GROWTH AND FLOWERING RESPONSES TO ABIOTIC PARAMETERS OF *AMARYLLIS BELLADONNA* L. FOR HORTICULTURAL APPLICATIONS

by

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DECLARATION

I, Carolyn Margaret Wilmot, declare that the contents of this thesis represent my unaided work and that the thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it presents my opinions, not necessarily those of the Cape Peninsula University of Technology.

07 March 2025

Signed **Date**

ABSTRACT

Amaryllis belladonna L. is an endemic bulbous species from the opulently diversified Cape Floral Region of the Western Cape, South Africa. Previously a monotypic genus of the Amaryllidaceae family, it has naturalised in many Mediterranean regions worldwide. The hysteranthous autumn flowering geophyte displays white to pink trumpet-shaped florets in a seasonal single-harvest inflorescence following a summer dormancy. However, the species faces development constraints of protracted bulb juvenility, offset generation for competent flowering size, and inconsistent and transient flowering behaviours upon reproductive bulb maturity. Likewise, there is a lack of scientific research and quantitative empirical data on cultivation methods, from planting to flowering, which has irrefutable economic potential. This study investigated the cultivation methodology and environmental conditions of *A. belladonna* at different bulb development phases, focusing on the effects of abiotic parameters on growth, development, and seasonal flowering. A literature review, four descriptive reviews, a field study, and three greenhouse experiments were included, forming a coherent body of work on related research questions and hypotheses testing for *A. belladonna*. The study objectives were:

Chapter 3 determined the factors stimulating flower initiation in *A. belladonna*. Findings revealed several factors associated with bulb size, age, dormancy, bulb planting establishment, cultivation methods, and environmental variables, such as temperature, hydration, day length, and seasonal fire, to promote flower initiation in the species. Chapter 4 determined the horticultural and floricultural market potential of *A. belladonna*. Findings established that the species has attracted international interest because of its adaptability, attractiveness, drought resilience, and fire-stimulated flowering attributes. Likewise, it alluded to the applications and design uses of the species within the broader fringes of the floriculture and horticulture arena. Among these are the ornamental functional design and use of *A. belladonna* in garden landscapes, naturalistic and roadside plantings, packaged retail flower bulbs, potted plants, and cut flowers. Chapter 5 evaluated the hydroponic cultivation capacity of ornamental bulbous species. Findings established limited accounts of scientific studies and cultivation of species variety, vegetation induction, and bulb regeneration to expand bulb size and yield and offset production compared to flowering-forcing under these conditions. Chapter 6 determined the impact of fire-stimulated flowering on South African geophytic biodiversity. Findings of initiated flowering and regenerative growth of selected geophytic taxa that inhabit different regions and vegetation habitats of South Africa following wildfires have been documented; however, these are primarily denoted in the species' natural habitats, with little account for those under cultivation. Moreover, there is limited knowledge and studies on how fire-associated factors initiate geophytic flowering mechanisms and their distinctive roles in preserving species richness and biodiversity, ecotourism, and the survival and well-being of

natural above- and below-ground ecosystems. Chapter 7 assessed the inhabited bulb planting life strategy and flowering prolificacy of *A. belladonna* by examining the population attributes, habitat features, and cultivation practices under *ex situ* garden conditions. The two-year study used purposive sampling to recruit six *ex situ* bulb populations from the Pinelands residential area. Results found bulbs to have enduring longevity and were recruited primarily through vegetative offsets. Flowering heterogeneity ranged from 4.9% to 58.3% within and between seasons; however, commonalities alluded to a broad influence of temperature. The study concluded that in addition to favourable habitat features and climatic growing conditions, population attributes (bulb size, structure, position, density, and establishment) and cultivation practices (premature defoliation, soil amendments, planting interference, and re-establishment) were significant synergistic constituents of flowering proficiency. Chapter 8 determined the effects of Kelpak® seaweed extract on the morphological and physiological growth and yield of *A. belladonna* bulbs grown in a greenhouse. The 24-week study comprised Kelpak® concentration dilutions of 0%, 0.2%, 0.4%, and 1% (*v/v*), administered to 5 consecutive juvenile bulb age groups as a monthly soil drench. Results showed that Kelpak® treatment improved phyto-stimulatory responses in bulb aerial and below-ground storage organs. Moreover, bulb age varied, with older bulbs establishing higher yields than their younger counterparts; however, bulb circumference, weight coefficients, and chlorophyll content showed that 1- and 2-year-old bulbs were most receptive to treatment. This study concluded that 1% Kelpak® is applied at an early developmental stage within the first two years to maximise the efficacy and proliferation rate of *A. belladonna*. Chapter 9 determined the effects of root zone water temperature and soilless media on bulb yield and offset *A. belladonna* bulb production in a deep water culture hydroponic system. The 18-month study included dormant juvenile bulbs that were planted in plastic cavity trays filled with soilless media (silica sand or Leca clay) and suspended in heated water reservoirs at different temperatures (16 °C, 22 °C, 28 °C, and 34 °C). Results found that the autonomous analysis of water temperature, as opposed to soilless media and combinations, was significant. Warm root zone temperatures from 16 °C to 28 °C promoted the growth and development of larger juvenile mother bulbs and offset generation without premature detachment; however, bulbs were depleted at an excessively high temperature of 34 °C. This study concluded that a water temperature of 22°C is needed for long-term sustainable production of optimal reclaimable bulbs and offsets to abridge the timeous cultivation of continuous vegetative bulb stock of *A. belladonna*. Chapter 10 determined the effects of a warm storage period on *A. belladonna* bulbs' flowering yield, flowering time, quality characteristics, and foliage growth. The 10-month study involved dormant flower-sized bulbs placed in storage regimes of 0-, 4-, 6-, 8-, 10-, or 12-weeks at a continuous warm temperature of 23 ± 1 °C before greenhouse planting. Results showed that flowering production (64.3% flowering after 12-week storage), flowering time (anthesis 9 days after 10- and 12-week storage), and quality attributes (inflorescence floret

numbers, fullness ratio, pot longevity and scape diameter) of *A. belladonna* were significantly influenced by warm bulb storage, but not foliage growth. Extended bulb storage did not advance flowering time despite greater harvest and shorter cultivation periods after planting. Bulbs should be stored at elevated temperatures for 8–10 weeks for optimal floret quality and longevity. However, this study concluded that 12 weeks of warm storage would be needed for economically sustainable greenhouse and specialty cut flower production of *A. belladonna*. The current study's comprehensive findings and recommendations contribute valuable and novel material towards developing and advancing cultivation practices, perpetuating prospects for enhanced economic value, quality, and reproducible commercial production for the competitive differentiation of *A. belladonna* in the floricultural and horticultural markets.

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To our Heavenly Father, for his abundant blessings, daily provisions, and abiding grace shown to me.

DEDICATION

…… This thesis is dedicated to my parents, Rodger and Margaret Wilmot ……

"Where flowers bloom, so does Hope"

Lady Bird Johnson

PREFACE

This thesis is organised into several chapters/publications addressing various aspects of the *Amaryllis belladonna* bulbous species. This thesis is written in an article-based format, and, where relevant, chapters are prepared according to the specified journal guidelines (including references) for publication or submission for review. Thus, repetition and content overlap appear across the chapters to maintain each chapter's/publication's authenticity and validity as an independent manuscript. Likewise, chapters are not chronologically ordered but are collated in the logical progression of information. The peer-reviewed publications and submission titles are listed in the research outputs and appear as page headers. The first page of each publication is included in the appendices.

The research activities presented in this thesis were conducted at the greenhouse and laboratory research facilities of the Department of Horticultural Sciences at the Cape Peninsula University of Technology's Bellville Campus in Cape Town, South Africa. Fieldwork was conducted at private property dwellings within the residential area of Pinelands, Cape Town, South Africa.

This thesis consists of 12 chapters arranged and described as follows:

Chapter 1: Presents the general introduction, which comprises the background of the study, research problem statement, research questions, hypotheses, aim and objectives, justification of the study, delimitations, and thesis layout and structure.

Chapter 2: Presents a detailed literature review that underlines the taxonomy, botanical description, cultivation, horticultural and habitat traits and economic significance of *A. belladonna*. In addition, the review outlines challenges and addresses prospective cultivation research gaps and opportunities from planting to seasonal flowering.

Chapter 3: Determines the factors influencing flower initiation in *A. belladonna* L.

Chapter 4: Establishes the horticultural and floricultural market potential of *A. belladonna* L.

Chapter 5: Evaluates hydroponic cultivation on ornamental bulbous species to enhance bulb development, size and flowering production.

Chapter 6: Establishes the impact of fire-stimulated flowering on South Africa's geophytic biodiversity.

Chapter 7: Assesses the effects of population attributes, habitat features, and cultivation practices on the flowering response of inhabited *A. belladonna* L. under ornamental garden conditions.

Chapter 8: Determines the effects of an exogenously applied seaweed extract on the morphological and physiological growth and yield in juvenile *A. belladonna* L. bulbs.

Chapter 9: Determines the effects of regulated root zone temperatures and soilless media in deep water hydroponics on bulb yield and offset *A. belladonna* L. production.

Chapter 10: Determines the effects of warm bulb storage on the flowering responses and foliage growth in *A. belladonna* L.

Chapter 11: Summarises the findings, contributions and further research opportunities in each chapter, along with the study's overall conclusions, recommendations, and contribution made to the body of knowledge.

Chapter 12: A compilation of the sources referenced in the preceding chapters following the Harvard referencing style.

RESEARCH OUTPUTS

The following research outputs acknowledge the doctoral candidate's progress and contribution to scientific knowledge while pursuing a Doctor of Horticulture postgraduate qualification. Manuscripts were compiled for submission, and scientific articles were published between 2019 and 2024 during candidacy. An appendix details the doctoral candidate's role as lead author and the roles and contributions of co-authors to each manuscript compiled for submission and publication.

South African DHET-accredited journal articles published (ascending order)

Wilmot, C.M. & Laubscher, C.P. 2019. Flowering initiation in *Amaryllis belladonna*. *Acta Horticulturae*, 1237: 137–144. https://doi.org/10.17660/ActaHortic.2019.1237.18

Wilmot, C.M. & Laubscher, C.P. 2019. *Amaryllis belladonna*: A potential urban landscape wonder. *Acta Horticulturae*, 1237: 287–293.https://doi.org/10.17660/ActaHortic.2019.1237.37

Wilmot, C.M. & Laubscher, C.P. 2023. Evaluating hydroponic cultivation for ornamental bulbous species to enhance flowering and bulb production in a changing climate. *Acta Horticulturae,* 1377: 663–670. https://doi.org/10.17660/ActaHortic.2023.1377.81

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2023. Warm bulb storage optimises flowering attributes and foliage characteristics in *Amaryllis belladonna* L. *Horticulturae*, 9(12): 1271. https://doi.org/10.3390/horticulturae9121271
(MDPI Editor's Choice article publication award – May 2024)

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2024. Stimulatory effects of an exogenously applied seaweed extract on the morphological and physiological growth and yield in juvenile *Amaryllis belladonna* L. bulbs. *The Egyptian Journal of Botany,* 63(3): 52–68. http://doi.org/10.21608/ejbo.2024.220974.2395

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2024. Regulated root zone water temperatures and soilless media improve bulb yield and offset production of hydroponically cultivated *Amaryllis belladonna* L. *Scientia Horticulturae,* 338: 113823. https://doi.org/10.1016/j.scienta.2024.113823

Manuscripts accepted, submitted or prepared for submission

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2024. Fire-stimulated flowering among South African geophytes: implications for biodiversity in a changing climate.
(Full text accepted for publication to *Acta Horticulturae*)

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2024. Flowering prolificacy of *Amaryllis belladonna* L. under ornamental garden conditions: influence of population attributes, habitat features, and cultivation practices.
(Submitted for publication to *Horticulture, Environment, and Biotechnology,* ID: HEAB-D-24-00217)

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2024. *Amaryllis belladonna* L. – The Cape Floral Region's hysteranthous geophyte: A review. **(Manuscript prepared for submission)**

International conference attendance

Wilmot, C.M. & Laubscher, C.P. 2019. Flowering initiation in *Amaryllis belladonna*. International Society of Horticultural Science Conference, XIII International Symposium on Flower Bulbs and Herbaceous Perennials held in Seoul, South Korea, 1-3 May 2019. **(Poster presentation)**
http://flowerbulb2019.org/

Wilmot, C.M. & Laubscher, C.P. 2019. *Amaryllis belladonna*: A potential urban landscape wonder. International Society of Horticultural Science Conference, XIII International Symposium on Flower Bulbs and Herbaceous Perennials held in Seoul, South Korea, 1-3 May 2019. **(Poster presentation)**
http://flowerbulb2019.org/

Wilmot, C.M. & Laubscher, C.P. 2023. Evaluating hydroponic cultivation for ornamental bulbous species to enhance flowering and bulb production in a changing climate. 31st International Horticultural Congress (IHC 2022): International Symposium on Innovative Technologies and Production Strategies for Sustainable Controlled Environment Horticulture held in Angers, France, 14-20 August 2022. **(Poster presentation)**
https://www.ihc2022.org/

Wilmot, C.M., Jimoh, M.O. & Laubscher, C.P. 2024. Fire-stimulated flowering among South African geophytes: implications for biodiversity in a changing climate. The III International Symposium on Greener Cities: Improving Ecosystem Services in a Climate-Changing World (GreenCities 2024) will be held in Wisley, Woking (United Kingdom), 25-28 September 2024. **(Poster presentation)**
https://www.rhs.org.uk/science/green-cities-2024

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ABBREVIATIONS AND ACRONYMS

Afr.	Afrikaans
ANOVA	Analysis of variance
CAGR	Compound annual growth rate
cv.	cultivar
CFK	Cape Floral Kingdom
CFR	Cape Floral Region
CPUT	Cape Peninsula University of Technology
CRBD	Completely randomised block design
DAP	Days after planting
DHET	Department of Higher Education and Training
DWC	Deep water culture
EC	Electrical conductivity
Eng.	English
FSF	Fire-stimulated flowering
GI	Geographical indication
GPS	Global positioning system
IKS	Indigenous Knowledge Systems
IUCN	International Union for Conservation of Nature
Leca®	Lightweight expanded clay aggregate
L.	Linnaeus
LC	Leca clay
LCA	Life cycle assessment
LPDE	Low-density polyethylene
LSD	Least significant difference
ME	Montgomery equation
NFT	Nutrient film technique
NS/ns	Not significant
PPFD	Photosynthetic photon flux density
RBD	Randomised block design
RGC	Rapid generation cycling
RH	Relative humidity
RO	Reverse osmosis
SANBI	South African National Biodiversity Institute
SAM	Shoot apical meristem
SE	Standard error
SCF	Specialty cut flower
SGT	Suspended growing tray
SS	Silica sand
SWE	Seaweed extract
TCF	Traditional cut flower
USO	Underground storage organ

CHAPTER 1

INTRODUCTION

INTRODUCTION

1.1 Background of the study

The prodigious flora of South Africa has long been of worldwide interest, with approximately 70% of the world's bulbous species, notably those from the Cape Floral Region (CFR), being unrivalled elsewhere in the world (Manning *et al.*, 2002; Manning, 2007; Reinten *et al.*, 2011; Barnhoorn, 2013; Duncan *et al.*, 2020). Geophytes are a diverse class of flora, and their global collective multiplicity is increasing because of omnipresent market changes, competitive demands for timely stock, and the purposeful breeding of new cultivars and hybrids with specialised and desirable qualities for many divisions of the agriculture, horticulture and floriculture, sectors (Anderson, 2006; Anderson, 2019; Slezák *et al.*, 2020; Marasek-Ciolakowska *et al.*, 2021). Although the selection and necessity of plant species are subjective and depend on specific conceptions and markets, biodiversity and diversification are paramount. Moreover, climate change's ramifications on geophytic production pose new challenges (Barnhoorn, 2013; Kamenetsky-Goldstein, 2019). The abundance of South African endemic bulbous species contributes a relatively small fraction to the number of commercial crops found within the global bulb industry and thus is not operative to its fullest potential (Matthee *et al.*, 2006; Reinten *et al.*, 2011; Barnhoorn, 2013; Darras, 2021). Complex fundamentals are involved in effectively developing South African flora rather than only their unique attractiveness and aesthetic qualities. Moreover, these species require long-term funding and interdisciplinary research strategies for their accessible development (Bester *et al.*, 2009; Reinten *et al.*, 2011; Barnhoorn, 2013).

As bulbous genera demonstrate significant associative dissonance and consume a variety of multifaceted economic impacts and statutory demands, geophytic cultivation methodologies cannot be extrapolated, although inferences can be made (Duncan, 2010; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013). Likewise, the inherent composition and genetic variability of geophytes are becoming more valuable (Kamenetsky & Miller, 2010; Reinten *et al.*, 2011; Marasek-Ciolakowska *et al.*, 2021), and greater emphasis will be directed towards species and those of indigenous and underutilised flora with potential sustainable production and health-promoting benefits (Duncan, 2010; Darras, 2020; Thörning *et al.*, 2022). In addition, contributions to local ecosystem biodiversity and the well-being of society and culture will further promote the abundance of these species (Ingram *et al.*, 2019; Darras, 2020; Thörning *et al.*, 2022). Undoubtedly, such efforts will increase the dependency on and demand for species-sustainable cultivation, conservation, and health. For these intentions, novel and heterogeneous scientifically based research with academic distinction is imperative to broaden the understanding of plant-environment interactions and cultivation practices from planting to flowering (Khodorova & Boitel-Conti, 2013; Darras, 2020). Moreover, these are essential in addressing existing and emerging challenges in advancing crop species under a changing climate (Le Nard & De Hertogh, 2002; Manning *et al.*, 2002; Reinten *et al.*, 2011; Duncan *et al.*, 2016; Kamenetsky-Goldstein, 2019; Darras, 2020; Slezák *et al.*, 2020).

These assertions are particularly pertinent to the profitable viability of the indigenous and underutilised *Amaryllis belladonna* L. bulbous species. *A. belladonna* is an attractive amaryllid endemic to the richly diversified Cape Fynbos Floral Region of the Western Cape, South Africa (Manning *et al.*, 2002; Duncan *et al.*, 2020). As one of only two species within the genus, the unassuming presence of the hysteranthous, early autumn flowering geophyte is well-known in many Mediterranean regions worldwide (Adams, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020). Several research studies have focused on underpinning the species alkaloidal activities (Pettit *et al.*, 1984; Evidente *et al.*, 2004; Nair *et al.*, 2013; Chavarro *et al.*, 2020; Nair & Van Staden, 2022; Evidente, 2023), improving its desirable floral attributes through interspecific and intergeneric breeding (Bryan, 2002; Duncan, 2004; Salachna *et al.*, 2020), propagation through tissue culture (De Bruyn *et al.*, 1992; Veeraballi *et al.*, 2017), and postharvest qualities of cut flower scapes (Gul *et al.*, 2020). However, the growth of the bulbous species is hindered by the lack of scientific and quantitative empirical data that perpetuate the cultivation methodology of various bulb development phases, harbouring indubitable commercial potential. Thus, novel and workable cultivation techniques of scientific merit are required to enhance the potential of *A. belladonna* for optimal growth and sustainable development and, more fervently, to stimulate seasonal flowering. These measures will strengthen species' capacity for sustained biodiversity and competitive economic differentiation in local and international flower bulb and cut flower markets.

1.2 Research problem statement

Amaryllis belladonna L. is comparatively unexplored in terms of cultivation methodology and environmental conditions at various phases of bulb development, from planting to flowering, which perpetuates bulb growth and stimulates seasonal flowering to ensure ornamental economic viability. During various bulb development stages, this study investigates the effects of abiotic parameters and environmental conditions on *A. belladonna* growth and seasonal flowering to improve the species' economic value and capacity for competitive differentiation and sustainable biodiversity in local and international flower bulb and cut flower markets.

1.3 Research questions

<u>The research questions that guided this study were:</u>

- Which factors influence flower bud initiation in *A. belladonna* L.?
- What is the horticultural and floricultural market potential of *A. belladonna* L.?
- How can the bulb size and productivity of *A. belladonna* L. be increased?

- What is the capacity of hydroponically cultivating bulbous species?
- How does fire-stimulated flowering affect the general biodiversity of South African geophytes?

1.4 Hypotheses

The hypotheses tested in this study were:

- Population attributes, habitat features, and cultivation practices affect the flowering prolificacy of established garden *A. belladonna* L.
- An exogenously applied seaweed extract affects morphological and physiological growth and yield in juvenile *A. belladonna* L. bulbs.
- Regulated root zone temperature and soilless media affect the bulb yield and offset production of *A. belladonna* L. in deep water hydroponic cultivation.
- A warm storage period affects the flower responses and foliage growth of *A. belladonna* L.

1.5 Research aim and objectives

1.5.1 Aim

This study aimed to investigate the effects of abiotic factors on the growth and seasonal flowering of *Amaryllis belladonna* L. at various bulb development stages to improve the species' economic value and capacity for commercial flower bulbs and cut flower production in local and international markets.

1.5.2 Specific objectives

The specific objectives of this study were to:

- Determine the factors that influence flower initiation in *A. belladonna* L.
- Determine the horticultural and floricultural market potential of *A. belladonna* L.
- Evaluate the general hydroponic cultivation of ornamental bulbous species to enhance bulb development, size, and flowering productivity.
- Establish the impact of fire-stimulated flowering on South African geophytic biodiversity.
- Assess the effects of population attributes, habitat features, and cultivation practices on the flowering responses of established *A. belladonna* L. under ornamental garden conditions.
- Determine the effects of an exogenously applied seaweed extract on the morphological and physiological growth and yield in juvenile *A. belladonna* L. bulbs.
- Determine the effects of regulated root zone temperatures and soilless media in deep water hydroponics on bulb yield and offset *A. belladonna* L. production.

- Determine the effects of warm bulb storage on flowering responses and foliage growth in *A. belladonna* L.

1.6 Justification for the study

South Africa's fynbos cut flower industry's annual value is close to ZAR 1 billion, with 30 million stems shipped from the Western Cape. Approximately 2500 individuals, primarily rural women, are directly employed by the sector (Mayhew, 2023; South Africa. Department of Trade, 2023). The largest market for exported goods, which total ZAR 766 million annually, is the European Union (67% of total exports); nevertheless, in recent years, exports to the Middle and Far East (combined, 24%) have increased (Mayhew, 2023; South Africa. Department of Trade, 2023). South Africa is presently the third-largest cut flower exporter on the African continent and is recognised as the pioneer and leader in the production of fynbos cut flowers; however, several other nations, including Australia, Israel and Ecuador, also export these crops (Mayhew, 2023; South Africa. Department of Trade, 2023). The Fynbos cut flower group, Cape Flora SA, reports that South Africa's flower exports mainly consist of indigenous flora, with the majority grown in the Western and Eastern Cape and ethically harvested and collected from the wild (Mayhew, 2023; SA Government, 2023). According to the South African Minister of Trade, Industry and Competition, Mr Ebrahim Patel, the sector is an important niche with the potential to grow and expand in response to rising worldwide demand (Mayhew, 2023; SA Government, 2023).

