect of warm bulb storage duration on *Amaryllis belladonna* bulbs inflorescence potted longevity. Bars represented by mean values followed by a different letter(s) are significantly different at $p \leq 0.05$, according to Fisher's least significant difference (L.S.D).

3.2. Effect of Warm Bulb Storage Period on Flowering Time Course of Visible Flower Buds, Anthesis, Opening of 50% Florets, and Complete Floral Senescence

The results in Figure 5 show a significant difference ($p \leq 0.05$) in the occurrence of visible flower buds in response to storage treatments and subsequent planting. Compared to the immediately planted control, the bulbs stored for 10 and 12 weeks, and the last to be planted were the first to show flower buds 9 days after planting. In addition, the flower buds of the 10-week storage bulbs emerged two weeks earlier than those of the 12-week storage, although they were statistically similar. Compared to the control, the onset of flower bud emergence was delayed by an average of 7 days for shorter storage periods of 4 and 6 weeks.

The timing of the first floret opening (anthesis) occurred between 17.9 and 101.0 days after storage intervals and subsequent planting in the greenhouse. It was significantly reduced compared to days after planting in the control bulbs ($p \leq 0.05$) (Figure 5). The first anthesis was observed three days earlier in the 8 and 10-week treatments than in the control bulbs. In addition, the opening of the first floret was delayed by about 5 days in the 12-week storage and 10 days in the 4- and 6-week storage compared to the control. Although the developmental course of anthesis differed by a few days between treatments, it occurred 7.4–13.0 days after flower bud emergence.

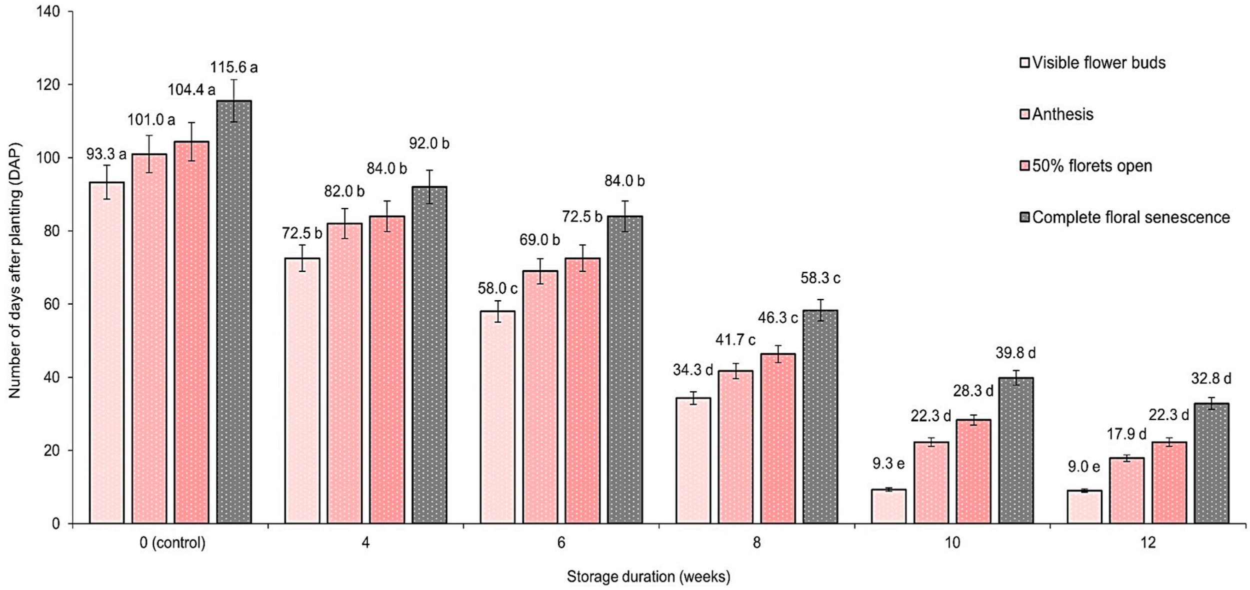

Figure 5. The effect of warm bulb storage duration on the number of days until the emergence of visible flower buds, anthesis, the opening of 50% florets, and complete floral senescence of the potted inflorescence of *Amaryllis belladonna* after planting. Bars represented by mean values followed by a different letter(s) are significantly different at $p \leq 0.05$, according to Fisher's least significant difference (L.S.D).

The influence on the opening of 50% florets on an inflorescence showed similar trends to the effect of the storage treatments on anthesis compared to the control. Figure 5 shows the flowering event between 22.3 and 104.4 days after storage intervals and subsequent planting. However, this trend was observed between 2 and 6 days after the first anthesis. The maximum number of days (6 days) was shorter than the minimum duration (7.4 days) observed for anthesis in all storage treatments, indicating that this period was shorter than the interval between the appearance of the visible flower bud and the opening of the first floret.