Moreover, Cape Flora SA manager, Ms Karien Bezuidenhout, stated, "The international market expansion has prompted modernisation and innovation within the sector, resulting in greater product quality". As a result, sales have increased in domestic and foreign markets (Mayhew, 2023; SA Government, 2023). An increase in fynbos production is commencing abroad; therefore, protecting and supporting the "Cape Flora" brand and its logo is critical to ensuring that South Africa's distinctive resources and quality are identifiable and protected (Mayhew, 2023; South Africa. Department of Trade, 2023). Recent developments to apply and secure a Geographical Indication (GI) for "Cape Flora" will ensure that South Africa's rich cultural heritage and biodiversity are recognised, promoted, and preserved (Mayhew, 2023; South Africa. Department of Trade, 2023).

The South African Indigenous Plant Knowledge Systems is a powerful and valuable agroecological and economic tool with a competitive advantage in terms of floral biodiversity that represents an untapped resource of an inestimable proportion (Reinten & Van Wyk, 2018; Duncan *et al.*, 2020; Darras, 2021). Thus, it is essential to examine, promote, and expand sustainable biodiversity and the stewardship of natural heritage and ecosystems (Donaldson & Scott, 1994; Manning *et al.*, 2002; Reinten *et al.*, 2011; Duncan *et al.*, 2020). Although new research instruments are being sought to resolve specific outcomes, sustainable cultivation, propagation, and postharvest management improvements remain necessary to make South African plant species more accessible (Niederwieser *et al.*, 2002; Reinten *et al.*, 2011; Duncan *et al.*, 2020). Similarly, there is a growing movement to develop sustainable novel approaches that leverage the innate characteristics and fundamental cultivation scheduling ramifications of South Africa's distinctive dispensation of underutilised indigenous flora (Reinten *et al.*, 2011; Duncan *et al.*, 2016; Reinten & Van Wyk, 2018; De Pascale & Romano, 2019).

The indigenous *A. belladonna* is widely recognised and utilised in a variety of planting palettes and functional applications as a low-maintenance, drought-tolerant, and intermittent seasonal late bloomer within the horticulture and floriculture framework (Theron & De Hertogh, 2001; Bryan, 2002; Brown & Duncan, 2006; Maree & Van Wyk, 2010; Van Jaarsveld, 2010; Pierce, 2011; Reinten *et al.*, 2011; Honig, 2014). Emphasis on the species' hysteranthous evolutionary marking makes it an inconspicuous and valuable bulb that permits flowering and ecosystem biodiversity when there appear to be fewer flowers in bloom than at any other time of the year (Manning *et al.*, 2002; Honig, 2014). Irrevocably, emphasis and differentiation may be placed on its use as containerised flowering potted plants or as fragrant cut flowers lasting up to a week or longer in floral arrangements (Theron & De Hertogh, 2001; Bryan, 2002; Brown & Duncan, 2006; Maree & Van Wyk, 2010; Reinten *et al.*, 2011; Barnhoorn, 2013; Gul *et al.*, 2020; Darras, 2021). Efforts to increase global recognition of South African indigenous floral genera and sustainable cultivation from planting to flowering, including species such as *A. belladonna,* would benefit ecosystem biodiversity, conservation, and social well-being. Furthermore, it will engage in Indigenous Knowledge Systems (IKS), technology transfer, and training opportunities, and it will boost the South African economy by creating employment and redistributing wealth and knowledge.

1.7 Delimitations of the study

- A single species, *Amaryllis belladonna* L., from the genus *Amaryllis,* was investigated.

- Fieldwork was conducted at site-specific private property dwellings within the Pinelands residential area, Cape Town, South Africa, as described in the materials and methods.

- Each experimental investigation used plant materials from a specified source, as described in the materials and methods.

- Plant populations in the *ex-situ* field study were manually monitored and observed. The research activities were conducted at the greenhouse and laboratory research facilities of the Department of Horticultural Sciences, Cape Peninsula University of Technology, Bellville Campus, South Africa.

1.8 Thesis layout and structure

This thesis, initially described in the preface, is compiled differently from the traditional thesis format. The article-format thesis showcases published, co-published, and/or "ready-for-publication" articles (including references) prepared during the candidacy and applied to the format prescribed by the Cape Peninsula University of Technology for a 100% doctoral study, which observes the following principles:

1. The overriding principle of the thesis is that it remains an original contribution to the discipline or field by the candidate.

2. Chapters containing journal articles form a coherent and integrated body of work focusing on a single project or set of related questions or propositions. All journal articles (including references) form part of the sustained thesis with a coherent theme.

3. This study does not include work published before the start of the candidature.

4. The number of included articles depends on the content and length of each article. It takes complete account of the university's requirements and recommendations for a doctoral degree, with at least three journal articles and the candidate as the primary contributing author, of which at least two have already been published. A third article, "ready-for-publication", should also be included if not published.

5. The thesis should be examined according to the requirements set out by the "Guidelines for Examiners of Dissertations and Theses" (using form HDC 1.7D).

As described in the preface, this thesis is organised into 12 chapters, including an introduction, a literature review and four descriptive reviews focusing on specific aspects of *Amaryllis belladonna*. Following this, a field study and three greenhouse experiments on *A. belladonna* at different stages of bulb development were conducted to fulfil the study's aim and objectives. These chapters are followed by the overall conclusions, recommendations and the sources referenced in this thesis.

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CHAPTER 2

AMARYLLIS BELLADONNA L. – THE CAPE FLORAL REGION'S HYSTERANTHOUS GEOPHYTE: A REVIEW

(LITERATURE REVIEW)

AMARYLLIS BELLADONNA L. – THE CAPE FLORAL REGION'S HYSTERANTHOUS GEOPHYTE: A REVIEW

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2.1 Abstract

Amaryllis belladonna L. is an attractive amaryllid species endemic to South Africa's richly diversified Cape Floral Region. As one of only two species within the genus, the hysteranthous, early-autumn flowering geophyte's unassuming presence is well-known and modest in many Mediterranean regions worldwide. This review underlines the provenance of the unique fynbos habitat of Amaryllidaceae, taxonomy, botanical description, seasonal life cycle, distribution, propagation, cultivation, horticultural traits, and economic significance of the *A. belladonna* species. Furthermore, it identifies challenges and constraints of life cycle assessment and prospective opportunities for cultivation research from planting to seasonal flowering imperative to advance the underutilised *A. belladonna*'s prospects for sustainable development, economic differentiation and biodiversity in local and international flower bulb and cut flower market sectors.

Keywords: Anthesis, Amaryllidaceae, bulb development, floral induction, ornamental bulb

2.2 Introduction

Amaryllis belladonna (L.) (Amaryllidaceae) is an indigenous geophyte to the Western Cape of South Africa (Manning *et al.*, 2002; Duncan *et al.*, 2016). Opportunistic flowering occurs in the hysteranthous bulb of *A. belladonna* for six to nine weeks in late summer to early autumn, followed by burgeoning vegetative growth in winter before it transcends into late spring dormancy. This species' seasonally rhythmic growth cycle contrasts with the flowering schedules of many other bulbous species, which generally flower in late autumn, winter, spring, and early summer (Manning *et al.*, 2002; Duncan, 2010; Duncan *et al.*, 2016). Emphasis on the species' hysteranthous evolutionary marking makes it an inconspicuous and valuable bulb that permits flowering and ecosystem biodiversity when there appear to be fewer flowers in bloom than at any other time of the year. This review seeks to elucidate the alluring character, ecological importance, economic potential, challenges, and research opportunities of the early-autumn flowering *A. belladonna* to improve its candidature as a bulbous ornamental species of the Cape Floral Region (CFR) for local and international commercial flower bulbs and cut flower market sectors.

2.3 Fynbos habitat of Amaryllidaceae

The prodigious South African flora has long been of worldwide interest, with approximately 70% of the world's bulbous species, notably those from the CFR, being unrivalled elsewhere in the world (Manning *et al.*, 2002; Manning, 2007; Reinten *et al.*, 2011; Barnhoorn, 2013; Duncan *et al.*, 2020). The Cape Floral Region is the smallest of the six floral kingdoms, making up only 0.04% of the Earth's surface, yet it has the highest levels of floral diversity and endemism (Cowling & Richardson, 1995; Manning *et al.*, 2002).

The Amaryllidaceae plant family comprises 75 genera and 1600 species worldwide (Christenhusz & Byng, 2016), with the second-largest collection of 18 genera found in Southern Africa (Snijman, 2004; Duncan *et al.*, 2020). The CFR is home to 14 genera, mainly deciduous and autumn-flowering bulbous species, several of which are endemic (Duncan *et al.*, 2020). These endemic amaryllids have been unequivocally reported on the Red Lists of South African Plants and the International Union for Conservation of Nature (IUCN) with categories ranging from 'Vulnerable' to 'Critically Endangered', indicating the need for endorsed conservation action (IUCN, 2020; SANBI, 2020). According to Duncan *et al.* (2020), the significant contributing factor to the deterioration of these Amaryllidaceae species, particularly in Southern Africa, is the exponential destruction of their natural habitats through a wide range of anthropogenic activities and their consequential peripheral effects. This decline is further compromised by the threat and spread of alien vegetation, the collection of wild plants for the traditional medicinal plant trade, and the pressures of climate change (Manning *et al.*, 2002; Manning, 2007; Duncan *et al.*, 2020). While species of Amaryllidaceae have significant commercial ornamental value, several are renowned and sought after for their distinctive amaryllid alkaloid compounds, representing a wide range of biological activities (Snijman, 2004; Duncan *et al.*, 2020).

2.4 *Amaryllis belladonna,* a taxon of the Amaryllidaceae family

Amaryllis belladonna is an indigenous geophyte of South Africa's Western Cape (Manning *et al.*, 2002; Duncan *et al.*, 2016). The bulb is well-recognised by numerous vernacular names locally and abroad by way of the "Belladonna lily" or "March lily" in English, or the "Belladonnalelie", "Maartblom" or "Maartlelie" in Afrikaans, or as the "Naked Lady", "Madonna Lily", or "Jersey Lily" in other parts of the world (Adams, 2001; Manning *et al.*, 2002; Duncan, 2004). The appearance of the tall, floral stalks without paired leaves gives rise to the common name “Naked lady”, while the “March lily” refers to March in which it habitually flowers in its endemic region (Adams, 2001). *Amaryllis* is derived from the feminine Greek word *amarullis*, which refers to a lovely Roman shepherdess, while the epithet *belladonna* means "beautiful lady" in Italian (Adams, 2001; Duncan, 2004).

2.5 Species, cultivars, and hybrids

For approximately two centuries, *A. belladonna* was considered a monotypic taxon of the genus *Amaryllis* (Campos-Rocha *et al.*, 2017). A second species, *A. paradisicola*, was discovered in the dry Richtersveld region north of the Cape Floral Region in 1997 (Snijman & Williamson, 1998; Manning *et al.*, 2002). This species is distinguished by its broad tongue-shaped leaves, inattentive offset generation, and smaller, less aromatic blooms that flower only after autumn rains (Snijman & Williamson, 1998; Barnhoorn, 2013; Duncan *et al.*, 2016).

For decades, a discourse surrounded the correct identification of the *A. belladonna* species among plant scientists, as the genus *Amaryllis* was denoted as the tropical South American species *Hippeastrum*. The matter was ultimately concluded in 1987 when the name for the South African bulb was universally approved (Duncan, 2004; Barnhoorn, 2013; Duncan *et al.*, 2016). Inopportunely, the abundant, vibrant, summer-flowering *Hippeastrum* and its hybrids cultivated in South Africa and worldwide continue to be sold under incorrect taxonomic names and have become entrenched in many attentive minds as ‘amaryllis’ (Adams, 2001; Bryan, 2002; Duncan, 2004). *A. belladonna* has been successfully bred with other Amaryllidaceae species, including *Brunsvigia, Crinum*, and *Nerine,* to produce various intergeneric hybrids. These hybrids are popular because of their varied flowering periods, hues, forms, and prolificacy, as well as bulb hardiness, vigour, and adaptation to year-round irrigation and fertilisation (Bryan, 2002; Duncan, 2004; Salachna *et al.*, 2020).

2.6 Botanical description of *Amaryllis belladonna*

A. belladonna is a large brown ovoid bulb with spongy, brittle outer tunics and perennial, fleshy, contractile roots that allow it to root itself securely. Once mature, the perennial offset-forming bulb has a neck 15–30 mm long and a diameter of 750 mm (Hartsema & Leupen, 1942; Pienaar, 1987; Adams, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020). Each bulb has one inflorescence on a solid naked, purplish-red scape (420–950 mm) enclosed by two sheathing bracts, with the outer bract overlapping the inner at the base (Figure 2.1a) (Manning *et al.*, 2002; Duncan *et al.*, 2020). The inflorescence produces four to seventeen or more sweet-scented florets of white to varied shades of pink arranged within an umbel configuration (Theron & De Hertogh, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2016). Pedicels range in length from 30 to 100 mm during flowering and extend to 250 mm when in fruit. Each trumpet-shaped floret comprises six tepals approximately 10 cm long that apically open to 8 cm, with dark pink veins and a pale lemon-centred throat (Figure 2.1b) (Johnson & Snijman, 1996; Adams, 2001; Theron & De Hertogh, 2001; Manning *et al.*, 2002; McMaster, 2007; Duncan *et al.*, 2020). A long-upturned style protrudes from the centre of each floret, surrounded by six anthers that are initially black and glossy before splitting to reveal masses of sticky white pollen (Fig. 1b) (Johnson & Snijman, 1996; Adams, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2016).

Each bulb has six to twelve or more arching, lanceolate (15–75 mm wide) leaves with a pronounced midrib encased inside a maroon aerial leaf sheath found at the leaf base (Manning *et al.*, 2002; Duncan *et al.*, 2020). While in active leafage, the plant may reach a height of up to 90 cm and a spread of 60 cm (Figure 2.1c) (Manning *et al.*, 2002; Barnhoorn, 2013; Duncan *et al.*, 2016). The constituents of the entire bulbous species are toxic to humans and livestock, causing respiratory paralysis and psychoactive effects when consumed in large quantities (Snijman, 2004; Duncan *et al.*, 2016).

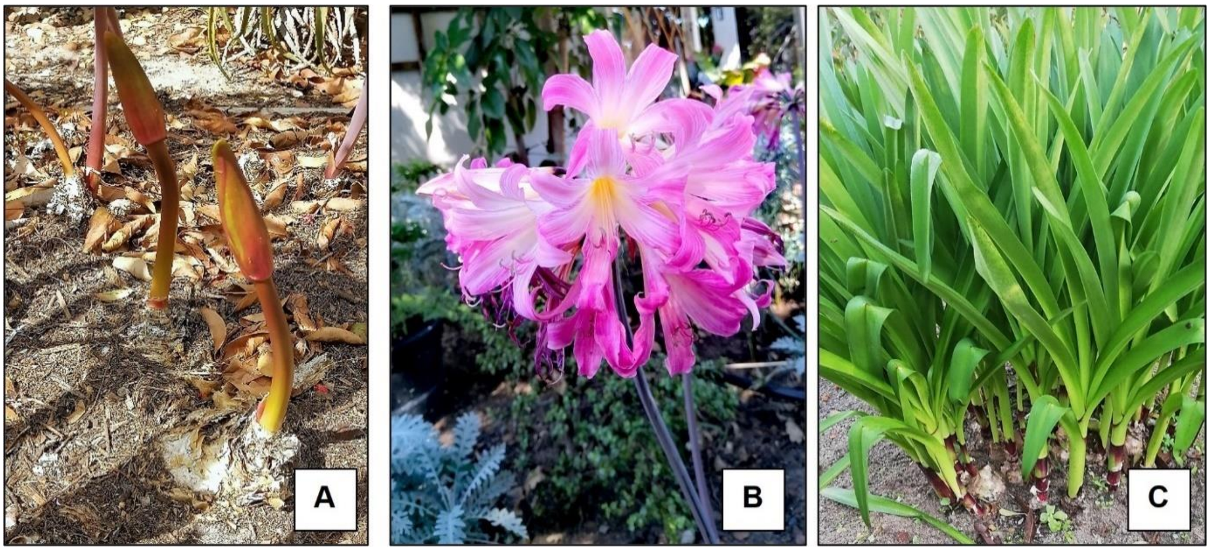

Figure 2.1: *Amaryllis belladonna*: (a) emergence of enclosed sheathing floral bracts, (b) floral structure, and (c) channelled leaves with distinct midrib and maroon aerial leaf sheaths (Photographs: C Wilmot)

The mature *A. belladonna* bulb's intrinsic morphology consists of numerous scales of the basal portions of foliar leaves from previous years. The newly produced leaves and inflorescence buds form in the bulb centre direction; after eight to ten leaves have formed, the growth point produces a new inflorescence (Hartsema & Leupen, 1942). Subsequently, an axillary bud at the base of the inflorescence will initiate a new series of leaves for the following season. The bulb initiates a single inflorescence each year during summer dormancy approximately 1 month before the preceding inflorescence emerges, equivalent to 12–13 months before flowering. The bulb measuring between 20 and 26 cm in circumference at the flowering stage can have up to five visible growth units (Hartsema & Leupen, 1942; Theron & De Hertogh, 2001). Likewise, in 70–80% of these bulbs, an aborted inflorescence can be observed between growth units at any time (Theron & De Hertogh, 2001).

2.7 Seasonal life cycle

As described within the Southern Hemisphere, the flowering stage *Amaryllis belladonna* bulb has a hysteranthous nature, showcasing the arrival of naked flower stalks in late summer to early autumn (Adams, 2001; Manning *et al.*, 2002; Duncan, 2010; Duncan *et al.*, 2016; Garland & Nicolson, 2016). The visible candelabrous pair of spear-headed bracts that rise above the ground is the first sign of flowering. As the flower scape reaches maximum height, the bracts part and systematically in coordinated succession, the floret buds begin to open (Johnson & Snijman, 1996; Manning *et al.*, 2002). The flowering period occurs between 6 and 9 weeks of the year (Manning *et al.*, 2002; Duncan *et al.*, 2016). Moreover, flowering occurs when very few other plants are in flower and is an advantageous evolutionary development in maximising the pollination of the species to ensure a successful seed bank soon after (Cowling & Richardson, 1995; Manning *et al.*, 2002; Duncan *et al.*, 2016). Once ripened, the large fleshy, recalcitrant, white-pink seeds are shaken from the dry globular capsules and scattered by the wind, typically landing adjacent to the parent bulb (Manning *et al.*, 2002). The green embryo does not enter dormancy and germinates while sustained by internal seed reserves. Therefore, coinciding with milder autumn temperatures and anticipated winter precipitation, the seedlings are quickly established (Johnson & Snijman, 1996; Manning *et al.*, 2002; Duncan, 2004; Duncan *et al.*, 2016; Pacific Bulb Society, 2018).

As the bulb inflorescence begins to fruit and the seed set disperses, the leaves emerge and expand into the winter rainfall months of the active vegetative growing season. During this photosynthetically active period, the bulb accumulates the necessary starch reserves to retain underground during harsh, dry, and hot summers (Manning *et al.*, 2002; Duncan *et al.*, 2016). Towards late spring to early summer, the onset of the rest period commences, ceasing photosynthesis and compelling the bulb into dormancy. This process is characterised and evident by the gradual yellowing, browning, and loss of turgidity in the senescing foliage and limited drying up and death of contractile roots (Seale, 1985; Warrington *et al.*, 2011; Kamenetsky & Okubo, 2012; Barnhoorn, 2013). It is essential to allow the foliage to perish to ensure that the underground storage organ has reabsorbed sufficient nutrients (Manning *et al.*, 2002; Barnhoorn, 2013; Honig, 2014; Solomon, 2018). Although aerial bulb growth is suspended during dormancy to preserve its delicate tissues from adverse environmental circumstances, its subterranean metabolic activity and desire for water and nutrients allow it to remain in an active yet shutdown mode (Manning *et al.*, 2002; Filippi, 2008; Barnhoorn, 2013; Kamenetsky-Goldstein, 2019).

Bulb latency during the hot, dry summer continues in anticipation of cooler autumnal night air and soil temperatures, shorter days, and the impending winter rains when dormancy is likely released and the flowering lifecycle resumes (Manning *et al.*, 2002; Duncan, 2010; Kamenetsky & Okubo, 2012; Barnhoorn, 2013; Duncan *et al.*, 2020). Juvenile bulbs undergo several years of seasonal vegetative growth and development until the intrinsic and extrinsic conditions that favour maturation and flowering competency are reached (De Hertogh & Le Nard, 1993; Thompson *et al.*, 2011). At this flowering stage, certain forms are inherently open to flower than others, and even in the more floriferous forms, not every bulb commences flowering each year (Pienaar, 1987; Manning *et al.*, 2002; Duncan *et al.*, 2020). Likewise, flowering is more pronounced under cultivation because it offers gentler treatment than those growing under natural (wild) circumstantial conditions (Manning *et al.*, 2002).

2.8 Geographical distribution

The Cape bulb is endemically confined to the Fynbos vegetation of the Western Cape of South Africa, from the northern Cederberg to the Cape Peninsula, and east to Nature’s Valley, where it encounters a Mediterranean climate (Figure 2.2) (Manning *et al.*, 2002; Duncan *et al.*, 2016). The term ‘Cape’ is limited to climatic conditions rather than the Cape Province's geographical locations, as several climatic types are found within its boundaries (Eliovson, 1959). The distinctive Fynbos Mediterranean climate is characterised by mild, wet winter rains, alternating with hot, dry summers accompanied by desiccating southeasterly winds (Cowling & Richardson, 1995; Manning *et al.*, 2002; Duncan *et al.*, 2020). The bulb is, therefore, acclimatised and accustomed to an annual warm (16 ˚C – 27 ˚C) to cool (5 ˚C – 13 ˚C) to warm (16˚C – 27˚C) thermoperiodic life cycle. As such, the species has naturalised and flowers in many lower elevations and coastal areas of other Mediterranean climatic regions around the world, including Mexico, California, Australia, Spain, Portugal, Tunisia, New Zealand, and the Channel Island of Jersey (Adams, 2001; Duncan, 2004; McMaster, 2007; Pierce, 2011; Duncan *et al.*, 2016; Pacific Bulb Society, 2018; El Mokni *et al.*, 2020).