Complete floral senescence was observed in all potted inflorescence florets, showing a turgidity loss followed by complete wilting. The storage interval and subsequent DAP significantly ($p \leq 0.05$) affected this occurrence in the greenhouse and was observed between 32.8 and 115.6 DAP in all storage treatments (Figure 5). Compared to the control and the 8- and 10-week treatments, the bulbs in the 4-, 6-, and 12-week treatments were the last to show flower senescence.

3.3. Effect of Warm Bulb Storage Period on Leaf Morphological Growth

3.3.1. Number of Leaves

As shown in Table 3, there was no significant difference ($p > 0.05$) in the number of leaves after the storage treatments and subsequent planting time during the vegetative growth phase of the bulbs. In contrast to the control and 4- and 10-week treatments, the

12-week stored bulbs had the most significant number (13.1) and the least variability. In addition, 11 or more leaf sets were identified in the bulbs under all storage conditions.

Table 3. Effects of warm bulb storage period on leaf characteristics of the number of leaves, leaf length, width, and area of *Amaryllis belladonna*.

Bulb Storage (Weeks)	**Leaf Characteristics**			
	Number of Leaves (n)	**Leaf Length (cm)**	**Leaf Width (cm)**	**Leaf Area (cm^2)**
0 (control)	11.9 ± 0.43 ab	47.1 ± 2.21 a	3.1 ± 0.12 b	148.6 ± 10.40 b
4	11.9 ± 0.28 ab	49.4 ± 3.02 a	3.4 ± 0.13 ab	170.0 ± 13.30 ab
6	11.7 ± 0.34 b	47.1 ± 2.11 a	3.4 ± 0.12 ab	160.90 ± 12.0 ab
8	11.7 ± 0.66 b	50.6 ± 2.28 a	3.5 ± 0.11 a	178.6 ± 11.20 a
10	12.2 ± 0.43 ab	45.9 ± 2.08 a	3.4 ± 0.06 ab	154.22 ± 7.69 ab
12	13.0 ± 0.42 a	47.1 ± 1.41 a	3.5 ± 0.09 a	165.14 ± 8.17 ab
		One-way ANOVA F-statistic		
Bulb storage	1.26 ns	0.62 ns	1.59 ns	1.03 ns

Mean values ± standard error (S.E.) in the same column with a different letter(s) are significantly different at $p \leq 0.05$ based on Fisher's least significant difference (L.S.D); ns = not significant.

3.3.2. Leaf Length, Leaf Width, and Leaf Area

The leaf morphology assessment of bulbs of *A. belladonna*, as measured by leaf length, width, and area, was not significantly affected by the number of weeks of extended warm storage ($p > 0.05$), as shown in Table 3. Despite similar results in all treatments, leaf expansion ranged from 45.9 to 50.6 cm. Notably, leaf blade expansion was slightly broader in all storage treatments than in the control (3.1 cm). Although 8-week storage presented the highest total leaf area (178.6 cm^2), the differences were comparable and less pronounced in all storage conditions.

4. Discussion

This study found that a warm bulb storage period and the subsequent planting significantly impacted flowering precocity, flowering time, and visual characteristics of *A. belladonna* scapes in the greenhouse. Irrespective of the storage treatment and subsequent planting, flower abortion (blindness) was observed, as not all bulbs successfully flowered. This finding is consistent with the physiological anomaly of inflorescence abortion noted in the species [12,49] and seen in other bulbous species of *Hippeastrum*, *Iris*, *Lachenalia*, and *Nerine*, where an after-storage planting resulted in the cessation of flower development [31,50,51]. Aspects of cultivation and climatic conditions may have influenced this flowering anomaly before and during the bulb harvest in the previous season(s). Moreover, root disturbances may have caused flower abortion, as seen in many Amaryllidaceae species [46]. According to [35,52], contingent on the cultivation and environmental growth circumstances, which are not always contemporaneous, the shoot apical meristem (SAM) may take a different trajectory to reach a physiological stage. Furthermore, these authors deduce that the timing and form of this transition vary depending on the species. Authors [44,52,53] reached similar conclusions.