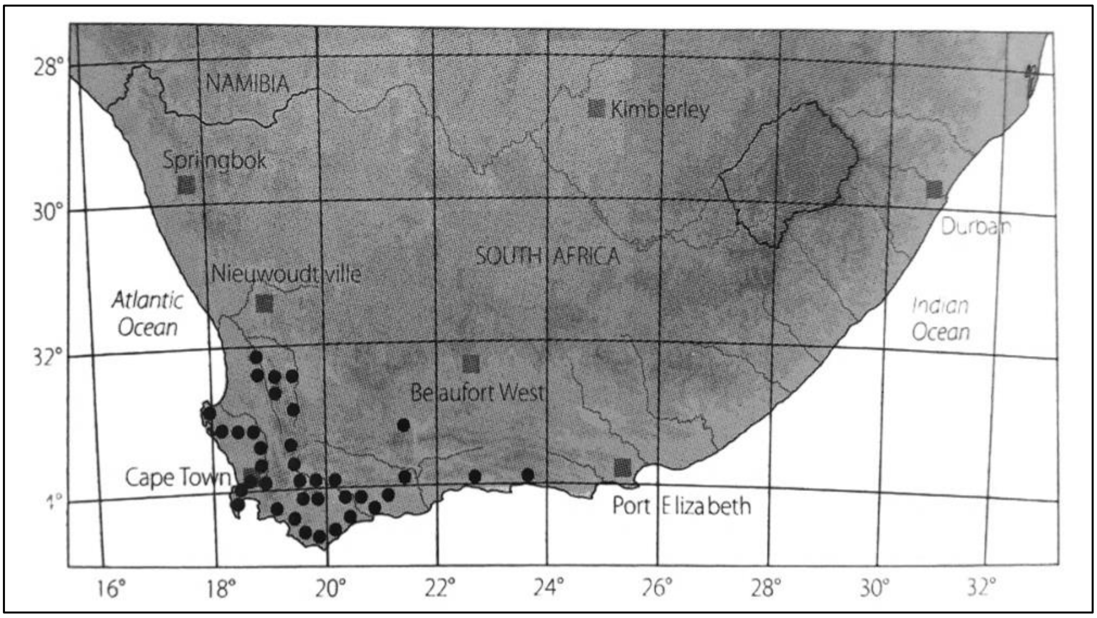

Figure 2.2: Map of the endemic distribution of *Amaryllis belladonna* within the Cape Floral Region (Duncan *et al.,* 2020)

2.9 Habitat and conservation status

Within their natural (wild) habitat, *A. belladonna* grows on lower hilly slopes, rocky hillsides, and in low-growing bush composed of Peninsula Shale Renosterveld, Cape Flats Sand Fynbos, and Sandstone Fynbos vegetation types (Manning *et al.*, 2002; Duncan *et al.*, 2016). The species flourish in nutrient-deprived, sandy soils with a slightly acidic pH and can withstand salty ocean spray in coastal locations (Adams, 2001; Manning *et al.*, 2002; Pacific Bulb Society, 2018). During the flowering period, carpenter bees (*Xylocopa* species) are the primary flower pollinators throughout the day but are only active on a few plants within a population (Adams, 2001; Duncan, 2004), whilst in the evening when the flowers are more heavily scented the noctuid moths are present (Manning *et al.*, 2002).

Amaryllis belladonna is well adapted to the flammable fynbos environment. It is often only seen flowering profusely in the open and mountainous areas of its natural habitat in a year or two following summer fires (Figure 2.3a) (Manning *et al.*, 2002; Duncan, 2004; Duncan *et al.*, 2016). This phenomenon is characterised and observed by abundant clusters of fragrant white and pink flower colonies transforming the blackened remains of the recently burned fynbos arena (Figure 2.3b) (Johnson & Snijman, 1996; Duncan, 2004). The species' shallow-seated bulbs endure quick, fast-moving fires; however, fire is not integral to its flowering as intermittent flowering occurs during inter-fire periods (Manning *et al.*, 2002; Duncan *et al.*, 2020). What exactly leads these species to blossom efficiently is unclear, especially following recent bushfires (Philips & Rix, 1989). It is suggested that fire is essential in eliminating the smothering vegetative moribund overgrowth, overshadowing the bulbs, and thus activating latent flower buds, leading to a profusion of mass flowering (Johnson & Snijman, 1996; Manning *et al.*, 2002; Duncan, 2004; Manning, 2007; Pierce, 2011; Duncan *et al.*, 2020).

Amaryllis belladonna is classified as 'Least Concern' on the ICUN Red List and the Red List of South African plants (IUCN, 2020; SANBI, 2020). Although this level of risk poses no threat to species' vulnerability, the ever-increasing pressures of habitat degradation and destruction caused by various anthropogenic activities and the collective harvesting demands of the medicinal plant trade are apparent. Moreover, this concern extends to the influence and prominence of the widespread peril of alien vegetation within the species' natural habitat of the Western Cape region of South Africa (Duncan, 2010; Duncan *et al.*, 2020).

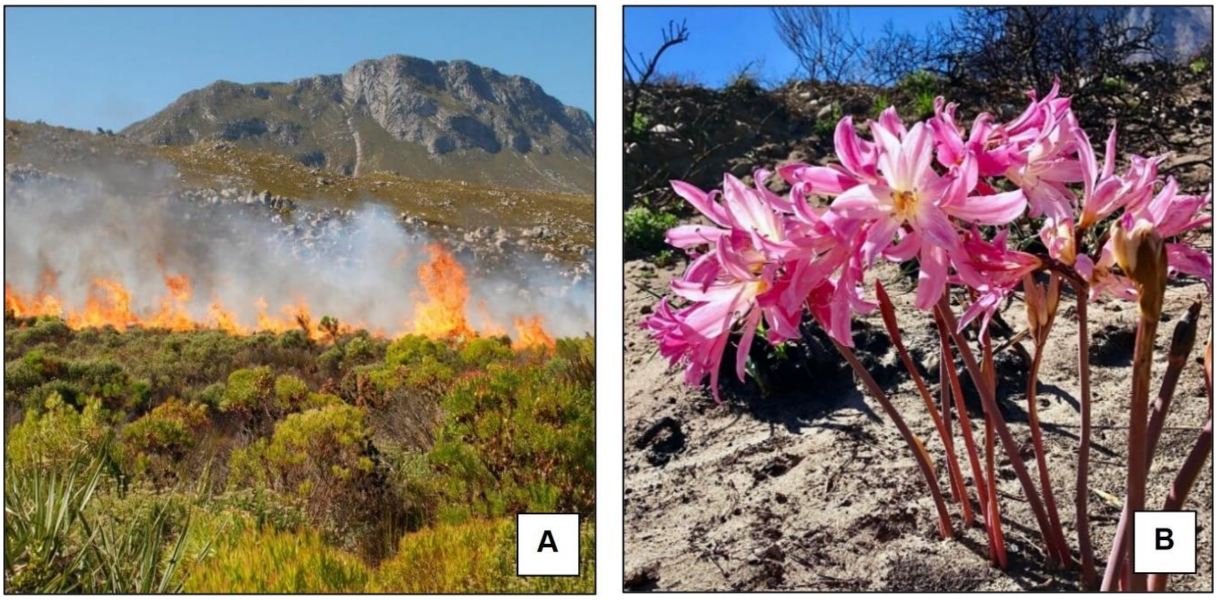

Figure 2.3: An archetypal mountainous fynbos fire (a); and *Amaryllis belladonna*'s abundant floral clusters emerging from bare soil following a fire (b) (Photographs: J Fil and J Parsons)

2.10 Cultivation and planting establishment

In the southern hemisphere, *A. belladonna* favours a warm to a hot, dry, north-to-north-eastern facing aspect to obtain adequate morning sun or the provision of a significant amount of warmth throughout the day to encourage flowering (Adams, 2001; Bryan, 2002; Duncan, 2010; Pacific Bulb Society, 2018). Seale (1985) and Gildemeister (1995) liken the warmth requirements to a 'summer roasting'. Although bulbs can withstand partially shaded areas, once the surrounding vegetation becomes too dense, fewer flower blooms are produced, and vegetation clearing is necessitated (Seale, 1985; Johnson & Snijman, 1996; Duncan, 2004; Barnhoorn, 2013; Duncan *et al.*, 2016).

The bulb grows befittingly in poor to moderately fertile and well-drained sandy soils with a slightly moderate acidic to neutral (5–7) pH (Adams, 2001; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). The bulb has moderate nutritional requirements, should not be grown in highly fertile soils, and receives little to no supplementary feeding (Duncan, 2010). According to Bryan (2002), Manning *et al.* (2002), Duncan (2010), and Barnhoorn (2013), feeding is not discouraged; instead, bulbs can undertake minimal supplementary feeding from flowering time in late summer until the onset of dormancy in spring. Naturally, improving the soil requires lifting the bulbs, but top-dressing may be done after growth begins, for which kraal manure and gently pierced phosphatic fertiliser are useful (Thorns, 1944). While the regular winter rains on the Cape Peninsula are generally adequate, periods of extreme dryness necessitate supplemental irrigation. Water resources must be available and accessible during the growing season, from May to October; however, many bulbs will induce early sprouting when heavy rainfall commences in February or March (Thorns, 1944; Manning *et al.*, 2002; Duncan, 2010). The subsequent flowering season is thus often not as prolific as a result (Thorns, 1944). As dormancy approaches, water should be gradually reduced; nevertheless, during spring and summer latency, the bulb can tolerate a modest quantity of water provided the soil is permeably well-drained (Seale, 1985; Duncan, 2010; Pierce, 2011; Barnhoorn, 2013).

The bulb should be shallowly planted with the neck at or elevated above soil level, with an optimal spacing of 10–15 cm; however, they can be placed closer for a massed impression (Seale, 1985; Duncan, 2010; Barnhoorn, 2013; Duncan *et al.*, 2016). Over time, this leads to gregarious and dense bulb concentrations and a decline in flowering (Adams, 2001; Manning *et al.*, 2002). As long-established bulbs resist disturbance, they can hinder flowering for several seasons. The lifting, dividing, and replanting frequency should be limited to every 4–6 years or when flowering declines (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). Moreover, this is pertinent because of the timeframe for the contractile roots to regenerate (Manning *et al.*, 2002; Duncan, 2010). Several sources indicate that lifting, dividing, and transplanting of established *A. belladonna* bulbs should be undertaken in autumn, just as new foliage emerges, allowing the bulb to re-establish during its active growing season and sending out new roots before the onset of dormancy in early summer (Duncan, 2004; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). In addition, bulbs lifted and reset without the perennial contractile roots drying soon after the flower stems have perished will often flower the following season (Manning *et al.*, 2002; Duncan, 2010).

However, Seale (1985) and Pienaar (1987) indicated that the bulbs should be lifted during early dormancy, stored, and replanted at least 3–4 weeks before the new season's flower buds appear. Suitable storage can be undertaken by placing the bulbs in cardboard trays, wire baskets, or paper bags in a moderately cool, dry, and well-ventilated location between 20 °C and 22 °C (Duncan, 2010; Barnhoorn, 2013). The *A. belladonna* bulb is thus regarded as a drought-tolerant specimen because it has longevity and has grown effectively for decades in various unmaintained and undisturbed landscapes for lengthy periods with little or no attention (Adams, 2001; Carter, 2007; Pierce, 2011).

2.11 Pests and diseases

The *A. belladonna* bulb is habitually destroyed by the destructive lily borer (*Brithys crinii*), a black and yellow-striped caterpillar readily seen attacking the leaves and sections of the bulb, hollowing out the soft, pithy scapes, pedicels, and fleshy seeds (Figures 2.4a–c) (Duncan, 2010; Barnhoorn, 2013). The caterpillar, well-known to attack many amaryllids throughout South Africa, is ostensibly immune to the toxic alkaloids found in Amaryllidaceae species (Johnson & Snijman, 1996; Duncan, 2010; Barnhoorn, 2013). To a lesser extent, leaf margins are nibbled by nocturnal snout beetles (Duncan, 2010). The bulb is reportedly disease-free (Barnhoorn, 2013).

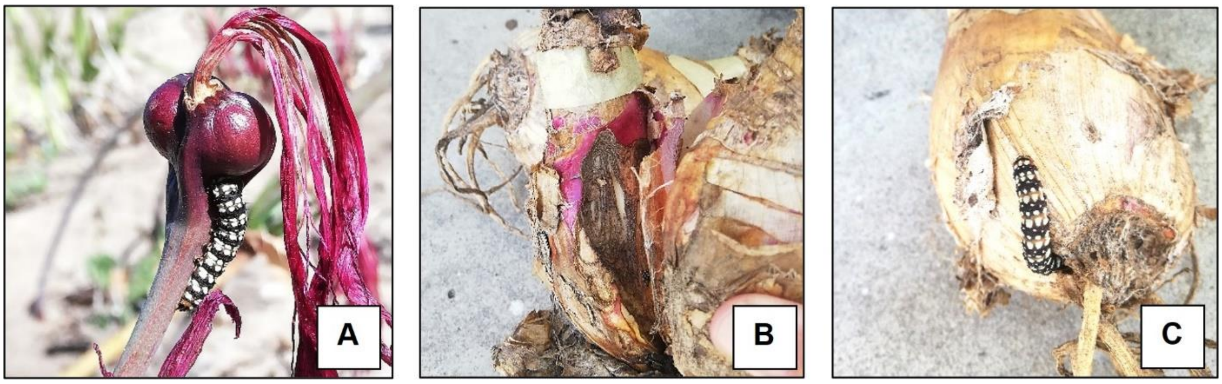

Figure 2.4: Lily borer caterpillar (a) piercing the fruiting capsule to consume fleshy seeds; (b) rasping of bulb scales (c) penetrating the bulb basal plate of *Amaryllis belladonna* (Photographs: C Wilmot)

2.12 Propagation

Seed and division of bulb offsets (daughter bulbs or bulblets) are the most accustomed and cost-effective forms of *A. belladonna* proliferation (Adams, 2001; Theron & De Hertogh, 2001; Manning *et al.*, 2002; Duncan, 2010; Pacific Bulb Society, 2018). However, more expensive alternative tissue culture techniques have been successfully documented (De Bruyn *et al.*, 1992; Veeraballi *et al.*, 2017). Seed capsules of *A. belladonna* develop rapidly after successful pollination in autumn and mature within 4–5 weeks (Amico Roxas *et al.*, 1994; Duncan, 2010). Once opened, seeds of significant size and colour variation are revealed (Figures 2.5a and c) (Amico Roxas *et al.*, 1994). The fleshy, recalcitrant seeds fail to withstand desiccation and do not enter a resting period; instead, the embryo continues to develop, relying on the nutrients stored in the copious endosperm for immediate germination (Figure 2.5b) (Manning *et al.*, 2002; Duncan, 2010). Once established, the bulb seedlings require several years to reach bulb maturity (Figure 2.5d).

Large enough offsets are gathered from the species' mother bulb basal periphery with contractile roots intact to augment clonal bulb stock material; however, their regeneration is limited in number (Figure 2.5e) (Duncan, 2010; Barnhoorn, 2013). Offsets should, if possible, remain attached to the parent bulb for a few years because premature detachment slows their maturation rate (Duncan, 2010). Like those grown from seed, offsets mature relatively slowly, taking 4–6 years under ideal conditions, if not longer, before maturity and flowering competency are reached (Johnson & Snijman, 1996; Manning *et al.*, 2002; Duncan *et al.*, 2016).

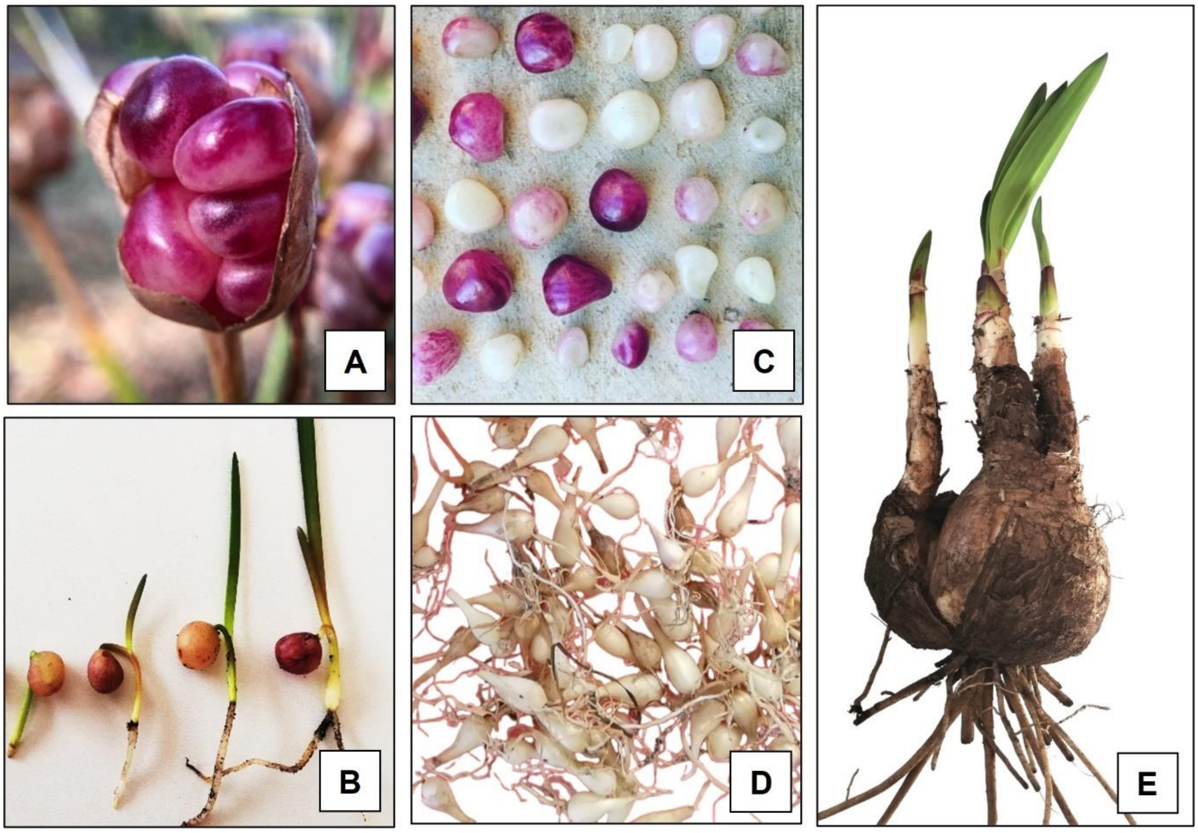

Figure 2.5: *Amaryllis belladonna:* (a) rounded fruiting capsule revealing recalcitrant seeds; (b) green embryonic, radicle emergence, and early bulb development from seed; (c) variation in seed colour, size, and shape; (d) juvenile bulb seedlings and (e) a typified mature mother bulb with two unattached offsets (Photographs: C Wilmot)

2.13 Economic significance of *A. belladonna*

A. belladonna is widely recognised and utilised in a variety of planting palettes and functional applications as a low-maintenance, drought-tolerant and intermittent seasonal late bloomer within the horticulture and floriculture framework (Theron & De Hertogh, 2001; Bryan, 2002;

Brown & Duncan, 2006; Maree & Van Wyk, 2010; Van Jaarsveld, 2010; Pierce, 2011; Reinten *et al.*, 2011; Honig, 2014). The species' seasonal landscape design use and function may include incorporating the bulbous species to explicitly accentuate, complement, or contrast various plant materials within landscaped entrance features, raised planters, rockeries, grass and gravel gardens, herbaceous beds, and borders, as well as to define clipped hedges and walkways. Moreover, they are prominent in unmaintained slopes, naturalistic gardens, and roadside plantings. Likewise, the flowering bulb attracts pollinators to the surrounding habitat, increasing ecosystem biodiversity (Manning *et al.*, 2002; Honig, 2014). Irrevocably, emphasis and differentiation may be placed on its use as containerised flowering potted plants or as fragrant cut flowers lasting up to a week or longer in floral arrangements (Theron & De Hertogh, 2001; Bryan, 2002; Brown & Duncan, 2006; Maree & Van Wyk, 2010; Reinten *et al.*, 2011; Barnhoorn, 2013; Gul *et al.*, 2020; Darras, 2021).

The species has likewise garnered scientific attention within the pharmacological arena because of its isolated alkaloid constituents, some of which exhibit anti-bacterial, anti-fungal, anti-neoplastic, and anti-parasitic properties (Pettit *et al.*, 1984; Evidente *et al.*, 2004; Nair *et al.*, 2013; Chavarro *et al.*, 2020; Nair & Van Staden, 2022; Evidente, 2023). Over 30 *A. belladonna* alkaloids have been discovered thus far, with 1-O-acetylcaranine, amarbellisine, buphanamine, hippeastrine, hydroxyvittatine, lycorine, and pancracine being a few among them (Evidente *et al.*, 2004; Nair *et al.*, 2013; Nair *et al.*, 2016; Tallini *et al.*, 2017; Nair & Van Staden, 2022; Evidente, 2023). In addition, over several decades, it has been used as a traditional medicine in African cultures (Nair *et al.*, 2016; Tallini *et al.*, 2017).

2.14 Horticultural challenges

Geophytes are a diverse class of flora, and their global collective multiplicity is increasing due to omnipresent market changes, competitive demands for timely stock, and the purposeful breeding of new cultivars and hybrids with specialised and desirable qualities for many divisions of the agriculture, horticulture and, floriculture sectors (Anderson, 2006; Anderson, 2019; Slezák *et al.*, 2020; Marasek-Ciolakowska *et al.*, 2021). While the selection and necessity of plant species are subjective and dependent on specific conceptions and markets, biodiversity and diversification are paramount. Moreover, climate change's ramifications on geophytic production pose new challenges (Barnhoorn, 2013; Kamenetsky-Goldstein, 2019). The abundance of South African endemic bulbous species contributes a relatively small fraction to the number of commercial crops found within the global bulb industry and thus is not operative to its fullest potential (Matthee *et al.*, 2006; Reinten *et al.*, 2011; Barnhoorn, 2013; Darras, 2021).

Complex fundamentals are involved in effectively developing South African flora rather than only their unique attractiveness and aesthetic qualities. According to Reinten *et al.* (2011), to compete globally, ornamental crops must be true to type, accessible in large numbers for a reasonably lengthy marketing period and consume a suitable vase life. With specific emphasis on certain Amaryllidaceae species, Niederwieser *et al.* (2002) and Duncan (2010) pointed out difficulties regarding flower initiation, floral longevity, bulb heterogeneity, and colour selection limitations for commercialisation. Reinten *et al.* (2011) further underlined that these challenges are partly caused by the limitations of erratic blooming and short flowering periods. These are imperative obstacles to overcome, coupled with a lengthy juvenile-to-maturation timeframe for large-scale commercialisation and distinct niche markets.

Moreover, these species require long-term funding and interdisciplinary research strategies for their accessible development (Bester *et al.*, 2009; Reinten *et al.*, 2011; Barnhoorn, 2013). The numerous limitations and restraints imposed by the *A. belladonna* species at different bulb development phases make it challenging to fulfil time-consuming obligations for the competitive requirements of the horticultural and floriculture frameworks. These are most notably related to the species' prolonged bulb juvenility, low offset production, and, more emphatically, the erratic flowering disposition once maturity and reproductive competence are reached.

2.15 Research prospects

As bulbous genera demonstrate significant associative dissonance and consume a variety of multifaceted economic impacts and statutory demands, geophytic cultivation methodologies cannot be extrapolated, although inferences can be made (Duncan, 2010; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013). Likewise, the inherent composition and genetic variability of geophytes are becoming more valuable (Kamenetsky & Miller, 2010; Reinten *et al.*, 2011; Marasek-Ciolakowska *et al.*, 2021), and greater emphasis will be directed to species and those of indigenous and underutilised flora with prospective sustainable production and health-promoting benefits (Duncan, 2010; Darras, 2020; Thörning *et al.*, 2022). In addition, contributions to the local ecosystem biodiversity and the well-being of society and culture will further promote these species (Ingram *et al.*, 2019; Darras, 2020; Thörning *et al.*, 2022). Such endeavours will undoubtedly increase the dependency and demand for species-sustainable cultivation, conservation, and health. For these purposes, novel and heterogeneous scientifically based research of academic distinction is imperative to broaden the knowledge of plant-environment interactions and cultivation practices from planting to flowering (Khodorova & Boitel-Conti, 2013; Darras, 2020). Moreover, these are essential in addressing existing and emerging challenges in sustainably advancing crop species in a changing climate

(Le Nard & De Hertogh, 2002; Manning *et al.*, 2002; Reinten *et al.*, 2011; Duncan *et al.*, 2016; Kamenetsky-Goldstein, 2019; Darras, 2020; Slezák *et al.*, 2020).

South African Indigenous Plant Knowledge systems are a powerful and valuable agroecological and economic tool with a competitive advantage in floral biodiversity that represents an untapped resource of inestimable proportion (Reinten & Van Wyk, 2018; Duncan *et al.*, 2020; Darras, 2021). Thus, it is essential to examine, promote, and expand the sustainable biodiversity and stewardship of its natural heritage and ecosystems (Donaldson & Scott, 1994; Manning *et al.*, 2002; Reinten *et al.*, 2011; Duncan *et al.*, 2020). Although new research instruments are sought to resolve specific outcomes, sustainable cultivation, propagation, and postharvest management improvements remain necessary to make South African plant species more widely accessible (Niederwieser *et al.*, 2002; Reinten *et al.*, 2011; Duncan *et al.*, 2020). As such, there is a growing movement to develop sustainable novel approaches that leverage the innate characteristics and fundamental cultivation scheduling ramifications of South Africa's distinctive dispensation of underutilised indigenous flora (Reinten *et al.*, 2011; Duncan *et al.*, 2016; Reinten & Van Wyk, 2018; De Pascale & Romano, 2019).

These assertions are particularly pertinent to the profitable viability of the indigenous and underutilised *A. belladonna* bulbous species. Several research studies have focussed on underpinning the species' alkaloidal activities (Pettit *et al.*, 1984; Evidente *et al.*, 2004; Nair *et al.*, 2013; Chavarro *et al.*, 2020; Nair & Van Staden, 2022; Evidente, 2023), improving its desirable floral attributes through interspecific and intergeneric breeding (Bryan, 2002; Duncan, 2004; Salachna *et al.*, 2020), propagation through tissue culture (De Bruyn *et al.*, 1992; Veeraballi *et al.*, 2017), and postharvest qualities of cut flower scapes (Gul *et al.*, 2020). Nevertheless, the growth of bulbous species is hampered by the lack of scientifically grounded and quantifiable empirical data to perpetuate the cultivation methodology of various phases of bulb development, harbouring indubitable commercial potential. Thus, novel and workable cultivation techniques of scientific merit are required to enhance the potential of the *A. belladonna* species for optimal growth and development and, more fervently, to stimulate seasonal flowering. This will strengthen the species' competitive differentiation and biodiversity in local and international flower bulb and cut flower markets.

2.16 Intrinsic factors affecting bulb and flower development

2.16.1 Bulb yield

Bulb size and uniformity are categorically graded and rigorously scrutinised to ensure that bulbs are at an acceptable grade level for commercial production because bulb size impacts output quality, yield and flowering productivity (Khodorova & Boitel-Conti, 2013; Kapczyńska, 2014; Manimaran *et al.*, 2017). This grade level is attained according to species-specific biomass; however, in most cases, bulb circumference is used (Seale, 1985; Barnhoorn, 2013). Flowering-sized bulbs vary considerably, and circumferences from 4 to 26 cm and above are recorded (Seale, 1985; Theron & De Hertogh, 2001; Barnhoorn, 2013). Bulbs are grown from seed or vegetatively and undergo numerous vegetative growth seasons (age) that serve as a source and sink of internal carbohydrate reserves to achieve species-specific critical reproductive maturation biomass, number of leaves, and/or size before flowering competency is initiated and induced (Rees, 1966; Seale, 1985; Le Nard & De Hertogh, 1993; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013). This timeframe varies significantly depending on the species, growth circumstances, and flower-promoting inducive stimuli encountered (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). However, inductive cues that promote flowering are ineffective for juvenile bulbs (Levy & Dean, 1998; Proietti *et al.*, 2022).

Smaller geophytic species of the *Amaryllis, Hyacinth,* and *Iris* families will flower for the first time from seed in 2–3 years (Seale, 1985; Barnhoorn, 2013). However, larger species, particularly from the amaryllid family, such as *Boophone, Brunsvigia*, and *Crinum*, can take up to 12 years or more to reach flowering size (Manning *et al.*, 2002; Duncan, 2010). Bulbous species and hybrids with long juvenile phases have important scheduling implications for economic profitability. Furthermore, the demand for adequate stock material and maintaining species in cultivation with selected traits for long-term production is increasing (Anderson, 2019). Current geophytic research focuses on procuring vegetative propagation (Marković *et al.*, 2021) and gradual reduction in the juvenile phase of species cultivation to provide optimal bulb 'ripening' or 'bulking' for planned production lines, bulb growth, homogeneity, and yield within prescribed periods (Anderson, 2019; Marasek-Ciolakowska *et al.*, 2021). Thus, to justify *A. belladonna*'s compelling and timely proliferation, determining effective cultivation practices is essential to augment the species' prolonged juvenile bulbs and offset development for greater capacity yields and flowering fitness.

2.16.2 Bulb dormancy

Dormancy is an essential part of a bulb's seasonal rhythmic life cycle, whose onset, duration, and release are species-specific and regulated by hemispheric seasonal changes or adverse conditions (Duncan, 2010; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013; Kamenetsky-Goldstein, 2019). During this yearly interval, ongoing internal morphological and physiological processes are sustained in preparation for growth and development once favourable circumstances materialise (Filippi, 2008; Duncan, 2010; Kamenetsky-Goldstein, 2019). For true bulbs of the *Amaryllis* and *Hyacinth* families, this is especially pertinent because it is during this time that the leaves and inflorescence for the upcoming season(s) are formed (Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). Therefore, while bulb latency offers a constructive handling, treatment, and shipping timeframe (Rees, 1966; Barnhoorn, 2013), circumstances and practices that disrupt the necessitated bulb dormancy processes can either inhibit or promote the successive growth and flowering sequence of events in the season(s) to follow (Manning *et al.*, 2002; Warrington *et al.*, 2011; Barnhoorn, 2013). Therefore, establishing a deeper knowledge of *A. belladonna* dormancy, the affecting factors, and prospective development and flowering performance dynamics is imperative to facilitate the species' capacity for profitable cultivation and seasonal viability.

2.17 Extrinsic factors affecting bulb and flowering development

2.17.1 Temperature

Temperature is a fundamental environmental factor regulating the many active growth processes of bulbs, development, dormancy induction and release, and flowering (Hartsema, 1961; Manning *et al.*, 2002; Duncan, 2010; Khodorova & Boitel-Conti, 2013; Capovilla *et al.*, 2015; Kamenetsky-Goldstein, 2019; Proietti *et al.*, 2022). Natural seasonal day and night (air and soil) temperature and duration fluctuations are among the many warm-cold-warm thermoperiodic differentials experienced by distinct hemispheric climatic regions, rainfall patterns, and topographical aspects (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013; Kamenetsky-Goldstein, 2019).

The floriculture industry's progressive understanding of the warm-cold-warm temperature signalling pathways, which are tightly associated with regulating the convoluted flowering induction and differentiation of many bulbous species, has resulted in the advancement of bulb storage and vernalisation techniques (Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013; Capovilla *et al.*, 2015). Commercial growers employ these multifaceted tactics to maximise flowering yields by bulb forcing or holding to satisfy specific and timely market demands and quality traits over extended periods (Barnhoorn, 2013). However, these are modified explicitly to coincide with each genus's cardinal temperature range, needs, and outcomes (Theron & De Hertogh, 2001; Khodorova & Boitel-Conti, 2013; Kamenetsky-Goldstein, 2019). During dormancy, methods of warm storage are well-established; in addition to accelerating or delaying bud growth and flowering, they increase quality attributes, enhance percentage yield, and stimulate root development (Barnhoorn, 2013; Capovilla *et al.*, 2015).

Saffron (*Crocus sativus* L.) bulbs flowered earlier when stored at warmer temperatures just after leaf withering (Molina *et al.*, 2005). Similarly, after warm storage, flowering was hastened in *Eucomis* (Carlson & Dole, 2015), *Hippeastrum* (Inkham *et al.*, 2019), and *Nerine sarniensis*

(Warrington *et al.*, 2011). Warm storage (25 °C – 30 °C) increased percentage yields and earlier flowering in various species of *Ornithogalum* (Roh & Hong, 2007). *Watsonia* corms exhibited improved vegetative growth, inflorescence maturity, and flower bud opening when stored at temperatures as high as 25 °C (Thompson *et al.*, 2011). As standardised forcing techniques make analysis and comparison difficult, defining the mechanisms that affect these characteristics in species-specific floricultural crops is crucial to attaining sustainable production and improved product quality (Roh & Hong, 2007; Barnhoorn, 2013; Reinten *et al.*, 2011). Therefore, determining the effects of temperature differentials and bulb storage practices on the flowering productivity of *A. belladonna* is fundamental to optimising the species' capacity for seasonal competence of inflorescence quality attributes and flowering yield. Furthermore, it is anticipated to provide data on prolonging the flowering season.

2.17.2 Water

Water availability and accessibility are paramount in geophytic cultivation and are among the most critical factors affecting bulb growth and flowering productivity (Seale, 1985; Duncan, 2002; Barnhoorn, 2013; Kamenetsky-Goldstein, 2019; Inkham *et al.*, 2022). Bulb growth occurs when conditions are favourable, and although they respond to temperature variations, they awaken with the anticipation and expectation of available and accessible water through various natural, seasonal, and anthropogenic precipitative pathways during active growing periods (Duncan, 2010; Barnhoorn, 2013). Climate change, drought, flooding, and incorrect watering regimes have been major pitfalls in losing many wild and cultivated bulbs (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013; Kamenetsky-Goldstein, 2019). Moreover, this has been evident to mimic growing conditions between different rainfall and seasonal and hemispheric climatic regions without carefully considering species-specific water requirements. Soil water potential within the bulb root zone is crucial for many intrinsic physiological and morphological processes because bulb roots facilitate the uptake of nutrients and water from the soil for seasonal bulb growth, development, and flowering. (Duncan, 2010; Ndhlala *et al.*, 2012; Barnhoorn, 2013; Inkham *et al.*, 2022). Conversely, water deficit and dryness inhibit absorption, causing bulb stress and stunted growth and development (Seale, 1985; Barnhoorn, 2013; Kamenetsky-Goldstein, 2019). Furthermore, signs of early dormancy, premature desiccation of the leaves and roots, decreased photosynthesis, an increase in the abscission rate, and embryonic flower abortion are among these (Ndhlala *et al.*, 2012; Barnhoorn, 2013).

Increased watering frequency resulted in more vegetative growth and larger bulbs of *Eucomis autumnalis* (Ndhlala *et al.*, 2012). At higher water frequencies, *Ornithogalum longibracteatum* and *Tulbaghia violacea* exhibited comparable responses (Kulkarni *et al.*, 2005). Similarly, optimum bulb growth and quality were found in *Hippeastrum* 'Red lion' at higher water frequencies (Inkham *et al.*, 2022). According to Duncan (2002), an initial heavy soaking of water after a dry summer in early fall accelerates the growth and emergence of flower buds in *Nerine* species. Soil moisture regulation can support the timely growth of bulbous plants and their below-ground biomass development. Therefore, increasing our knowledge of *A. belladonna* moisture requirements and response mechanisms in regulating the provision of soil-water-nutrient uptake is essential to augment the species' potential for optimal growth, development, and flowering.

2.17.3 Nutrients

Nutritional delivery is critical for producing, cultivating, and retaining bulbs throughout several seasons (Seale, 1985; Barnhoorn, 2013). Following flowering and during the active growth season, nourishment is required when bulbs regenerate in preparation to see them through periods of dormancy, increase biomass, and supplement the embryos for the next season(s) flowering in their advanced maturation stage (Duncan, 2010; Barnhoorn, 2013). However, fertiliser applications should be withheld near dormancy as those containing nitrogen may stimulate undesirable leaf growth at the loss of flowering when foliage production naturally declines (Seale, 1985; Duncan, 2010; Barnhoorn, 2013). Profitable plant production originates with quality, nutrient-filled soils and healthy seedlings, allowing them to establish themselves in the field and improve their survival rate under adverse conditions (Elsadek & Yousef, 2019).

Bulbous species respond effectively to fertiliser treatments when appropriate macro- and micronutrient and species-specific demands are recognised (Seale, 1985; Duncan, 2010; Barnhoorn, 2013). While several South African bulb species effectively gain from added nutrition, many winter growers require very little, if any, as they occur naturally in nutrient-deficient soils, yet nutritional supplementation is not discouraged for optimal development and flowering (Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). Evergreen and summer-growing bulbs often require higher levels of supplemental nutrition than winter-growing varieties (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010). Although bulbs may be claimed to thrive in the wild in pure sand, nutrient-deficient soils, or standing in water, attempts to nurture them in such conditions under cultivation are unlikely to be effective (Thorns, 1944). Using low-phosphate organic fertiliser, high-potash liquid fertiliser, or liquid feeds containing seaweed extracts incorporated into the topsoil medium or as a soil drench or foliar spray during the growing season is recommended (Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013).

Optimal growth and flower production of *Hippeastrum hybridum* were obtained by applying N, P, and K at 200 kg N, 400 kg P, and 300 kg K per hectare (Jamil *et al.*, 2016). Potassium sulphate as a foliar spray and the simultaneous application of potassium soil dressing improved growth parameters in *Gladiolus hybrida* cv. “Rose Supreme” (El-Naggar & El-Nasharty, 2016). *Eucomis bicolor* ‘Baker’ bulbs attained enhanced growth, blooming, yield, leaf quantity and chlorophyll content with seaweed extract pre-soaking before planting (Byczyńska, 2018). *Eucomis autumnalis* (Mill.) Chitt (Aremu *et al.*, 2016) and *Erica verticillata* Bergius (Adams *et al.*, 2019), two economically valuable and well-known indigenous South African taxa, showed promising results from seaweed-based research. The influence of fertiliser application on *A. belladonna* has not yet been investigated. Therefore, determining the stimulating effects of fertiliser amendments and supplemental nutrition in cultivating *A. belladonna* is imperative to improve the species’ capacity for bulb growth, development, and flowering and support bulb health and survival.

2.17.4 Hydroponics

Hydroponic technology’s development has enabled year-round cultivation by resolving many plant crops’ challenges and inherent flaws across numerous latitudinal locations worldwide. (Wahome *et al.*, 2010; Sakamoto & Suzuki, 2015; Karagöz *et al.*, 2022). While eliminating the necessity for soil substrates, hydroponics permits precise governance, modification, and delivery of long-term environmental extrinsic factors such as temperature, nutrients, humidity, light, pH, EC, and water to plant crops (Wahome *et al.*, 2010; Fussy & Papenbrock, 2022; Karagöz *et al.*, 2022; Velazquez-Gonzalez *et al.*, 2022). This approach has fostered higher growth and development rates through rapid generation cycling (RGC), resulting in feasibly larger crop production yields per unit area (Wahome *et al.*, 2010; Sakamoto & Suzuki, 2015; Karagöz *et al.*, 2022). Although hydroponic culture is a viable alternative for optimising many crop varieties (Fussy & Papenbrock, 2022; Velazquez-Gonzalez *et al.*, 2022), production results—especially for bulbous species—have been used to promote flowering with minimal evidence of vegetative development (Barnhoorn, 2013). Flower-forcing species such as *Hippeastrum, Hyacinth, Leucojum,* and *Narcissus* are among them (Seale, 1985; Barnhoorn, 2013; Schroeder *et al.*, 2020). *Lilium* Asiatic hybrids cv. “Blackout” grown using a nutrient film technique (NFT) hydroponic system achieved optimal performance, producing flowers in 55 days (Asker, 2015). The highest rates of vegetative growth, flower formation, and quality characteristics were exhibited in *Gladiolus grandiflorus* cultivated in a bag culture hydroponics system (Wahome *et al.*, 2010), as did *Fritillaria imperialis* in soilless culture (Kahraman & Özzambak, 2006). Therefore, with advances in hydroponics, determining the feasibility of hydroponically cultivating *A. belladonna* would be beneficial in promoting workable solutions to alleviate and address the species’ requirement for timeous and adequate stock material and increased bulb yield.

2.17.5 Planting establishment

Incorrect and unfavourable species-specific planting depths often hinder certain functions and retard or weaken geophytic growth and flowering percentage (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). A perfectly well-drained medium with a moderately acidic to neutral pH (5–7) is one of the most important factors when cultivating Southern African bulbs (Manning *et al.*, 2002; Duncan, 2010).

As bulbs grow and expand, they compete for space and nutrients, eventually affecting their bulb development, quantity, and quality (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). Moreover, the leaving, lifting, dividing, storing, and resetting regimes of *in situ* or ex-situ bulbous species are considerably varied and can invigorate or inhibit several activities (offset production, flowering stimulation, bulb expansion) necessary for successful cultivation (Rees, 1975; Seale, 1985; Duncan, 2010; Barnhoorn, 2013). Selected bulbs are gregarious and prefer to grow closer together, whereas others prefer to be disturbed, spaced, and replanted more frequently to encourage an increase in growth and, more importantly, successful flowering (Seale, 1985; Duncan, 2010; Barnhoorn, 2013). Based on empirical evidence, bulbs that proliferate vegetatively will eventually grow congested, whereas those without this characteristic will become thin and patchy (Thorns, 1944). According to Thorns (1944), Manning *et al.* (2002), and Duncan (2010), because of their perennial contractile roots and the time to regenerate, amaryllids prefer to be left undisturbed for several years or until a decline in flowering is observed.

Kapczyńska (2013) found that a lower bulb planting in comparison with a denser planting density positively influenced the quality of four cultivars of *Lachenalia* bulbs (circumference and weight) without affecting their quantity; however, planting arrangements had little effect on inflorescence length and the number of florets produced. Field-grown *Nerine sarnensis* lifted every 4–6 years supports the invigoration and performance of flowering yields for commercial production (Warrington *et al.*, 2011). Knowledge of specific bulb genera, habitats, and requirements most favourable where they naturally occur is pertinent to successfully cultivating and establishing bulbs for commercial purposes (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). Moreover, it is imperative to discover the enduring ramifications of perturbations on the planting establishment, longevity, and densities of *ex situ* perennial bulbs. Additional research is necessary to comprehensively comprehend the appropriate timing for intentionally utilising these cultivation techniques, especially within *ex situ* settings. Thus, determining the population attributes, habitat features, and cultivation practices associated with *A. belladonna*’s *ex situ* bulb planting life strategy will better understand the species’ synergistic demands and capacity to promote commercial cultivation and prolific flowering yields. Furthermore, data from such investigations are anticipated to provide further knowledge of the species' survival strategies under cultivation.

2.17.6 Fire-stimulation

Numerous South African bulbous species are well-adapted and, in some cases, dependent on the occurrence of natural wildfires for flowering and to enhance reproductive growth (Cowling & Richardson, 1995; Saunders & Saunders, 2000; Manning *et al.*, 2002; Duncan, 2010; Lamont & Downes, 2012; Garland & Nicolson, 2016). A natural wildfire provides both physical and chemical changes to the ecosystem for a certain period during and after the fire, directly and indirectly affecting the induction of seed germination, re-sprouting, physical dormancy, and post-fire flowering of selected plant species (Cowling & Richardson, 1995; Manning *et al.*, 2002; Dixon *et al.*, 2009; Bradshaw *et al.*, 2011; Keeley *et al.*, 2011; Garland & Nicolson, 2016). The ensuing capabilities of mass flowering profusion by induced dormant flower buds of fire-stimulated flowering (FSF) geophytes are typically most abundant in the season immediately following a fire that diminishes throughout successive seasons (Le Maitre & Brown, 1992; Cowling & Richardson, 1995; Manning *et al.*, 2002; Duncan *et al.*, 2005; Garland & Nicolson, 2016). Bulbous species such as *A. belladonna, Bulbinella nutans, Boophone disticha, Brunsvigia* spp., *Cyrtanthus* spp., *Disa* spp., *Eucomis autumnalis, Haemanthus* spp., *Kniphofia uvaria, Lachenalia* spp., *Nerine* spp., and *Watsonia* spp. are among those that flower after fire (Keeley, 1993; Cowling & Richardson, 1995; Joubert, 1998; McMaster & McMaster, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2005; Filippi, 2008; Garland & Nicolson, 2016).

It was found that smoke, not heat, stimulates flowering in *Cyrtanthus ventricosus* Willd., and the species significantly correlates with fire, blooming within a few days following a fire, regardless of the season (Keeley, 1993; Cowling & Richardson, 1995; McMaster & McMaster, 2001; Manning *et al.*, 2002). *Hessea cinnamomea* and *Lachenalia sargeantii* displayed comparable obligatory tendencies after natural fires (McMaster & McMaster, 2001; Duncan *et al.*, 2005). A once-off treatment with 1:500 (*v/v*) smoke water increased the flowering of *Watsonia borbonica* from 20% to 90% (Light *et al.*, 2007). Smoke and fire are potential tools to encourage flowering biodiversity (Kulkarni *et al.*, 2011; Wagenius *et al.*, 2020); thus, any innovative insight into a species' behavioural attributes to such variables is necessary for its development (Le Maitre & Brown, 1992; Duncan, 2002; Slezák *et al.*, 2020). More research is needed to explore these possibilities for many profitable, endangered, rare and underutilised geophytes within the conservation and horticultural sectors (Pyke, 2017; Vlok, 2020). Therefore, determining how fire and its peripheral effects modify the flowering proficiency of *A. belladonna* and other bulbous geophytes may address ramifications and reveal characteristics that strengthen the species' capacity for ecosystem biodiversity, cultivation fitness, and recruitment.

2.18 Conclusion

This review has elucidated *Amaryllis belladonna'*s in-depth character, identified the myriad design uses, concepts and horticultural traits and emphasised the economic value, life cycle assessment challenges, constraints and opportunities for cultivation research. Although this genus has proven to be a valuable and distinctive indigenous taxon and resource of the Cape flora, the bulbous species is limited by a lack of scientifically based and quantified empirical data regarding practical cultivation approaches for various stages of bulb growth, from planting to seasonal flowering, which has irrefutable economic potential. This review concluded that numerous variables related to bulb yield, dormancy, temperature stimuli, water and nutrient availability, cultural practices, and seasonal fires, all of which synergistically shape the growth, development and flowering disposition of *A. belladonna*. These components are imperative in addressing the underutilised cultivation methodology and scheduling ramifications of *A. belladonna* for optimal growth and development and, more fervently, to stimulate seasonal flowering. This review recommends addressing these fundamental factors to strengthen the species' prominence and capacity for competitive economic differentiation in the local and international flower bulb and cut flower sectors.