In further elucidating this flowering oddity, the most intriguing finding was that the collective proportion of the 0 and 12-week storage treatments accounted for 59.3% (more than half) of the overall maturation performance yield. It can be inferred that in this study, the longer continuous warm bulb storage conditions for the completion of the rest period were met, and flower emergence was prompted by a particular cumulative temperature range and duration for the last stages of floral differentiation before planting [26,37,38]. However, the shorter storage periods and the timing of the subsequent greenhouse temperature fluctuations because of an earlier planting time after storage may have affected the receptive signalling pathways and transitional apical meristematic activity, resulting in noticeable aberrations of stunted spike emergence and inflorescence abortion [26]. Further insight into these findings suggests that there appeared to be a difference in bulb rest immediately after leaf senescence and harvesting when bulbs were sensitive to temperature changes and later when not. According to [31,54], when dormancy is established, species are at different stages of internal bulb development, and the degree of dormancy at harvest may be related to how receptive the bulbs are to temperature fluctuations. Similarly, *Nerine sarniensis* [38] and *Lachenialia* species [51] reported findings of varied dormancy degrees, storage, and association with flowering performance. This responsiveness may explain why the control (no-storage), with an immediate planting, had a better flowering capacity and regulation than those subjected to shorter storage treatments and earlier subsequent greenhouse temperature differentials because they were only exposed to greenhouse temperature variations from the onset and not both.

The capacity for a bulb to flower depends on an optimal species-specific temperature range and duration for growth and reproduction, and deviating from this can cause unmanageable stress, lowering the floral meristem development rate or abortion, and thus degrading the inflorescence's productivity and quality [25,55]. This finding validates the research that the capacity for a bulb to flower depends on the key storage intervals, and straying from these threshold parameters increases the risk of inflorescence abortion [50]. According to this study's findings, the timing, length, and variety of subsequent temperature regimes affected the flowering response, aligning with those of [52,56]. The timing of floral induction after leaf development is typically governed by vegetative growth and senescence under the influence of temperature during a phase of limited vegetative growth [31]. Ref. [49] estimated that the bulbs of *A. belladonna* initiate a single inflorescence each year during summer dormancy, about one month before the previously formed inflorescence appears. As a result, morphogenesis during dormancy is incomplete as different developmental stages of the imminent and subsequent seasons' inflorescence are initiated. Temperature fluctuations can adversely or favourably impact both phases, with the results only presenting in the following seasons [38]. As a result, factors that impact the dormant period essentially define the competitive character of the commencement of reproductive activities in the species.

Flowering periodicity, productivity, and market quality do not depend exclusively on thermal stimuli; additional criteria are necessary to promote anthesis signalling pathways. These criteria include age, bulb size, and weight, all affecting the flowering capability, with critical parameters differing between taxa, species, and cultivars [23,31,36]. The dynamic metabolic processes associated with shoot apical meristematic transition activity during bulb dormancy necessitate energy, water transfer and delivery. These resources can only be derived from subsurface organ sources, and temperature influences their mobilisation and distribution [57,58]. Therefore, as a perennial hysteranthous taxon, *A. belladonna* relies heavily on the vegetative growth seasons where the emergence of flowers and leaves are succinctly divided to accumulate and maintain adequate carbohydrate reserves in larger underground storage organs for flowering and fruiting [59,60]. Although this study utilised bulbs with a circumference of 30-33 cm, which did not attain 100% flowering, the minimum flower-size bulb for *A. belladonna* is approximately 26 cm in circumference [12,49]. This disparity is reinforced by the fact that, although having a sufficient bulb size, the accumulation, supply, and distribution of resources under the influence of temperature are numerous and may dictate the rate at which growth, development, dormancy, and flowering occur [26,61].

A significant finding from this study was the considerable variation in the number of scape florets after warm bulb storage and planting; however, it had little effect on the morphology since the floret diameter and length were unaffected. These findings contradict that of [51], who found that delayed planting altered the diameter of solitary florets, not the length. In another study, a later planting date in the same species of *Lachenalia* enhanced the number of florets per inflorescence [62]. The quantity of flowers on an ornamental plant greatly reflects its aesthetic value and impacts its qualitative characteristics, according to [63]. Other key factors influencing decorative quality include crown diameter [64] and fullness ratio [65]. Given the disparities in floret numbers, they were likely already formed in the bulb before storage treatments, and the discrepancies may be due to several other factors, such as the genetic disposition of floriferous clones [66] and carbohydrate assimilation [56,61].

Interestingly, despite the variation in floret numbers across treatments, none of the bulbs showed evidence of floret bud atrophy. Observations from this study suggest that the differentiation of inflorescence emergence is more susceptible to exogenous temperature changes than the differentiation of florets opening after planting. Further results from this study found that flowering scapes of *A. belladonna* may retain their aesthetic appeal for at least 10 days, if not longer. *A. belladonna* floret's lifespan is about 2.5 days, opening in coordinated succession for an overall display in the vase [18]. The authors added that this is comparable to the longevity of florets attached to the bulbs, making them attractive to growers, sellers, and buyers as specimens for cut flowers and potted plants. The study also found that the inflorescence scape diameter was thicker in storage treatments compared to the control but minimal compared to commercial quality standards. Furthermore, the minimum stem length was 37 cm, although insignificant, making it a suitable and positive attribute for the cut flower market.