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CHAPTER 3

FLOWERING INITIATION IN *AMARYLLIS BELLADONNA*

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FLOWERING INITIATION IN *AMARYLLIS BELLADONNA*

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3.1 Abstract

Understanding the initiation and influencing factors is necessary to develop forcing techniques for flowering plants. The March lily (*Amaryllis belladonna*) is a late summer flowering bulbous plant in South Africa. The inflorescence bears 2–12 soft pink fragrant funnel-shaped flowers on 'naked' (leafless) stems. It makes an excellent potted plant and fresh-cut flower lasting up to a week in a bouquet. Preliminary data on the factors influencing morphological changes to promote flower-bud initiation are discussed. These include physical traits such as bulb size, age, dormancy, planting establishment relevant to methods and bulb disturbance, and environmental factors such as temperature, watering, day length, and seasonal fire. This review encourages further research and popularisation of *A. belladonna* to enhance its year-round growth and expand its economic and commercial potential.

Keywords: Amaryllidaceae, cut flower, hysteranthous bulb, initiation, naked ladies

3.2 Introduction

Amaryllis belladonna flowers in late summer, unlike many other bulbous species that flower in autumn, winter, spring, and early summer. *A. belladonna* exhibits active growth in winter, with leaf senescence occurring before dormancy at the beginning of summer. Several environmental factors can affect bulb development and play a significant role in flower development (De Hertogh & Le Nard, 1993). However, it remains unclear which contributing factors initiate flower development in *A. belladonna.*

The Amaryllidaceae family consists of 59 genera and approximately 850 species, with the diversity found in South America (28 genera), South Africa (18 genera), the Mediterranean region (8 genera), and Australia (3 genera) (Adams 2001; Snijman, 2004). Amaryllidaceae bulbs such as *Galanthus*, *Leucojum,* and *Narcissus* are more adaptable to cooler temperate climates. *Amaryllis, Clivia, Hippeastrum, Nerine,* and *Zephyranthes* are more suitable for warm temperate and subtropical climates (Snijman, 2004). Southern Africa has 210 endemic species, consisting of 111 species in Namaqualand and the Cape Region, with 77% found nowhere else worldwide (Snijman, 2004). Most species in South Africa are well-adapted and dependent on the occurrence of natural wildfires for their flowering and reproductive phases.

Unfortunately, 59 species have become endangered and/or vulnerable due to natural habitat loss, while 58 are near threatened. Habitats consist mainly of ephemeral pools, riverbanks, seasonally dry places, and rainforest understoreys (Snijman, 2004). Species such as *Clivia, Cryptostephanus,* and *Scadoxus* have rhizomes, whereas most other Amaryllidaceae species have bulbous storage organs which grow well below ground (Snijman, 2004). While most Amaryllidaceae species have ornamental economic value, many are traded as Traditional African Medicines. Most bulbs are highly toxic in large dosages and were mainly used for their psychoactive effects, *Amaryllis,* which was used as an arrow poison by the Khoi and San tribes (Snijman, 2004; Duncan, 2010; Solomon, 2018). This mini-review explores factors that affect morphological changes in the flower initiation of *A. belladonna* to expand future research on improving flowering for economic and commercial potential.

3.3 *Amaryllis belladonna* L.

Most Amaryllidaceae species, especially *Amaryllis. belladonna* L., are highly valued as garden plants, potted plants, and excellent cut flowers; however, their commercial potential remains unexplored (Bryan, 2002). A complete understanding of the factors that influence morphological changes to initiate flowering in *A. belladonna* is necessary to establish methods to develop forcing techniques in this species. *Amaryllis* is a feminine Greek word named after a beautiful shepherdess, meaning beautiful lady (Adams, 2001). The genus consists of two species, *A. belladonna* and *A. paradisicola. A. belladonna* L., commonly known as the "Belladonna lily, March lily, Naked lady (Eng.); and the Belladonnalelie, Maartblom, Maartlelie (Afr.)" are one of the most beautiful of all species (Bryan, 2002).

Several crossbreedings of *Amaryllis* have been performed with *Brunsvigia, Crinum,* and *Nerine* to produce intergeneric hybrids. Some of these are Var Blanda with large white blossoms and Var Spectabilis with rose-coloured tepals and white inside. Several cultivars include Baberton: dark rose pink; Cape Town: deep rose red; Hathor white; Jagersfontein: deep pink; Johannesburg: pale pink with a lighter throat; Kewensis: pink with a yellow throat; Kimberley: deep carmine red with a white centre; Major with dark stems and dark pink flowers: Pallida a rose pink; Purpurea: purple-rose; Rosea: white stripes on rose tepals; Rubra: has more red than pink and Windhoek shows lovely rose pink with a white centre (Bryan, 2002). As amaryllis has so much potential as cut flowers, more crosses are expected in the future (Bryan, 2002). While some forms of *A. belladonna* are more naturally free flowering, some with rapid vegetative growth rates tend not to flower readily (Duncan, 2004).

Figure 3.1: *A. belladonna* flowering in nature, showing a striking, intense pink flower colour of the flowers [http://www.biodiversityexplorer.org/plants/amaryllidaceae/amaryllis_belladonna.htm]

3.4 Growing cycle, bulb maturity, and planting requirements

3.4.1 Understanding the natural growth cycle and flower initiation

Amaryllis belladonna is indigenous to the Mediterranean climate of South Africa and grows on lower slopes and rocky hillsides, in low-growing bushes, and by rivers. The species is endemic to the south-western Cape (Olifants River to Cape Town) and southern parts of the Western Cape to George and the Richtersveld in the Northern Cape (Philips & Rix, 1989; Mustart *et al.*, 1997; Adams, 2001; Duncan 2010). *A. belladonna* has gained international popularity with naturalisation in many Mediterranean climates (Manning *et al.*, 2002). The species consists of a large, brown, rounded ovoid bulb that is 750 mm in size and is covered with spongy, brittle outer tunics with perennial fleshy roots (Pienaar, 1987; Adams, 2001). The bulbs are poisonous to livestock and humans, causing respiratory paralysis if eaten (Bryan, 2002). During late summer, flower stems emerge from the bare ground to signal the end of a hot summer in the region. The bulbs flower at a specific time when a few other plants are in flower (Adams, 2001; Duncan, 2010). Bulbs produce 2–12 soft white, pink to rose pink intensely fruity and sweet-scented trumpet-shaped flowers on 'naked' (leafless flower stalks) and purplish-red stems (50–90 cm tall) (Philips & Rix, 1989; Johnson & Snijman, 1996; Mustart *et al.*, 1997; Adams, 2001; Bryan, 2002; Manning *et al.*, 2002; Duncan, 2010) (Figure 3.1). The flowers appear before the leaves (hysteranthy) and continue to flower over three months with the arrival of the first rains and the change in season (Adams, 2001).

After flowering and during the wet winter growing period, bulbs produce six to eleven long strap-like channelled leaves, which remain green throughout the winter (Johnson & Snijman, 1996; Mustart *et al.*, 1997; Manning *et al.*, 2002). These leaves grow through photosynthesis, while starch reserves are built in the bulb (Johnson & Snijman, 1996; Mustart *et al.*, 1997)

(Figure 3.2). Bulb senescence occurs as summer arrives, the leaves die back, and the bulb becomes dormant and uninteresting during this season (Figure 3.2) (Adams, 2001). Notably, *A. belladonna* does not flower yearly in its natural habitat (Pienaar, 1987). The irregular flowering of this species shows the potential for experimental trials to explore flowering initiation under several conditions, as further indicated.

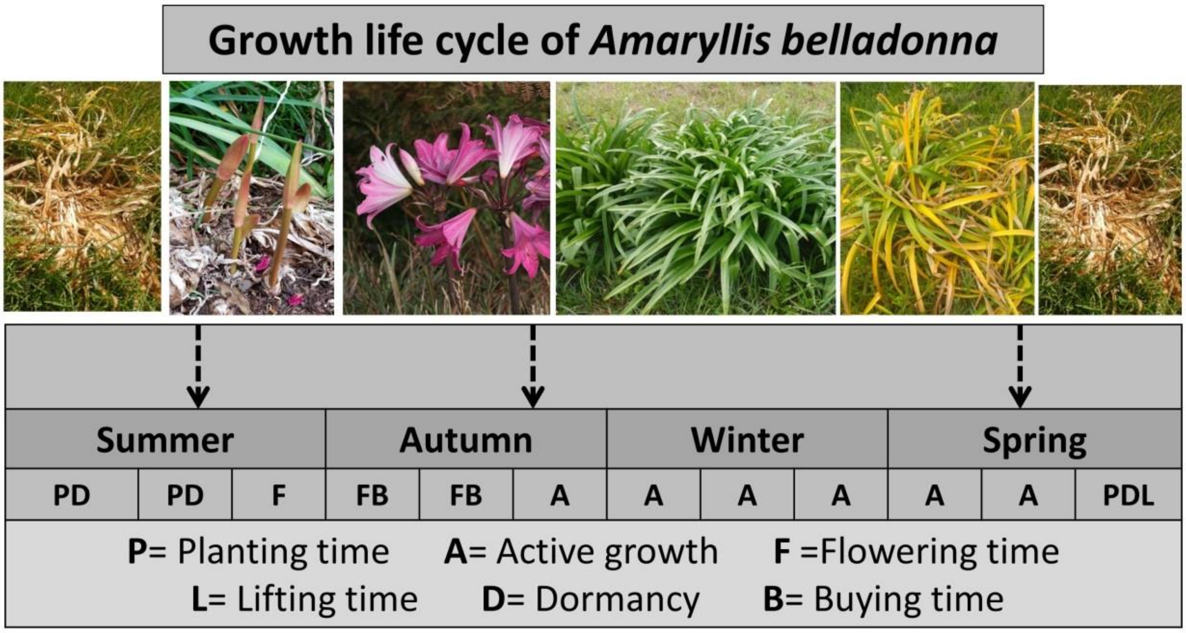

Figure 3.2: Photographic representation of the annual growth cycle and cultivation periods of *Amaryllis belladonna* during climatic seasons
[Pictures: Laubscher C; https://www.houseplantsexpert.com/growing-belladonna-lily-plants indoors.html;http://www.biodiversityexplorer.org/plants/amaryllidaceae/amaryllis_belladonna.htm]

3.4.2 Bulb maturity, avoiding disturbance, and flower initiation

As specific genotype variances could favour the initiation of inflorescence, development stages such as bulb size (500–750 mm), age (4–5 years) and possibly a minimum number of leaves (6–9) could indicate when a critical bulb size is reached. This is when flowering is initiated in *A. belladonna* (Figure 3.3). During active growth above ground, carbohydrates accumulate to enhance bulb development. The planting of bulbs is essential to synchronise flower initiation. Although it is recommended to plant bulbs when they are dormant, the exact planting time of *A. belladonna* seems to vary (Pacific Bulb Society, 2018). Some sources recommend that bulbs be planted from mid-summer to the beginning of the last summer month of a year to ensure that they have settled in the ground before the inflorescences appear (Pienaar, 1987; Duncan, 2010); others indicate that bulbs should be planted with the emergence of new leaves to bloom the following year (Pacific Bulb Society, 2018). Planting *A. belladonna* bulbs during different seasons could result in a total decline in flowering for consecutive years, as some summer-planted bulbs could not flower for at least two years after planting (Pacific Bulb

Society, 2018). Before lifting, bulbs should be watered, and after that, they can be lifted. Clump division is performed in late spring or summer, saving as many roots as possible and ensuring they are kept moist to prevent bulbs from drying out (Solomon, 2018). When bulbs mature, offsets develop, or new plants can be raised from freshly sown seeds, which could take between 4 and 6 years to flower. *A. belladonna* bulbs do not favour disturbance and may not flower the first summer or after several seasons after replanting (Barnhoorn, 2013; Solomon, 2018). *A. belladonna* bulbs prefer to be left in the ground undisturbed for several years to flower more readily (Duncan, 2010). On the other hand, bulbs left undisturbed for a longer period could also decrease flowering; therefore, it is recommended that bulbs be lifted and replanted after several years to improve flowering (Duncan, 2010). Flowering can be affected when roots are damaged or exposed to air (Duncan, 2010).

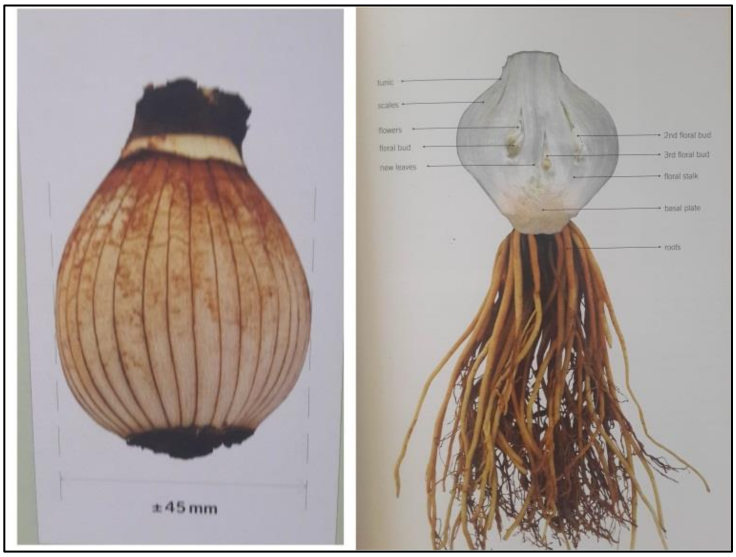

Figure 3.3: Presentation of the bulb size, root growth, and flower bud development of *Amaryllis* (Barnhoorn, 2013)

3.4.3 Planting requirements and flower initiation

Although *A. belladonna* requires very little attention to grow, it prefers a hot, sunny position if flowering quantity is to be attained (Philips & Rix, 1989; Adams, 2001; Barnhoorn, 2013; Solomon, 2018). Bulbs grown in full sun should be more floriferous in bloom than those grown in the shade (Bryan, 2002; Pacific Bulb Society, 2018). *A. belladonna* should be planted in well-drained sandy to fertile loam soil with added compost (Pienaar, 1987; Rix, 2006; Barnhoorn, 2013; Solomon, 2018). The bulbs should not be cultivated in rich soils or receive supplementary feeding because they have low nutritional requirements (Duncan, 2010). A top dressing of 10-10-10 can be beneficial when flowers fade and foliage emerges (Bryan, 2002). Bulb leaves should not be removed until they completely perish (Solomon, 2018). *Amaryllis* is suitable for water-wise plantings; however, in arid conditions, regular watering is required (Bryan, 2002; Duncan, 2010). Begin watering as the flower spikes appear and increase watering after flowering until the foliage dies down and allow pots to dry out (Bryan, 2002). *A. belladonna* is ideally suitable to be grown in large pots (30–25 cm) that can accommodate the large bulbs and root systems, especially suitable for cold climates where bulbs could be spaced 5–6 cm away from the pot wall (Bryan, 2002; Duncan, 2010; Pacific Bulb Society, 2018; Solomon, 2018).

Amaryllis belladonna bulbs should be planted with the neck of the bulb exposed or planted at soil level where light and heat may encourage inflorescence emergence (Adams, 2001; Bryan, 2002; Duncan, 2010; Barnhoorn, 2013; Solomon, 2018; Pacific Bulb Society, 2018). Bulbs should be planted deeper where temperatures drop below freezing; while adding lightweight mulch on top of the bulbs is beneficial in preventing them from freezing (Bryan, 2002). Unfavourable planting methods could greatly affect flowering percentage (Figure 3.4). Therefore, further studies are essential to establish a suitable planting protocol to ensure the successful flowering of this popular flowering bulb.

Figure 3.4: *A. belladonna* cut flower with dark red stems at a flower market [https://www.newcoventgardenmarket.com/blog/flowermarketreport-oct-2012]

3.5 Environmental and climatic conditions

3.5.1 Temperature changes and flower initiation

Proper environmental growing conditions could stimulate the successful flowering of *A. belladonna* as a potential commercial cut flower. The inflorescence emergence could be stimulated by a long dry summer resting period of high temperatures (15 ˚C – 27 ˚C) and then possibly triggered by cooler autumn temperatures (5 ˚C – 13 ˚C). The bulbs are dormant during summer and exposed to higher (27 °C) day temperatures, which support flowering (Manning *et al.*, 2002) (Table 3.1). Simulated conditions could be induced by heated storage of bulbs followed by vernalisation at cooler temperatures. This cooling period is essential for flower development or spring flowering bulbs to prevent root growth functions and flowering disorders (Kamenetsky & Okubo, 2013). Growing *A. belladonna* in Mediterranean climates experiences flowering more readily (Pacific Bulb Society, 2018). As bulbs lose their leaves, the plants act like sclerophyllous plants, acting with a strategy of becoming dormant during the hot summer period. Some dry-climate plants use this strategy of extremes to cope with survival where no leaves allow photosynthesis, hence no water loss (Filippi, 2008). The bulbs remain underground and are ready to signal flower production as a survival mechanism with changes in temperature and the possible first arrival of autumn rains.

Amaryllis tolerates moisture during summer rain if bulbs have good drainage (Barnhoorn, 2013). Many species of the Mediterranean climate regions have developed a range of remarkable strategies to cope with dry conditions (Filippi, 2008). *A. belladonna* occurs naturally in this climate type with hot, dry summers and mild, wet winters (5 °C to 22 °C). The species is also frost-hardy and can withstand temperatures up to -5 °C (Duncan, 2010) and has adapted to the southern parts of England, where it can survive up to -15 °C, although it requires a very warm position to flower (Philips & Rix, 1989). Climatic requirements should be simulated for commercial planting, as the example in Northern California indicates where bulbs have survived in receiving moisture during autumn and a hot, dry summer period (Bryan, 2002).

Table 3.1: Climatic conditions depicting the season, maximum and minimum temperatures, humidity, and average rainfall of natural habitat for *A. belladonna* L. in the Western Cape province of South Africa
Source adapted: [http://www.signaturetours.co.za/south-african- information/weather-and-climate]

	Summer	**Autumn**	**Winter**	**Spring**
Temperature	Max 27 °C Min 15 °C	Max 25 °C Min 14 °C	Max 22 °C Min 7 °C	Max 19 °C Min 9 °C
Humidity	77%	77%	80%	80%
Average monthly rainfall	17 mm	25 mm	82 mm	53 mm

3.5.2 Seasonal rain, moisture, and flower initiation

Amaryllis belladonna bulbs receive an average of 17 mm of rain during the hot summer months in their natural Mediterranean climate-type habitat (Table 3.1), indicating that low amounts of watering in summer are required to initiate flowering. Because *A. belladonna* is known for its difficulty in flowering, it is important to protect plantings from excessive summer rain to prevent bulbs from rotting (Pacific Bulb Society, 2018). Bulbs are remarkably resilient to garden irrigation during summer dormancy when grown in well-drained soils (Duncan, 2010). Occasional summer watering should keep fleshy roots from drying out and could trigger flowering at the end of summer; however, dry summer dormancy after leaf senescence could also be responsible for flowering initiation. Similarly, the advance of early autumn rain could also trigger flower initiation (Bryan, 2002; Pacific Bulb Society, 2018). Begin to water as soon as the flower spike appears. During the wet winter growing conditions with a short-day length (8–11 hours/day) and full sun exposure, the leaves actively grow to produce and store starch energy for the next flowering season (Honig, 2014). While thermoperiodicity is an important factor in flowering and not a photoperiod for many species, only a few bulbous species respond to both temperature and day length (Ofir & Kigel, 2006). Winter freezing in cold climates should be avoided as bulbs could perish from freezing conditions (Pacific Bulb Society, 2018). *A. belladonna* occurs mainly along South Africa and California coastal areas and is widely grown in Australia. It is uncertain whether improved flowering along coastal regions is due to milder temperatures, higher humidity during summer, or fog along the coast (Pacific Bulb Society, 2018). It is possible that withholding water could induce flowering or that the arrival of the first moisture after a long summer could trigger flowering initiation.

3.5.3 Wildfire, heat, vegetation clearing, and flower initiation

The ecological cycle of Cape flora has a natural occurrence of frequent natural fires, which result in burning areas in the habitat that provide spectacular flowering of a diversity of bulbous plants after bushfires (Mustart *et al.*, 1997; Filippi, 2008). *A. belladonna* produces a showstopper display against a background of sun/fire-scorched vegetation (Pienaar, 1987) (Figure 3.5). It remains uncertain why species such as *A. belladonna* flower successfully, especially after bushfires (Philips & Rix, 1989). Bulbs can also completely render flowering for possibly 5–40 years and then be triggered to flower en masse, possibly due to the heat of wildfires and or the exposure to smoke (Johnson & Snijman, 1996; Adams, 2001; Duncan 2004; Pacific Bulb Society, 2018). During cultivation, dry plant material can be burned over the bulbs to assimilate wildfires and induce flowering (Duncan, 2010). Smoke treatments induced in other bulbous species, such as *Cyrtanthus ventricosus,* have initiated flowering (Johnson & Snijman, 1996), and a top dressing of hot wood ash followed by watering in early autumn could encourage the flowering of *A. belladonna* (Rix, 2006).

It remains uncertain what triggers flowering in some *A. belladonna* bulbs to ensure that they flower year after year (Johnson & Snijman, 1996). *A. belladonna* requires bright light, preferably in a warm position with morning to full-day sun to flower (Duncan, 2010). Often, bulbs become overgrown with vegetation, which reduces flowering. Therefore, it is essential to remove overgrowth and shading regularly to encourage the flowering of *A. belladonna* (Johnson & Snijman, 1996; Duncan, 2010). Studying these and other plant strategies is necessary to understand the species' survival techniques in plantings to enhance commercial cultivation and ensure flowering at its fullest potential (Filippi, 2008).