Except for the 10-week treatment, this study found that staggered bulb planting by extended storage treatments did not significantly accelerate the flowering morphogenesis of *A. belladonna*. Instead, they dramatically reduced the period following planting in a storage-dependent manner. This can be ascribed to the fact that the immediately planted bulbs of the control required 93 days (almost ten times as long) to reach this developmental stage, even though flower buds emerged simultaneously (calendar date) with the later greenhouse plantings in the 8- and 12-week treatments. As a result, compared to the immediately planted control, the 12-week-treated bulbs required at least one month to complete the flowering cycle after planting. In contrast, the immediately planted control took nearly four times as long (115.6 days) to achieve this last seasonal greenhouse development stage. This finding may be explained by the fact that long-term bulb storage reduced the time of floral events after planting due to the advanced internal morphogenesis of elongation and the altered carbohydrate content of the inflorescence during storage [57,58]. Similar results were obtained in *Lachenalia* species [62], *Nerine sarniensis* [38], and *Ornithogalum dubium* [67].

Conversely, shorter storage intervals and subsequent planting would have postponed or halted the final stages of flower development, resulting in delayed inflorescence bud emergence. In addition, the proportion of flowering bulbs would have been much lower if inflorescence abortion and lodging had occurred due to arrested development. Interestingly, both results were observed in this study; however, this shorter timeframe contradicts the findings that a 6-week storage period resulted in a quicker sprouting of Asiatic lily cv. "Royal Trinity" [68] and accelerated growth and flowering of *Ornithogalum thyrsoides* hybrids [24]. In this study, the total duration of the flowering cycle, from the appearance of visible buds to the complete senescence of florets, was about 7.5 weeks, consistent with numerous authors' conclusions about the species short flowering season [3,46].

The hysteranthous leaf emergence occurred after flowering and correlated with the onset and decline in temperature as the autumnal season approached. However, the precise physiological processes that initiate the onset are unclear. This study found that warm bulb storage did not affect the foliage quality parameters of the leaf number, length, width, and area. It is proposed that the leaf set had already been established before the bulb harvest and would not have changed significantly during the vegetative growth phase. However, [31] explains that the rate of expansion and production may have been impacted. Visual observations of emerging leaves initially made in the control and shorter storage treatments of 4 and 6 weeks support this finding. In addition, leaf emergence was slightly delayed in bulbs that flowered during the seasonal study period compared with those that remained vegetative in all treatments. According to [69,70], this delay is caused by mobilising compounds and ions from wilting tepals to other organs through the degradation of macromolecules when flowers perish.

This study unveils that the innocuous observation and proclivity of the emerging *Amaryllis belladonna* flower bud, seemingly appearing out of nowhere and rapidly extending to create a prescient curiosity of the imminent and lasting floral display and a conscious awareness of the seasonal shift that heralds the end of summer cannot be undervalued. This study highlights that focusing on market-driven initiatives, as opposed to the product-based strategies of the past, is the solution to SCF's success [4,6,71]. Focusing on the attractive qualities of unique native flora and underutilised species like *A. belladonna*, the potential of the SCF may be invigorated and conserved [4,10]. Along with [4,16], this study demonstrates the high potential of *A. belladonna* as a cut flower and potted plant, promoting its candidacy for local and international SCF markets as a seasonal and sustainable niche product, emblematic of South Africa's unique floral heritage.

5. Conclusions

This study found that warm bulb storage after lifting significantly affected the flowering production, flowering time, and flower quality attributes of *A. belladonna* but not the foliage growth. Aside from favouring a higher flowering capacity and shorter intervals under greenhouse cultivation after planting, extended warm bulb storage did not typically advance the flowering time. The control and shorter storage periods exhibited an unsustainable and uneven pattern. The findings of this study advocate that a cumulative temperature range during bulb dormancy is crucial for supporting inflorescence maturity's energy demands and floret buds' opening. If not adequately maintained during bulb storage and cultivation, *A. belladonna*'s flowering ability is compromised. Ideally, bulbs should be stored at an elevated temperature for 8–10 weeks after the harvest to achieve the highest floret-quality attributes and longevity. However, for optimal anthesis in the shortest interval, sustainable and economical greenhouse, and specialty cut flower production, 12-week warm bulb storage is recommended for this seasonal single-harvest species. Additionally, we recommend investigating a broader range of storage temperatures, durations, and initial lifting dates during dormancy to identify patterns and develop a more precise protocol for improving flowering competency and quality attributes, potentially extending the season.

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