Figure 3.5: *A. belladonna* flowering after fire in a natural habitat [http://www.biodiversityexplorer.org/plants/amaryllidaceae/amaryllis_belladonna.htm]

3.6 Conclusion

Almost all data on the aspects influencing morphological changes to promote flower-bud initiation have shown many possibilities for increasing flowering in *A. belladonna*. Physical traits such as bulb size, age, dormancy, planting establishments relevant to methods and bulb disturbance, and environmental factors such as temperature, watering, day length, and seasonal fire may all be important for stimulating flower initiation. Although there have been many studies on the storage of bulbs, the data found on aspects that trigger the flowering of *A. belladonna* show great variation. Further studies are required on the stages from planting to flowering and the post-flowering period of the species. Understanding the influencing factors is necessary to establish the factors responsible for initiating the flowering of *A. belladonna*. This could lead to the development of flower-forcing techniques and extend the short-lived flowering period to enhance year-round growth and expand the economic cut flower potential of *A. belladonna.*

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CHAPTER 4

AMARYLLIS BELLADONNA: A POTENTIAL URBAN LANDSCAPE WONDER

Manuscript published in *Acta Horticulturae*

AMARYLLIS BELLADONNA: A POTENTIAL URBAN LANDSCAPE WONDER

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4.1 Abstract

Amaryllis belladonna is an indigenous bulb endemic to the southwestern Cape of South Africa and is one of two members of the Cape genus. This species is closely associated with *Brunsvigia* and *Nerine* bulbous species. The bulb has a hysteranthous nature, showcasing the arrival of white to different shades of pink-scented trumpet-shaped flowers in late summer to early autumn. By losing its leaves and going into dormancy at the height of summer, it conserves its resources, making it a drought-tolerant perennial found in nutrient-poor soils. The species is well adapted to the fire-prone fynbos environment of its natural habitat, after which it sends out blooms in abundance. In cultivation, the species is an impressive and reliable garden and landscape ornamental that requires minimal attention. *A. belladonna* has proven to be a popular plant that has naturalised in Mediterranean climates worldwide. This review focuses on the prospective design use and application of *A. belladonna* in urban landscapes.

Keywords: bulbous ornamental, endemic, fynbos, hysteranthy, Mediterranean

4.2 Introduction

South Africa boasts a diverse array of over 2700 indigenous bulbous species suitable for different climatic conditions. Countless of these endemic genera have been popularised locally and internationally for various ornamental purposes (Manning *et al.*, 2002; Barnhoorn, 2013). Many evergreen species are taken up and are familiar plants in many garden landscapes; however, deciduous species are much less cultivated. These deciduous bulbs add colour, interest and detail to areas briefly and then go into dormancy, vanishing but surviving underground (Honig, 2014). Changes in temperature and seasonal rainfall are fundamental to a bulb’s success in any landscape environment, and understanding how a bulb responds in and out of season requires patience. This is necessary to improve the plant and to overcome the problems mainly associated with relocation and adaption between different hemisphere climatic conditions (Reinten *et al.*, 2011). Some South African plants have not been well researched in all fundamental aspects; thus, questions relating to propagation, cultivation, natural behaviour, landscape use and design are often absent. These aspects are required to fully understand a plant’s marketable potential (Seale, 1985; Manning, 2007; Reinten *et al.*, 2011; Barnhoorn, 2013). This review explores the use and design potential of *Amaryllis belladonna* L. (Amaryllidaceae) in urban landscapes.

4.3 *Amaryllis belladonna* L. description

4.3.1 Botanical description

Amaryllis belladonna is a South African indigenous true bulb more commonly known as the "Belladonna lily", "March lily" locally or the "Naked lady", "Madonna lily", or "Jersey lily" internationally. *A. belladonna* was considered the only species for over two centuries. In 1997, a second species, *A. paradisicola,* an equally beautiful specimen, was discovered in the arid Richtersveld, north of the Cape Floral region (Snijman & Williamson, 1998; Manning *et al.*, 2002). *A. paradisicola* differs from its sister species in that its flowers are smaller, less scented, flower only after autumn rains, do not produce any bulb offsets, and the leaves are broadly tongue-shaped (Snijman & Williamson, 1998; Barnhoorn, 2013; Duncan, 2016). Other genera from this family of high horticultural importance and similarities found in Southern Africa include *Clivia, Crinum, Cyrtanthus, Nerine, Brunsvigia, and Scadoxus* (Adams, 2001; Manning *et al.*, 2002).

This bulb has a hysteranthous nature, showcasing the arrival of white to different shades of pink sweet-scented trumpet-shaped flowers in late summer to early autumn. Typically, each bulb has one inflorescence, with each stem producing up to 12 flowers or more (Johnson & Snijman, 1996; McMaster, 2007; Duncan, 2016). Bees, particularly carpenter bees, are the primary pollinators of these flowers (Adams, 2001; Duncan, 2004). As the bulb begins to set seed, long strap-like leaves emerge during the winter rainfall months of its active growing season. During this time, the bulb builds up its starch reserves to store them underground during the harsh, dry summer. During the late spring, the leaves die back, and photosynthesis shuts down, sending the bulb into a state of dormancy (Seale, 1985; Barnhoorn, 2013). It is essential to allow the foliage to turn yellow and die entirely so the underground storage organ can reabsorb nutrients from the foliage (Honig, 2014). Flowering before the foliage emerges, known as hysteranthy, is common in Cape bulbs (Johnson & Snijman, 1996; Duncan, 2004; Manning *et al.*, 2002; Duncan, 2016). The plant has a growth height of up to 90 cm with a spread of 60 cm (Barnhoorn, 2013; Duncan, 2016).

Amaryllis belladonna is often seen flowering profusely in open areas of its habitat after summer fynbos fires, evident on the slopes of Lion's Head, Cape Town, on a few occasions (Duncan, 2004; Duncan, 2016). Evidence for this is observed by the emergence of many flower spears of fragrant white and pink blooms transforming the recent blackened remains of the burnt fynbos (Johnson and Snijman, 1996). This phenomenon is said to clear the upper vegetation, shading the bulbs below, thus exposing them to higher temperatures and harsh elements (Manning *et al.*, 2002; Manning, 2007; Peirce, 2011; Barnhoorn, 2013).

4.3.2 Distribution and habitat

The bulb is endemically confined to the Western Cape, from the northern Cederberg to the Cape Peninsula, and east to Nature's Valley (Duncan, 2016). *A. belladonna* has proven to be a popular plant that has become naturalised in many Mediterranean climates of winter rainfall and summer droughts throughout the world, such as Mexico, California, Australia, Spain, New Zealand, and the Channel Island of Jersey (Duncan, 2004; McMaster, 2007; Pierce, 2011; Duncan, 2016).

4.3.3 Position, soil type, fertilisation and, watering

Amaryllis belladonna prefers a full-sun location but can tolerate a semi-shaded area; however, it reduces flowering (Duncan, 2004; Barnhoorn, 2013; Duncan, 2016). It grows suitably in moderately fertile, light, well-drained soils (Barnhoorn, 2013). Bulbs should be fed sparingly from flowering time in late summer until the onset of dormancy in spring (Barnhoorn, 2013). The bulb requires minimum water in summer, yet it may withstand a modest amount of water if the soil is adequately drained, with most of its water received during the winter seasonal rainfall (Seale, 1895; Pierce, 2011; Barnhoorn, 2013). Thus, the drought-tolerant bulb can grow in unwanted, low-maintenance landscape areas (Carter, 2007; Pierce, 2011).

4.3.4 Planting

The *Amaryllis belladonna* bulb should be planted with the neck at or just above the soil level and exposed to the sun (Seale, 1985; Barnhoorn, 2013). An ideal spacing should be around 10 cm between bulbs, however, they may be spaced closely together for a mass effect (Barnhoorn, 2013; Duncan, 2016). The plants should not be disturbed as it hinders flowering for several seasons. The bulb reaches a diameter of approximately 750 mm upon maturity (Barnhoorn, 2013; Duncan, 2016).

4.3.5 Propagation and cultivation

In their natural habitat, the large and fleshy white-pink seeds are dispersed by the wind and land close to the parent plant, often germinating immediately (Johnson & Snijman, 1996; Duncan, 2004; Duncan, 2016). Propagation of the fresh seed sown in late autumn in trays of sand pressed just below the soil surface germinates within approximately two weeks. However, the seedlings will take three to six years or more to attain flowering (Barnhoorn, 2013). Offsets may be removed in late summer and planted immediately. Lifting and replanting bulbs should occur in early summer (Barnhoorn, 2013; Duncan, 2004). The new bulbs and offsets do not flower within the first few seasons because they require maturity and sufficient establishment within the landscape (Johnson & Snijman, 1996; Manning *et al.*, 2002; Duncan, 2016).

For many years, discussions among botanists surrounding the correct naming of *A. belladonna* occurred, as for decades, the name *amaryllis* had simultaneously been used for other bulbous plants with emphasis on the tropical South American species *Hippeastrum.* The matter was finally concluded in 1987 when the name for the South African bulb was unanimously supported (Duncan, 2004; Barnhoorn, 2013; Duncan, 2016). Unfortunately, the vivid, summer-flowering *Hippeastrum* hybrids cultivated in abundance both in South Africa and abroad continue to be sold under incorrect names and have been entrenched in many plant enthusiasts' minds as 'Amaryllis' (Adams, 2001; Bryan, 2002; Duncan, 2004).

Amaryllis belladonna has been used in crossbreeding with other species from the same family, such as *Brunsvigia, Crinum,* and *Nerine,* to produce different hybrids. This has been successful because it varies the flowering times, colours and shapes of showcased flowers (Bryan, 2002).

The plants are poisonous to humans and livestock and can cause respiratory paralysis if eaten because of their amaryllid alkaloid compounds. The Khoisan people used the sap from the poisonous bulbs at the end of their arrows for hunting purposes (Adams, 2001; Duncan, 2004; Barnhoorn, 2013).

4.3.6 Pests and diseases

Bulbs are readily destroyed by the lily borer, a black and yellow-striped caterpillar that bores into the plant stems, hollowing out the soft, pithy inside until it collapses. The fleshy seeds of the belladonna lily are likely to be eaten. This caterpillar is seemingly immune to the toxic alkaloids found in Amaryllidaceae species and attacks amaryllids all over South Africa (Johnson & Snijman, 1996; Barnhoorn, 2013). The caterpillars can be removed manually or using a full-cover spray (Adams, 2001). The plant is relatively disease-free (Barnhoorn, 2013).

4.4 *Amaryllis belladonna* use and design in urban landscape

The variety of blooms, colour, flowering time, plant height and shape make flowering bulbs an excellent addition to any landscape and garden (Sunset Magazine, 1968; Barnhoorn, 2013; Cornwell, 2018). Bulb design can be interpreted as mass plantings in parks, estates, and along roadsides to create visual impact. However, most people use them in smaller quantities as grouped accents or highlights rather than as landscape material (Sunset Magazine, 1968; Barnhoorn, 2013; Cornwell, 2018). *A. belladonna* is an adaptable bulb that can be utilised in various settings within the urban landscape (Figure 4.1 and Table 4.1). These functional design applications of *A. belladonna* are as follows:

4.4.1 Beds and borders

Plants reinforce the structure and circulation of a landscape design, either formally or informally. The design process is like interior design, which involves creating spaces and furnishing them using different colours and textures (Honig, 2014). Plants are often used as visual navigation cues, highlighting different transitional zones and hard landscaping features such as pathways and low brick walls (Sunset Magazine, 1968; Van Jaarsveld, 2010; Peirce, 2011; Honig, 2014). Steep slopes and, in some instances, roadsides in the landscape are often difficult to mow and maintain. Bulbous plants are practical for these areas because they eliminate the problems associated with constant attention and maintenance (Pierce, 2011; Cornwell, 2018).

Amaryllis belladonna, together with other plant types, have been successfully used and have further potential as foreground features against low- to medium-clipped hedges along roadsides, slopes, pathways, and bed borders as intermittent seasonal features, displaying their short-lived flowering season and lush-green textural foliage (Van Jaarsveld, 2010; Pierce, 2011; Honig, 2014) (Figure 4.1 and Table 4.1).

4.4.2 Potted plants and planters

A successful method of growing bulbs, mainly deciduous species such as *A. belladonna,* is planting them as a single species or grouped with other plants in pots (Figure 4.1 and Table 4.1). This allows the temporal positioning of the sunken pots in different sunny areas within the garden landscape or focal points as they come into flower, adding seasonal interest and colour (Barnhoorn, 2013; Honig, 2014). Once seasonal flowering is complete, the portable pots can be moved to a less visible area, allowing the foliage to die back to a dormant stage; after that, these pots may be stacked away, creating a suitable efficiency of space (Honig, 2014). This method ensures that bulb establishment is not disturbed, resulting in a delay in flowering over the next few seasons (Seale, 1985; Pierce, 2011; Barnhoorn, 2013; Honig, 2014). This can be especially useful in areas where seasonal rainfall may affect the dormancy and flowering of bulbs.

In recent years, container gardening has become more popular on decks, patios, windowsills, and balconies, often providing focused colour in these small areas (Barnhoorn, 2013). A pre-requisite to this planting style is to ensure a suitable and well-drained planting medium and that containers have adequate drainage holes (Seale, 1985; Barnhoorn, 2013; Honig, 2014). For pots and planters that remain in a desired location, a combination of different seasonal bulbs with the addition of suitable annuals and groundcovers can be used to extend the blooming time and seasonal interest.

4.4.3 Gravel and rock garden

Gravel and rock gardens favour the display of different seasonal deciduous bulbs. These xeriscape landscape environments are well-suited for bulbs adapted to nutrient-poor soils and low watering requirements (Carter, 2007; Honig, 2014). The area can be covered with different-sized and coloured gravel chip stones. Adding sculptural rocks as markers or features such as dry riverbeds enhances the barren ground, doubling as informal seating areas (Van Jaarsveld, 2010; Honig, 2014). During the season, the planted bulbs emerge through the gravel, creating an element of surprise. Once flowering ends, the seed set and the foliage have adequately died back, the gravelled area can attain its former state (Van Jaarsveld, 2010; Pierce, 2011; Honig, 2014). *A. belladonna* is a well-suited bulb in this type of drought-tolerant design (Figure 4.1 and Table 4.1).

4.4.4 Seasonal and colour

Growing evergreen and deciduous bulbs together provides an ongoing seasonal interest in the landscape, with their different flowering times and foliage types, which balance one another in various settings (Sunset Magazine, 1968; Manning *et al.*, 2002). An interplanting of blue agapanthus and pink belladonna is a classic combination (Sunset Magazine, 1968; Pierce, 2011). As *A. belladonna* flowers in late summer or early autumn, they often provide colour and interest when other plant species are out of season. The pastel shades of pink *A. belladonna* can be planted to complement an arrangement of grey-toned herbaceous perennials and ground covers (Sunset Magazine, 1968) (Figure 4.1 and Table 4.1).

4.4.5 Grassy effect

Grasses are often seen as weeds and animal fodder but have become popular landscape plants. They provide textural and structural interest, showcasing their often year-round inflorescence in the landscape (Honig, 2014). They work well in informal and naturalistic gardens and contemporary landscapes. Landscaping with grasses studded with flowering bulbs has become popular (Van Jaarsveld, 2010; Honig, 2014). Naturalistic bulb plantings may be performed by following the natural pattern of the bulbs, which occur in randomly spaced clusters throughout the landscape rather than in rows. Bulbs naturalise easily in grassy areas (Honig, 2014; Cornwell, 2018). *A. belladonna* integrally adds to the grassy effect during late summer as its long, slender stalks arise and sway in the summer breeze, requiring very little attention (Dean, 2015) (Figure 4.1 and Table 4.1).

4.4.6 Fragrance and cut flowers

Biodiversity is a sustainable and important component of landscape design, which requires careful, holistic consideration of all elements and role players (Van Jaarsveld, 2010; Honig, 2014). Fragrant plants, whether their foliage or flowers, provide an unusual interest to the landscape but are crucial in attracting suitable pollinators to the area, for which sexual reproduction would cease to exist (Manning *et al.*, 2002; Van Jaarsveld, 2010; Honig, 2014). *A. belladonna* is suitable for a fragrant landscape design as it attracts pollinators to its sweet-scented flowers in the garden (Johnson and Snijman, 1996; McMaster, 2007; Duncan, 2016). At the same time, even though flowering time is short-lived, between 6 and 9 weeks, these clusters of flowers make excellent fragrant cut flowers lasting up to a week in bouquets and arrangements (Adams, 2001; Manning *et al.*, 2002; Dean, 2015) (Figure 4.1 and Table 4.1).

It is imperative to recognise and understand the description and myriads of design functions of *A. belladonna* in the urban landscape. This informative material can promote species resourcefulness and lead to comparable studies on similar plant species and their interactive use and design within the urban landscape.

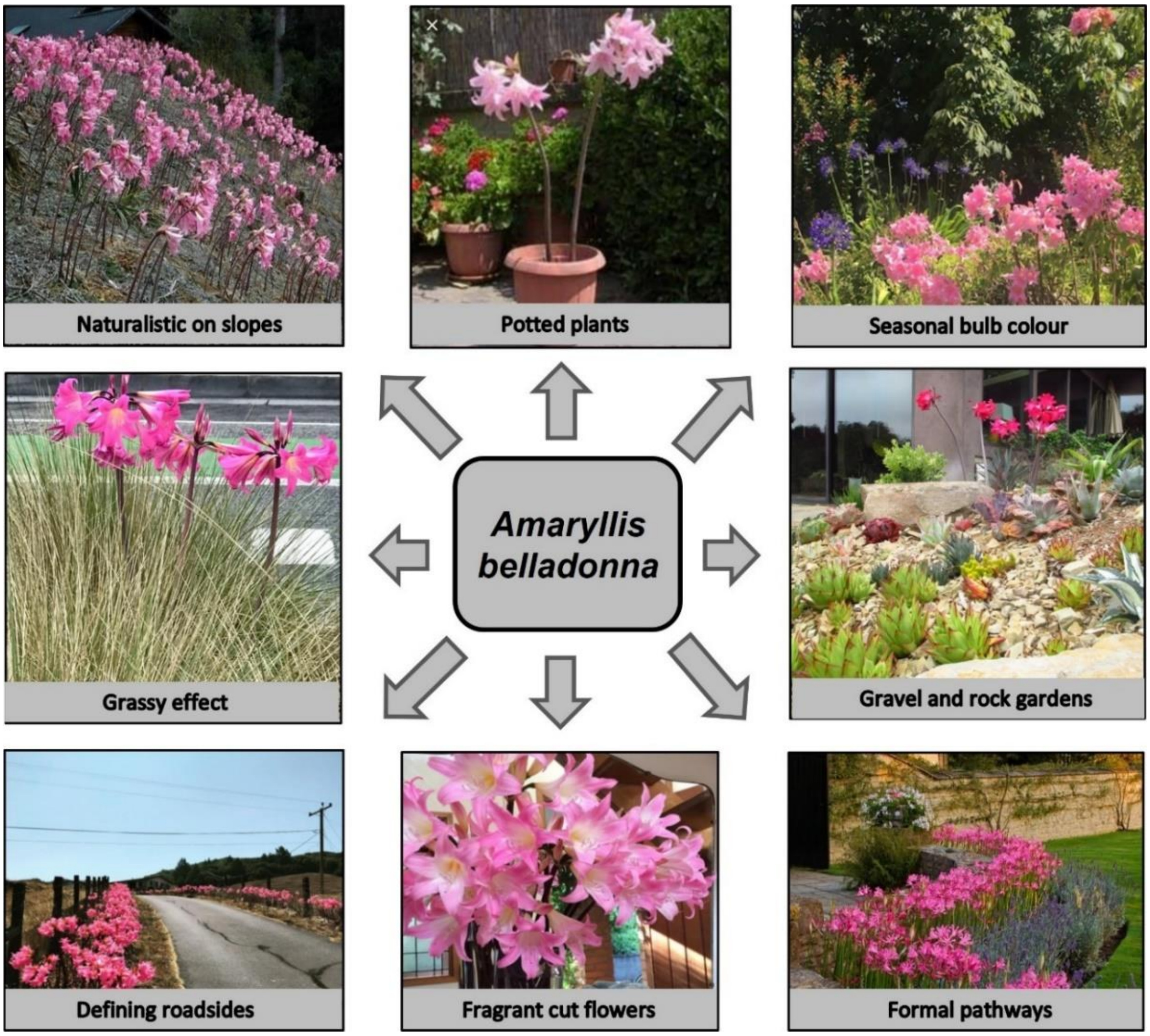

Figure 4.1: Diagrammatic representation of the versatility of *A. belladonna*'s use and design in urban landscapes

Table 4.1: Planting palettes using *A. belladonna* along with other plant species
Source adapted: (Sunset Magazine, 1968; Van Jaarsveld, 2010; Honig, 2014).

Planting palette	Function	Description	Suggested companion plant selection
Structure	Beds and borders	Used to accentuate behind low- to medium-clipped hedges and different boundary fences, slopes, pathways, and roadsides.	*Buxus macowanii(*)* *Searsia crenata(*)* *Plecistachys serpyllifolia(*)* *Lavender angustifolia(#)* *Santolina chamaecyparissus(#)*
Situation	Pots and planters	Used as a single species or combined with other bulbs, annuals, or ground covers in pots or planters on decks, patios, windowsills, balconies, and pots temporarily sunken into the landscape.	*Eucomis autumnalis (*)* *Petunia species (#)* *Lobelia* species (*#) *Hemerocallis species (#)* *Crassula spathulata (*)*
	Gravel and rock gardens	Used with other deciduous bulbs and succulents to intermittently accentuate the hard landscape.	*Aristea capitata*(*) *Haemanthus coccineus(*)* *Sedum* species(#) *Sempervivum* species(#)
Colour	Seasonal bulbs	Used to provide different flowering and seasonal interests in the same area.	*Agapanthus* species(*) *Chasmanthe aethiopica(*)* *Chasmanthe floribunda(*)*
	Grey scheme	Used as a sporadic seasonal burst of pink in a colour scheme with grey plants.	*Artemesia afra(*)* *Artemesia albula(#)* *Senecio leucostachys(#)* *Cerastium tomemtosum(#)* *Stachys olympica(#)*
Texture	Grassy effect	Used together with different grasses to create a natural, meadow-like style and accent to the landscape.	*Melinis nerviglumis(*)* *Chlorophytum saundersiae(*)* *Chlorophytum comosum(*)* *Cenchrus ciliaris(*)* *Carex* species(*#) *Dietes grandiflora(*)* *Dietes bicolor(*)*
The senses	Fragrance	Flowers are used to attract pollinators to the landscape.	---------------
	Cut flower	Used as a suitable cut flower.	*Agapanthus* species(*) *Seriphium plumosum(*)* *Asparagus densiflorus* ‘Meyersii’ (*)

Indigenous (*), Exotic (#).

4.5 Conclusion

This review concludes that research should focus more on the different potential markets of a plant species rather than on preconceived product concepts. It is apparent that the deciduous *Amaryllis belladonna* bulb provides variety in the landscape, regeneration, and hope in the aftermath of disastrous fires and creates knowledge of seasonal change marking the end of summer. *A. belladonna* has considerable scope to transform its use and design potential in different urban landscapes in South Africa and internationally.

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CHAPTER 5

EVALUATING HYDROPONIC CULTIVATION FOR ORNAMENTAL BULBOUS SPECIES TO ENHANCE FLOWERING AND BULB PRODUCTION IN A CHANGING CLIMATE

EVALUATING HYDROPONIC CULTIVATION FOR ORNAMENTAL BULBOUS SPECIES TO ENHANCE FLOWERING AND BULB PRODUCTION IN A CHANGING CLIMATE

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5.1 Abstract

The annual rhythmic cycle of ornamental bulbous species is highly dependent and tightly regulated by numerous abiotic signals for optimal bulb formation and flower production. A flower bulb's developmental and seasonal cycle, capacity, and timeframe to reach a critical flowering maturation stage, multiplication, and growing climatic regions are highly diverse and are contingent on the species. Utilising controlled, monitored and flexible mechanisms emphasising hydroponic cultivation can maximise favourable growing conditions and potentially increase geophytes' knowledge-demanding and sustainable production and yield. Accounts of scientific studies on species variety and product outcomes cultivated under these conditions are limited. This paper determines the prospective possibilities of research, development, and innovative approaches to enhance the commercial production and flowering of a range of bulbous species as climate-smart crops within a hydroponic context.

Keywords: bulb development, controlled environment, flower bulb, nutrient solution, soilless substrates

5.2 Introduction

Global climate change and its adverse effects have challenged the demand and supply of specialised horticultural crops in different climatic regions worldwide. Notwithstanding, the negative impacts of climate change have impacted geophytes' growth and development because the annual rhythmic cycle of ornamental bulbous species is highly dependent and tightly regulated by numerous environmental signals for effective bulb formation and flower production (Kamenetsky-Goldstein, 2019). Moreover, a flower bulb's developmental and seasonal cycle, capacity, and timeframe to reach a critical flowering maturation stage, multiplication, and growing climatic regions are highly diverse and are contingent on the species (Le Nard & De Hertogh, 1993; Duncan, 2010; Khodorova & Boitel-Conti, 2013). Modern technological and innovative advances require research and integration to improve commercial production that re-establishes, realigns, and overcomes the obstacles affecting bulbous geophytes. Hydroponics is a well-known alternative and innovative technology that has gained momentum and shown successful results in agricultural and ornamental crops (Hemathilake & Gunathilake, 2022). Successful hydroponic cultivation of geophytes has been documented through hydroponic forcing for the primary intention of flower production; however, the literature on a wider variety of species and specific developmental product target outcomes is limited. This study determines the potential research, development, and benefits of growing a more comprehensive range of bulbous species and their floricultural product types as an environmentally friendly and sustainable crop using precision innovative hydroponic techniques in a changing climate.

5.3 Effect of climate change on bulb development

Climate change is an extensively researched global phenomenon with varying degrees and magnitudes of influence experienced worldwide in different regions and locations (Malhotra & Srivastva, 2014; Barua *et al.*, 2021). Ornamental crops with an emphasis on geophytes are not excluded. Deviations and fluctuations of extrinsic factors due to climate change, namely but not limited to drought, flooding, photoperiod, temperature, salinity, pest and disease responses, and their peripheral effects, have been shown to impact bulb and flower production (Kamenetsky-Goldstein, 2019). Inevitably, these factors fundamentally affect the intrinsic factors and the closely related morphological and physiological properties and processes for successful vegetative and reproductive growth, activity, and yield (Rees, 1966; Le Nard & De Hertogh, 1993; Filippi, 2008; Duncan, 2010; Khodorova & Boitel-Conti, 2013). These issues pose difficulties to the horticultural cultivation and economic distribution chain.

As leading technologies of geophytic production predominantly occur and are conducive in the Mediterranean, temperate, and tropical climatic regions despite climate change (Barnhoorn, 2013), expanding the area of successful bulb production using different management approaches such as hydroponic culture can be advantageous. Furthermore, this can provide an opportunity to diversify the growing region where problems with climate or microclimate conditions hinder the sensitivity of bulbs from being cultivated to optimal capacity, particularly with northern and southern hemispheric disparities.

5.4 Hydroponic technology

Management practices could be implemented through technological evaluation and improvement to provide remedial and practical solutions to the immediate problems encountered in adapting to climate change (Malhotra, 2017). Innovative hydroponic advances in adjusting to climate change and its effects aim at creating viable and sustainable plant-environment interactions within unfavourable environments (Hemathilake & Gunathilake 2022). The global hydroponics market is forecasted to be valued at USD 22.2 billion in 2028, which is an increase of USD 12.7 billion from 2020, occupying a compound annual growth rate

(CAGR) of 11.3% throughout the estimated period (GlobeNewswire, 2021). Hydroponics is essentially an aqueous solution that provides essential nutrients, hydration, and oxygen to a plant species for adequate growth and production without using soil (Venter, 2010). Furthermore, temperature, humidity, aeration, light, pH, and EC factors allow maximum control, supply, modification, and regulation readily available to the plants for optimal growth (Wahome *et al.*, 2010; Barua *et al.*, 2021). Hydroculture systems, therefore, provide and maintain a conducive environment of abiotic parameters for enhanced plant production. The passive or active hydroponic structures often described are an aggregate system, aeroponics, ebb and flow, deep water culture (DWC), liquid system, wick system, nutrient film technique (NFT), and drip system.

The most significant hydroponic scientific research has been performed to cultivate crops year-round without limitations of locality, climate, and soil (Mandizvidza, 2017). Furthermore, it significantly mitigates the efficient and effective use of water during production (Olivier & Singels, 2015) when water availability and scarcity are rising (Wahome *et al.*, 2010). Hydroponic cultivation can be a costly investment upon initial system design and construction. However, returns are often recuperated from the reduced production time, labour, space, carrying capacity and density required and effectively utilised with these systems, as well as the costs associated with tolerating and withstanding the impairing effects of abiotic and biotic stresses (Miller, 2002; Venter, 2010).

Hydroponics emulates growing conditions between different rainfall and seasonal and hemispheric climatic regions. Utilising controlled, monitored, and flexible mechanisms emphasising hydroponic systems to maximise favourable abiotic growing conditions can increase geophytes' knowledge-demanding and sustainable bulb and flower production.

5.5 Benefits of growing bulbs in hydroponic culture

5.5.1 Selection environments

As bulbs inherently rely on temperature in addition to light and moisture as the most essential components to fulfil their annual life cycles, numerous phenotypic traits are affected by these warm-cold-warm temperature sequences. These include but are not limited mainly to the induction and release of bulb dormancy, leaf unfolding rates, photoperiod responses, timing of flower bud initiation and development, and flowering time (Le Nard & De Hertogh, 1993; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013; Anderson, 2019; Kamenetsky-Goldstein, 2019). In addition, the specific temperature and photoperiod signalling pathways are tightly associated with the flowering time regulation in many plant species (Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013; Capovilla *et al.*, 2015). Although several selection environments are necessary before planned production lines and objectives may be reached

(Anderson, 2019), hydroponic cultivation can provide a platform to implement and regulate seasonal theromoperiodic cycles in a more favourable and conducive manner for bulb development outside their precedented lifecycle (Miller, 2002).

5.5.2 Root systems

The cooling simulation, direct contact, and availability of nutrient-filled water temperatures effectively and efficiently stimulate root formation and encourage growth and development surrounding the critical root zone of bulbs (Barnhoorn, 2013; Anderson, 2019). Contractile and fibrous root systems can easily access water, oxygen, and nutrients without any soil barriers; therefore, less energy is spent searching for diluted nutrients. Consequently, the maximum capacity for nutrient-water uptake during their annual vegetative growth cycles is achieved (Mandizvidza, 2017). The basal plates must, however, not be submerged as rot and poor root formation will occur; thus, the bulb must remain clear from the water source from the onset (Barnhoorn, 2013). Therefore, hydroponics reduces the duration, time, energy, and cleaning procedures for harvesting compared with bulbs grown in a soil substrate.

5.5.3 Geophytic structure

For commercial production, bulb yield and uniformity are scrutinised to ensure that bulbs are at an acceptable grade level and size for the competitive flower bulb market (Barnhoorn, 2013). Critical bulb expansion ‘ripening’ each year is necessary to ensure successful bulb growth, uniformity, and yield within specified timeframes for planned production lines (Barnhoorn, 2013). In addition, mother bulbs induce and regenerate offsets (daughter bulbs) as part of their expansive growth (Duncan, 2010; Barnhoorn, 2013). As juvenile and mature bulbs are grown in inert substrates within hydroponic systems, visible variations in the morphological traits of bulbous material can be easily observed. It can aid in the quantitative prediction of competency and support calculated decisions around strong phenotypic traits and floriferous clones. Thus, a high throughput rate of phenotyping in a controlled environment can be achieved.

5.5.4 Generation time

The time frame of various bulbs, from the seed to flower maturation stage, ranges from 1 to 10 years and longer (Manning *et al.*, 2002; Khodorova & Boitel-Conti, 2013). Therefore, it takes several years to pass through warm-cold-warm sequences to reach a stage where the transition from juvenility to reproductive maturity is achieved (Khodorova & Boitel-Conti, 2013). The horticulture distribution chain requires further research and development to reduce the prolonged juvenile period and product delays at specific times. Hydroponic cultivation can be employed as a selection tool to fulfil these objectives at selected time-consuming growth phases.

5.5.5 Vegetative production

The juvenile growth phase is a period in which selection and rapid leaf unfolding can occur to minimise time by maximising growth rates (Anderson, 2019). Lower temperatures favour aboveground growth (Khodorova & Boitel-Conti, 2013) and a wider surface area, promoting enhanced photosynthetic capacity per unit area (Anderson, 2019). Leaf numbers may indicate a phase change from a vegetative to a reproductive state (Langens-Gerrits *et al.*, 2003). Hydroponics may provide suitable growing temperatures and environments that offer extended periods of aboveground growth, advance vegetative growth, and reduce the noncompetent period before flowering.

5.5.6 Flower production

Flower production is the ultimate developmental phase of flower crops. These phases are often short-lived and highly sought after. Reproductive flowering-sized bulbs vary considerably, and circumferences ranging from 4 to 26 cm and above have been observed and recorded (Theron & De Hertogh, 2001; Khodorova & Boitel-Conti, 2003; Barnhoorn, 2013). Forcing mature bulbs into flowering through hydroponic techniques can reduce storage time and stimulate flower bud initiation under these conditions. Furthermore, it can enhance the flowering traits of inflorescence stem length, flower number and diameter, floral internodes, and reflowering capabilities.

5.6 Challenges in growing bulbs in hydroponic culture

5.6.1 Multiplicity of geophytic species

Different geophytic genera have disparate economic attributes, influences, and optimal cultivation requirements (Le Nard & De Hertogh, 2002; Manning *et al.*, 2002; Reinten *et al.*, 2011; Barnhoorn, 2013). Reinten *et al.* (2011), Barnhoorn (2013), and Duncan *et al.* (2020) emphasised that South African species require new and alternative research methodologies, as well as modern technology, to increase plant production efficiency. These qualities are necessary to recognise and fully expand their marketable potential. Not every bulb can be grown in hydroponics (Barnhoorn, 2013). Moreover, the system choice, singular or collectively integrated and exercised, will depend on the bulb species, type (deciduous, winter rainfall and summer rainfall/evergreen varieties), production, and expected cultivation outputs.

5.6.2 Geophytic quality

Hydroponic culture is a technically controlled and monitored growing environment; therefore, high-quality, disease-free plant material must be sourced and thoroughly checked before successful cultivation (Miller, 2002; Barnhoorn, 2013). At the production output stage, the quality of flower production in tulips is reduced with shorter and lighter flower stems than those grown in a soil substrate (Miller, 2002). However, this limitation can be overcome by systematic adjustments. Careful consideration of floricultural traits throughout geophytic cultivation in hydroponics will need to be scrutinised for successful production in the commercial market.

5.6.3 Pests and diseases

Plant pests or infectious diseases are prone to rapidly escalate and infest the hydroponic growing system as plants grow at high densities. Preventative measures for hydroponic materials and sources, periodic systematic procedural checks, and technical knowledge are required to ensure that these obstacles are contained and remedied within limited timeframes from the onset.

5.7 Hydroponically grown bulbs

Globally, many bulbous species are grown for local and international markets for various ornamental purposes (Manning *et al.*, 2002; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013). Bulb growth and development is an intricate sequence of well-timed processes and has been extensively researched, documented, and studied by experts and specialists for years (Rees, 1966; Seale, 1985; Barnhoorn, 2013). There is a global trend and perception of the release and showcase of new and improved ornamental plants to the commercial market, which has shown and provided rapid movement throughout the growing stages of the supply chain (Wilkins & Anderson, 2007). Bulbous species well-known and researched for their successful cultivation in hydroponics for forced flowering include but are not limited to, *Crocus, Hippeastrum, Hyacinthus, Leucojum, Narcissus,* and cold-treated *Tulipa* species (Figure 5.1) for commercial trade (Barnhoorn, 2013). Literature has mainly documented the flower-forcing techniques associated with hydroponic cultivation, primarily for the aesthetics of cut flowers and potted plants (Miller, 2002; Barnhoorn, 2013) and for the culinary, cosmetic, and medicinal industries, as in the case of *C. sativus* (Schroeder *et al.*, 2020).

Wahome *et al.* (2010) found that the highest vegetative growth, flower formation, and quality parameters of *Gladiolus grandiflorus* were induced when grown using a bag culture hydroponics system. Results from a study of Asiatic lilies grown in an NFT hydroponic system showed optimal performance, with flowers produced in 55 days (Asker, 2015).

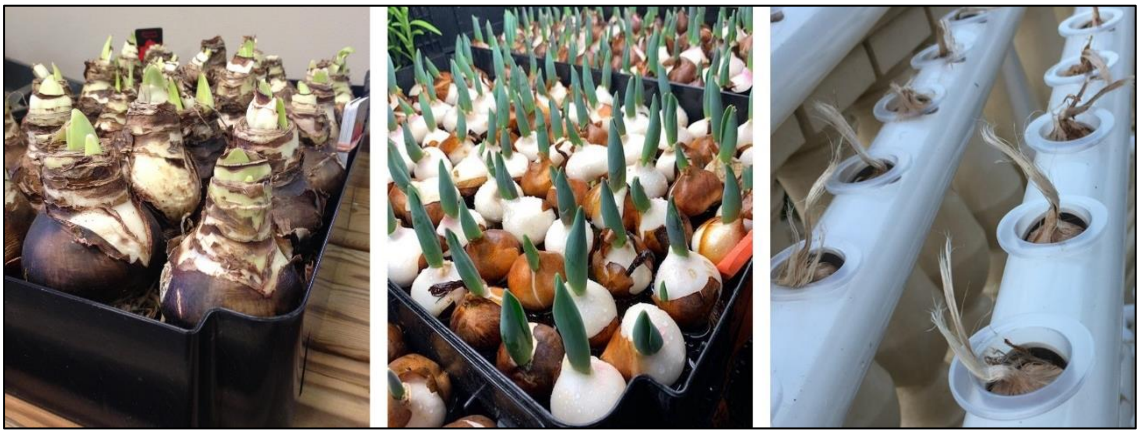

Figure 5.1. Bulb forcing in *Hippeastrum* (left), *Tulipa* (middle), and *Crocus* (right) species grown in different hydroponic systems for flower production
(Sources: https://www.berbeeus.com/plant/Hydroponic.
https://www.littlefarmhouseflowers.com/blog/2021/1/3/hydroponic-tulip-trial.
https://milankordestani.medium.com/hydroponic-saffron-cultivation-and-the-effects-of-soil-salinity-174774863451).

There is considerably less information on research and development related to practices of hydroponic cultivation employed in the induction and regeneration of bulbs for the primary function of expanding bulb yield and offset production. Bulb production other than seed propagation is readily advanced from conventional (asexual) vegetative methods such as chipping, scoring, twin-scaling, scooping, and tissue culture to expand production outputs. These vegetative methods have been promoted where robust attributes and varied genotypes are readily sought (Duncan, 2010; Barnhoorn, 2013; Anderson, 2019). The regeneration of bulbs using the asexual propagation methods mentioned above is inconsistent among species, as Yanagawa (2005) described, and is costly (Anderson, 2019). Hydroponics can support achieving various developmental outcomes for a particular stage (phase/s) throughout the bulb life cycle (Shroeder *et al.*, 2020). New experimental research methods and modifications can be supported with specialised equipment designed to accommodate these bulbs, such as prick/pin trays while growing in these systems (Shroeder *et al.*, 2020).

As Niederwieser *et al.* (2002) indicated, highlighting selected Amaryllidaceae species, research on cultivation, flower initiation, vase life, the lack of bulb uniformity, and limited colour variety for commercialisation has proven somewhat difficult. Exploring the effects of hydroponic culture on these challenging aspects of bulbous species that have not been well-researched or shown to have difficulties may prove successful. *Amaryllis belladonna*, an attractive early-autumn flowering geophyte, has a naturally low multiplication rate and lacks bulb uniformity and flowering potential. There is limited literature and research on alternative and innovative propagation and cultivation approaches to remedy these obstacles for this species (Wilmot & Laubscher, 2019a; 2019b). Experimental research using hydroponic techniques on species such as *A. belladonna* may offer new insights and methods of great return (Figure 5.2). These methods can augment and invigorate the need to trial a wider variety of bulbous geophytes.

Moreover, the wealth and abundance of geophytic species worldwide and the utilisation of new cultivation methods, such as hydroponics, can inherently not only increase developmental product outcomes for the trade; however, they can similarly be applied to conserving species listed on the ICUN Red List with a varying status of global extinction (IUCN, 2020).

Figure 5.2. *Amaryllis belladonna*: morphological growth and development of juvenile bulbs grown in inert substrates within a DWC hydroponic system, showcasing the expansive bulbs and offset yield after two months (left) and after the second growing season (right) (Source: Wilmot, C)

5.8 Conclusion

This paper has concluded that it is possible to recalibrate the cultivation of a wider selection of bulbous species under a skilful and controlled hydroponic regimen to improve adverse growing conditions in a changing climate. Furthermore, focusing on the different prospective markets rather than on predetermined product models can be profitable. Therefore, hydroponic integration can be a sustainable management approach to enhance bulb development, offset production, and increase flowering potential in local and international horticultural distribution chains.

5.9 Acknowledgements

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CHAPTER 6

FIRE-STIMULATED FLOWERING AMONG SOUTH AFRICAN GEOPHYTES: IMPLICATIONS FOR BIODIVERSITY IN A CHANGING CLIMATE

Abstract submitted to *Acta Horticulturae*

FIRE-STIMULATED FLOWERING AMONG SOUTH AFRICAN GEOPHYTES: IMPLICATIONS FOR BIODIVERSITY IN A CHANGING CLIMATE

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6.1 Abstract

Wildfires occur in many vegetation habitats within peri-urban peripheral areas, often with devastating consequences. However, a new cycle of initiated flowering and regenerative growth of selected geophytes has been established. Prolific and vibrant displays of flowering geophytes inhabiting different seasonal rainfall regions of South Africa have been documented. *Cyrtanthus ventricosus* is triggered to flower in as little as seven to nine days, whereas many others, such as *Amaryllis belladonna, Kniphofia uvaria,* and *Watsonia* species, flower *en* masse within an extended post-fire period. Geophytic flowering is most prevalent in the first flowering period following a fire, with a rapid decline in the latter seasonal phases. Certain species remain dormant for several years and rely solely on fire stimulation for long-term survival. There is limited knowledge and comprehension of how fire-associated factors initiate geophytic flowering mechanisms and their distinctive role in preserving species richness and biodiversity, ecotourism, and the survival and well-being of natural above- and below-ground ecosystems. This paper highlights the predominance of fire-stimulated flowering responses, challenges, and prospects among South African geophytes for future naturalistic planting. A changing climate may present horticultural opportunities and raise awareness of plant-environment relationships, translating into enhanced efforts for botanically endangered, rare, and underutilised geophytic species.

Keywords: biodiversity, flowering fitness, fire, fynbos, geophyte, recruitment

6.2 Introduction

Indigenous wild flora, particularly geophytes, are becoming increasingly popular in the global horticulture network largely because of their robust and long-lived ability to adapt to harsh local climatic conditions (Bradshaw *et al.*, 2011; Kamenetsky-Goldstein, 2019). Environmental cues closely govern geophytes' annual rhythmic phases, and a thorough understanding of the biological development and interplay between plants and their environments is paramount in a changing climate (Khodorova & Boitel-Conti, 2013; Kamenetsky-Goldstein, 2019).

Flower-stimulated flowering (FSF) of plant taxa, also known as post-fire flowering, is a well-known phenomenon after wildfires (Cowling & Richardson, 1995; Lamont & Downes, 2011; Vlok, 2020). South African geophytes are renowned for their floral heritage, diversity, high levels of endemism, widespread occurrence, and sought-after horticultural commodities. Several are well-adapted and, in some circumstances, rely on wildfire to activate latent flower buds in fire-stimulated flowering (FSF) geophytes, resulting in blossoming, revitalised development and recruitment (Manning *et al.*, 2002; Duncan *et al.*, 2020). This paper highlights the unique challenges that geophytic species and related ecosystems/habitats face in a changing climate and how horticulture can help mitigate some of the adverse effects, using the South African fauna as a case study.

6.3 Materials and methods

The study was conducted by searching the plant science H-Index for relevant and well-known scientific journals, books, and other sources using the research unit of the Cape Peninsula University of Technology (CPUT) library databases (Google Scholar, Science Journals, ScienceDirect, Scopus, Springer, Web of Science, and Wiley Online Library). Keywords were used to extract information from all pertinent publications.

6.4 Wildfire regimes

The prevalence of landscape fires, either from natural (wildfires) or anthropogenic activities, is a complex phenomenon; hence, they are ascribed and simplified as a four-factor regime comprising frequency, intensity, magnitude, and season (Cowling & Richardson, 1995; Van Wilgen *et al.*, 2010; Keeley *et al.*, 2012). Furthermore, the intricacies of numerous predisposing factors, including but not limited to site topography, source of ignition, climatic conditions, vegetation type, biomass fuel quality and load, pre-burn plant age, size, and circadian rhythms, are not overlooked (Cowling & Richardson, 1995; Lamont & Downes, 2011). Fire-prone environments are widely known and exist in several habitats worldwide; however, they are more frequent in Australia, the western regions of the Americas, South Africa, and countries contiguous with the Mediterranean Basin (Filippi, 2008; Van Wilgen *et al.*, 2010; Bradshaw *et al.*, 2011; Pyke, 2017; and references therein).

The direct effects include the loss of plant biomass, rapid heat pulses surging underground, and several biologically active chemical compounds present in plant-derived smoke (Van Staden *et al.*, 2000; Dixon *et al.*, 2009; Lamont & Downes, 2011; Elsadek & Yousef, 2019). The indirect effects (among others) constitute the removal of the often-dense competition of the upper vegetation canopy that exposes the region to greater diurnal air and soil temperatures as well as light differentials that were otherwise buffered (Keeley, 1993; Van Staden *et al.*, 2000; Manning *et al.*, 2002; Duncan *et al.*, 2020). Furthermore, it allows for higher nutrient availability in the soil from burnt residuals (mineral ash) and increased accessibility of precipitation to the soil surface, thus greater moisture penetration to the root zone (Keeley, 1993; Cowling & Richardson, 1995; Manning *et al.*, 2002).

Burning initiates various traits of selected plant taxa's life cycle phases, including seed germination, re-sprouting, serotiny, physical dormancy, and post-fire flowering (Cowling & Richardson, 1995; Manning *et al.*, 2002; Dixon *et al.*, 2009; Bradshaw *et al.*, 2011; Keeley *et al.*, 2011; Garland & Nicolson, 2016). It is apparent from the preceding that each fire is inimitable in its properties and effects.

6.5 Geophytes

6.5.1 Description of geophytes and their fire-stimulated flowering responses

Geophytes comprise regenerative or dormant buds from underground storage organs (USO), namely a bulb, corm, rhizomatous, or tuberous rootstock (Proches *et al.*, 2006; Duncan, 2010). Geophytic genera (vegetative or seed) can take 1-10 years, or longer, to acquire the necessary structural size, mass of carbohydrate reserves, and apical meristem(s) competence under inductive circumstances to reach reproductive flowering (Manning *et al.*, 2002; Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013; Anderson, 2019; Duncan *et al.*, 2020). Based on their growth, dormancy, and flowering phenologies, geophytes are classified as hysteranthous (flowering without leaves which appear afterwards), synanthous (primarily evergreen and new leaves appear before flowering), or proteranthous (leaves have partially/fully died back before flowering commences) (Duncan, 2010; Duncan *et al.*, 2020).

Geophytes produce attractive flowers that signal the onset of seasonal rhythms in the landscape. Despite their flowering brevity, the desire and demand for these flowering times are highly sought after for various horticultural commodities (Filippi, 2008; Barnhoorn, 2013). Geophytic taxa with specific physiological dispositions, patterns, and mechanisms of resource mobilisation exploit the direct or indirect effects of fire and the later post-fire successional phases (temporal environmental fluctuations and availability of resources, singularly or as a sum of interacting and synergistic factors) as a niche for optimal flowering fitness and recruitment (Cowling & Richardson, 1995; Manning *et al.*, 2002; Verboom *et al.*, 2002; Kraaij & Van Wilgen, 2014; Vlok, 2020). Hence, the appearance and profusion of flowering of these USOs following a fire have attracted scholarly attention. Due to the heterogeneity of the ecological re-establishment of the parched terrain vegetation, geophytic blooming is abundant in the first 12–18 months after a fire and then rapidly diminishes in subsequent seasons (Le Maitre & Brown, 1992; Cowling & Richardson, 1995; Manning *et al.*, 2002; Duncan *et al.*, 2005; Garland & Nicolson, 2016). The interval between the occurrence of a fire and the species-specific initiation and onset of pyrogenic-induced geophytic flowering varies greatly (Cowling & Richardson, 1995; Manning *et al.*, 2002; Duncan *et al.*, 2020).

Species flowering predisposition is obligate (fire-dependent) if it occurs exclusively in the first two years after a fire and continues to develop vegetatively (or is dormant) until the subsequent fire. However, if a prolific temporal increase in flowering is triggered by fire but persists at lower levels during the inter-fire period, flowering is facultative (not integral) (Lamont & Downes, 2011; Duncan *et al.*, 2020). Generally, facultative geophytes are shallow-seated and can tolerate fast-moving flames, whereas obligate species are likely deep-seated as a survival strategy in very intense fires (Duncan *et al.*, 2020).

6.5.2 Fire-stimulated flowering in South African geophytes

Numerous geophytic species from South Africa's subtropical, summer, and Mediterranean (fynbos) winter rainfall regions have been identified through sightings, communiqués, photographic imagery, or transcription to account for their similarities in flowering abilities and regenerative growth following fire disturbances. Representative discoveries of these botanically diverse FSF geophytic species are summarised in Table 6.1.

Wildfires are widespread across the peri-urban peripherals of the Cape Mediterranean fynbos region from early summer to autumn (November-March) because of high temperatures, strong winds, low humidity, and rainfall (Cowling & Richardson, 1995). However, in regions with summer rainfall, fires tend to occur during the cooler months of late winter transitioning into spring (July–September), when conditions are drier, coupled with frequent berg winds (Barnhoorn, 2013; Duncan *et al.*, 2020). FSF occurs at different times and is more prevalent in species from the Mediterranean fynbos region (Manning *et al.*, 2002; Lamont & Downes, 2011; Garland & Nicolson, 2016), and to a lesser extent in species from the summer rainfall and subtropical regions of South Africa (McMaster & McMaster, 2001; Duncan *et al.*, 2020).

Selected *Cyrtanthus* species, *C. ventricosus* (aptly named the "Fire Lily"), found that the initial effect of smoke (ethylene) triggers the stimulus of flowering and flowering as soon as 7–9 days after a fire (obligatory) irrespective of the season or gradation of burn (Keeley, 1993; Cowling & Richardson, 1995; McMaster and McMaster, 2001; Manning *et al.*, 2002). Similarly, *Hessea cinnamomea* and *Lachenalia sargeantii* exhibited similar obligate tendencies soon after a fire. These species can lie dormant (inactive) for over 15 years in anticipation of a fire, which is critical for their survival and, ultimately, flowering and seed production (McMaster & McMaster, 2001; Duncan *et al.*, 2005).

Burgeoning floral displays in vibrant colours of *Amaryllis belladonna, Kniphofia uvaria*, *Nerine angustifolia, Watsonia borbonica* and similar species of the genus are observed against a blackened backdrop during the first post-fire flowering season (Figure 6.1) (Le Maitre & Brown, 1992; Cowling & Richardson, 1995; McMaster & McMaster, 2001; Duncan, 2004; McMaster, 2008). This occurrence is caused by the wide variations in soil temperatures experienced by removing moribund vegetative overgrowth, not by variables directly related to fire (Cowling & Richardson, 1995; Duncan *et al.*, 2020). These extreme daytime and night temperature fluctuations are most noticeable in autumn (Cowling & Richardson, 1995). Up to 80% of the species bloom in response to a summer or autumn fire when the bulbs store the most reserves (Cowling & Richardson, 1995).

Figure 6.1: Profuse post-fire flowering of *Amaryllis belladonna* (left) and *Kniphofia uvaria* (right) in the Mediterranean Fynbos region (Photos: C. Paterson-Jones and Z. Poulsen)

The below-ground investment of carbohydrate returns in harvested geophytes is up to three times greater in the first few years after a fire (Botha *et al.*, 2020). These high levels of carbohydrate synthesis may have been a feasible tool that, historically, local inhabitants used by simulating fire in areas to “farm” out geophytes with a predilection for edible species (Cowling & Richardson, 1995; Vlok, 2020; Botha *et al.*, 2022). Observation of fire-induced flowering of South African geophytes is primarily noted in the species’ natural habitats, with little account for those found under cultivation.

The correlation between the morphophysiological and phenological anomalies, such as geophytic size, age, annual development lifecycle, and planting establishment, and the flowering mechanisms of the subtropical, summer, and winter rainfall species following the occurrence of fire, is not well defined. Not all geophytes flower post-fire, and variations within taxa, most notably species (*Watsonia* and *Cyrtanthus* spp.), exist (Cowling & Richardson, 1995; Manning *et al.*, 2002; Volk, 2020). Scientific evidence demonstrates that dormancy release and germination in many seeds of dormant non-bulbous South African species are triggered by fire (heat) or smoke treatment (Brown *et al.*, 2003; Newton *et al.*, 2021). However, exceptions like *Hypoxis* spp. and *Lanaria lanata* highlight the diversity of adaptive strategies among South African flora, showcasing the intricate ways in which these species have evolved to thrive in fire-affected ecosystems (McMaster & McMaster, 2001; Manning *et al.*, 2002).

6.6 Implications of biodiversity

Approximately 70% of the world's bulbous species, particularly those from the Cape Floral Region (CFR), endemic to South Africa, have long piqued attention from around the globe (Manning *et al.*, 2002; Manning, 2007; Reinten *et al.*, 2011; Barnhoorn, 2013; Duncan *et al.*, 2020). With a competitive advantage in species floral biodiversity, South African Indigenous Plant Knowledge Systems are an influential and valuable agroecological and economic instrument that constitute an untapped resource of incalculable size (Reinten & Van Wyk, 2018; Duncan *et al.*, 2020; Darras, 2021).

Through the earliest seasonal flowering of bulbous plants following the event of a fire, nectar and pollen are released, providing food resources and sustenance during periods when the flowering disposition of other species of floral genera is either absent or scarce (Manning *et al.*, 2002; Duncan *et al.*, 2020). Moreover, multifaceted proximal fire-associated factors synchronise the flowering of many species over inter-fire periods and significantly enhance seed production due to high levels of pollination and seed predator satiation (Cowling & Richarson, 1995; Manning *et al.*, 2002; Wagenhuis *et al.*, 2020). A high speciation flowering rate is critical to increasing the fitness of fauna and floral species biodiversity and genetic recruitment (Rundel *et al.*, 2018; Farinati *et al.*, 2022).

Climate change potentially increases wildfire frequencies. Therefore, plant species' biodiversity is compromised when those fires occur too soon (< 4–7 years) after the previous one, resulting in death and/or insufficient time for juvenile geophytes to re-establish themselves to a competent reproductive maturation, potentially rendering their productivity and survival (Garland & Nicolson, 2016; Duncan *et al.*, 2020) (these include species of Amaryllidaceae which take several years until maturity is reached). Conversely, some geophytic plant species (obligate) depend on fires for survival and recruitment, thus timely prescribed burns can mimic the benefits of wildfires while lowering the risk associated with larger uncontrolled fires (Rebelo *et al.*, 2011; Garland & Nicolson, 2016; Duncan *et al.*, 2020) (Taxa examples emphasised under the Fire-stimulated flowering in South African geophytes heading). These findings point to a potential strategy for using fire as a cue to improve South geophytic plant rejuvenation and reproduction, encouraging population expansion and preserving species biodiversity in

Table 6.1: Summary of the selected fire-stimulated flowering South African geophytes

Geophytic Taxa	Family	Reference(s)
Agapanthus africanus (L.) Hoffmanns, *A. africanus subsp. africanus, A. africanus subsp. walshii* (Leighton.)*, A. praecox*	Agapanthaceae	McMaster & McMaster, 2001; Manning *et al.*, 2002
Amaryllis belladonna	Amaryllidaceae	Duncan, 2004; Duncan *et al.*, 2020
Apodolirion buchananii	Amaryllidaceae	Duncan *et al.*, 2020
Aristea bakeri, A. racemose, A.spiralis	Iridaceae	Manning *et al.*, 2002; Vlok, 2020
Bobartia aphylla	Iridaceae	Vlok, 2020
Brunsvigia bosmaniae, B. joshephinae, B. marginata, B. orientalis	Amaryllidaceae	Garland and Nicolson, 2016; Duncan *et al.*, 2020; Cowling and Richardson, 1995
Bulbinella nutans	Asphodelaceae	Cowling and Richardson, 1995
Cyrtanthus aureolinus, C. breviflorus, C. debilis, C. odorus, C. suaveolens, C. tuckii var. viridilobus, C. ventricosus	Amaryllidaceae	Keeley, 1993; Cowling & Richardson, 1995; McMaster & McMaster, 2001; Duncan *et al.*, 2005; Duncan *et al.*, 2020
Dierama igneum	Iridaceae	McMaster & McMaster, 2001
Eucomis autumnalis subsp. *amaryllidifolia*	Hyacinthaceae	McMaster & McMaster, 2001
Geissorhiza hispidula, G. inconspicua	Iridaceae	Cowling & Richardson, 1995; Vlok, 2020
Gethyllis kaapensis	Amaryllidaceae	Duncan *et al.* 2020
Gladiolus longicollis, G. pubigerus, G. rogersii Baker	Iridaceae	McMaster & McMaster, 2001; Vlok, 2020
Haemanthus canaliculatus, H. coccineus, H. sanguineus	Amaryllidaceae	Manning *et al.* 2002; Duncan *et al.*, 2020
Hessea cinnamomea, H. monticola	Amaryllidaceae	Manning *et al.* 2002; Duncan *et al.* 2020
Hypoxis spp*	Hypoxidaceae	McMaster & McMaster, 2001, Manning *et al.*, 2002
Kniphofia uvaria	Asphodelaceae	McMaster, 2008
Lachenalia aloides, L. montana, L. sargeantii	Hyacinthaceae	Duncan *et al.*, 2005; Garland and Nicolson, 2016
*Lanaria lanata**	Linariaceae	Manning *et al.*, 2002
Moraea reticulata	Iridaceae	McMaster & McMaster, 2001; Duncan *et al.*, 2005
Nerine angustifolia, N. humils	Amaryllidaceae	McMaster & McMaster, 2001; Duncan *et al.*, 2020
Ornithogalum graminifolium	Hyacinthaceae	Vlok, 2020
Oxalis luteola	Oxalidaceae	Cowling & Richardson, 1995
Spiloxene capensis	Hypoxidaceae	Cowling & Richardson, 1995
Tritoniopsis parviflora, T. ramosa	Iridaceae	Manning *et al.*, 2002; Vlok, 2020
Tulbhagia acutiloba	Alliaceae	McMaster & McMaster, 2001
Wachendorfia paniculata	Haemodoraceae	Manning *et al.*, 2002
Watsonia borbonica, W. fourcadei, W. tabularis, W. vanderspuyiae, W. zeyheri	Iridaceae	Le Maitre & Brown, 1992; Cowling & Richardson, 1995; Vlok, 2020
Seeds of geophytic species that germinate after exposure to (fire) heat or smoke*		

fire-dependent ecosystems (South Africa as a case study) (Kulkarni *et al.*, 2011; Wagenhuis *et al.*, 2020). However, considerations are needed in planning, approvals, firebreaks, and firefighting readiness within the constraints of the urban and peri-urban periphery (Cowling & Richardson, 1995; Rebelo *et al.*, 2011). Moreover, these are essential in addressing existing and emerging challenges in advancing geophytic species in a changing climate (Le Nard & De Hertogh, 2002; Reinten *et al.*, 2011; Kamenetsky-Goldstein, 2019; Darras, 2020).

6.7 Prospects of fire simulation in naturalistic plantings

Naturalistic (or biophilic) planting continues to garner interest in the horticulture industry. In addition to its year-round interest, it can support the sustainable mitigation and incorporation of indigenous flora and plant communities that inhabit the indigenous climatic arena (Filippi, 2008; Barnes, 2019; Alizadeh & Hitchmough, 2020). Additional contributing factors of naturalistic planting include the potential reduced requirements and inputs of high maintenance, watering, weeding, and the addition of fertilisers; moreover, indigenous species are more resistant to the pressures of pests and diseases (Filippi, 2008; Barnes, 2019; Alizadeh & Hitchmough, 2020; Duncan, 2020). They also provide a conducive habitat that permits the inclusivity of wildlife, from pollinators like bees and butterflies to insects, invertebrates, birds, and mammals (Garland & Nicolson, 2016; Barnes, 2019; Alizadeh & Hitchmough, 2020). Naturalistic planting supports increased species biodiversity and promotes the health and equilibrium of the local ecosystem and ecological footprint (Barnes, 2019; Alizadeh & Hitchmough, 2020; Russo, 2024). Fundamentals of naturalistic plantings derive from their layering of plant forms, colours, shapes, and sizes, which depend on one another and flourish under similar conditions. These result in patterns and morphologies within these communities interlinked underground via extensive root communication, nutrient exchange, and mycorrhizae interaction (Cowling & Richardson, 1995; Filippi, 2008; Barnes, 2019; Alizadeh & Hitchmough, 2020; Duncan, 2020; Russo, 2024).

As fire provides a richness of peripheral synergistic effects within an ecosystem, so does the premise of naturalistic planting. Given these deliberations, integrating an FSF geophyte understudy into a simulated fire-dependent naturalistic tapestry with short-lived, self-sown, and long-lived plants may perpetuate genetic variability and biodiversity within the urban and peri-urban periphery of the South African landscape arena. Furthermore, it may re-establish habitat ecosystems that have been destroyed or harmed owing to urban sprawl.

6.8 Conclusions and recommendations

Wildfires' intricacies and morphophysiological vicissitudes in South African geophytes have been denoted. Fire-associated factors initiating geophytic flowering mechanisms play distinctive roles in preserving species richness and biodiversity, ecotourism, and the survival and well-being of natural above- and below-ground ecosystems. In a changing climate, numerous possibilities may be inaugurated in varying horticultural capacities for many profitable, endangered, rare, and underutilised South African geophytes. Research is needed to ratify the synergy between fire's direct and indirect ramifications on species flowering patterns and responses in future natural and experimental field settings.

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CHAPTER 7

FLOWERING PROLIFICACY OF *AMARYLLIS BELLADONNA* L. UNDER ORNAMENTAL GARDEN CONDITIONS: INFLUENCE OF POPULATION ATTRIBUTES, HABITAT FEATURES AND CULTIVATION PRACTICES

FLOWERING PROLIFICACY OF *AMARYLLIS BELLADONNA* L. UNDER ORNAMENTAL GARDEN CONDITIONS: INFLUENCE OF POPULATION ATTRIBUTES, HABITAT FEATURES, AND CULTIVATION PRACTICES

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7.1 Abstract

Amaryllis belladonna is a bulbous geophyte endemic to South Africa's Western Cape that blooms from late summer to early autumn before the winter leaves unfurl. Aside from its protracted bulb juvenility, the species is criticised for its unpredictable flowering behaviour once reproductive bulb maturity is reached. A two-year field study explored *A. belladonna*'s established *ex situ* bulb planting life strategy and flowering disposition by examining the population attributes, habitat features, and cultivation practices influencing flowering prolificacy under ornamental garden conditions within its endemic region. The study comprised six *ex situ* populations recruited using purposive sampling and predetermined criteria. The findings revealed that bulbs of *A. belladonna* populations have enduring longevity, and offsets, although slow, are the primary mode of bulb recruitment. Flowering heterogeneity ranged from 4.9% to 58.3% within and between seasons, yet several parallels were identified. These commonalities spoke to a larger impact of temperature. In addition to favourable habitat features and climatic growing conditions, population characteristics (bulb size, structure, position, density, and establishment) and cultivation practices (premature defoliation, soil amendments, planting interference, and re-establishment) were significant synergistic constituents of flowering proficiency. This study recommends that more scientific research be undertaken on the species' ex *situ* life strategy and bulb lifting, division, and repositioning behaviours to ensure seasonal single-harvest flowering reliability and continuity.

Keywords: Amaryllidaceae, anthesis, anthropogenic, cultivation, *ex situ* life strategy, planting establishment

7.2 Introduction

Amaryllis belladonna L. (Amaryllidaceae) is a hysteranthous geophyte indigenous to the Western Cape, South Africa's fynbos biome (Manning *et al.*, 2002; Duncan *et al.*, 2020). From late summer to early autumn, the austerity of summer dormancy is broken by stately clusters of pink-shaded florets appearing on a single *A. belladonna* inflorescence for 6–9 weeks before the burgeoning winter strap-like leaves unfold (Adams, 2001; Theron & De Hertogh, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020). Apart from their prolonged bulb juvenility, the seasonal single-harvest species is widely criticised for exhibiting erratic flowering behaviour once maturity and competence are attained (Theron & De Hertogh, 2001; Duncan, 2004; Duncan *et al.*, 2020). In their natural (wild) habitat, *A. belladonna* is observed festooning unspoiled mountainous landscapes with copious clusters of flower colonies in a year or two following habitually sighted summer fires that are otherwise stifled (Manning *et al.*, 2002; Duncan, 2004; Adams, 2001; Duncan *et al.*, 2020). These have been denoted within the Western Cape Province, including but not limited to the slopes of Lion’s Head (Johnson & Snijman, 1996; Duncan, 2010), Pardeberg Mountains (Garland & Nicolson, 2016), and Koegelberg Nature Reserve (pers. observe. C. Laubscher and C. Wilmot). However, fire is not integral to the species’ flowering, as intermittent flowering is observed during inter-fire periods (Johnson & Snijman, 1996; Manning *et al.*, 2002; Duncan, 2010). On the other hand, flowering appears more readily and reliably each year under cultivation and in open areas, provided they have adequate warmth (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Duncan *et al.*, 2020).

Despite its limiting and unpredictable floral demeanour, the *A. belladonna* bulbous species is durable and drought tolerant. Once established, it grows successfully in many unmaintained and undisturbed landscape areas for decades. In addition to its versatility, the species thrives in sandy soils devoid of nutrients and sunlit locations that require minimal attention (Adams, 2001; Manning *et al.*, 2002; Duncan, 2010). Hence, the species has proven popular, naturalised and cultivated in several Mediterranean regions worldwide (Adams, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020). The species, also widely known as the “March lily,” “Belladonna lily”, or “Naked lady”, likewise supports ecosystem biodiversity by attracting pollinators with its sweetly scented florets during a period when few other species are in bloom (Manning *et al.*, 2002; Gul *et al.*, 2020). Aside from its sought-after application as a cut flower and potted plant in floriculture markets, *A. belladonna* has been incorporated into wide-reaching planting palettes and landscape designs (Barnhoorn, 2013; Wilmot & Laubscher, 2019a; Gul *et al.*, 2020; Darras, 2021).

Geophytes exhibit a complex associative dissonance in size, vigour and multiplication, as well as cultivation methods, environmental cues and annual exogenous rhythmic sequences that regulate their intrinsic life cycles to attain optimal rates of development, growth and meristematic flowering (Le Nard & De Hertogh, 2002; Thompson *et al.*, 2011; Khodorova & Boitel-Conti, 2013; Kamenetsky-Goldstein, 2019; Marković *et al.*, 2021). These variances occur within many species’ genera and cultivars (Manning *et al.*, 2002; Khodorova & Boitel-

Conti, 2013; Kamenetsky-Goldstein, 2019); hence, while generalisations can be made, each species must be addressed independently. Identifying habitat features, characterising bulb structures, and analysing cultivation practices and environmental variables that drive regional variation in reproductive flowering success are not idle academic distinctions (Manning *et al.*, 2002; Barnhoorn, 2013). In addition to identifying gaps and unravelling shortcomings, this study may aid in a better understanding of flower-regulating factors. Furthermore, recognising and quantifying these aspects within the confined context of a species' native habitat or region of origin may offer a deeper understanding of the plant-environment binomial, perhaps revising unexplored facets of a species' life strategy and life cycle assessment. Researchers are encouraged to engage in collaborative study initiatives that improve geophytic species life cycle assessment (LCA) and uncover new knowledge to enhance their economic and sustainable viability ((Manning *et al.*, 2002; Thompson *et al.*, 2011; Anderson, 2019; Slezák *et al.*, 2020; Marasek-Ciolakowska *et al.*, 2021; Marković *et al.*, 2021).

There is insufficient information and descriptive accounts of *A. belladonna*'s *ex situ* bulb life strategy and flowering performance under garden cultivation. Moreover, Wilmot and Laubscher (2019b) emphasise that various factors affect the tendency of *A. belladonna* to flower. Therefore, this study explored *A. belladonna*'s established bulb-planting life strategy and flowering disposition under established ornamental garden conditions within the geographical confines of its endemic region to bridge this knowledge gap by examining the population attributes, habitat features, and cultivation practices that influence flowering prolificacy. These findings support calculated modifications and recommendations for commercial *ex situ* bulb planting protocols of *A. belladonna* to support flowering-regulating prolificacy and continuity.

7.3 Materials and methods

7.3.1 Study area

An *in-situ* field study was conducted from July 2020 to September 2022 in Pinelands, Cape Town, South Africa, 33°56'31" S, 18°30'24" E. Pinelands is a residential area in the southern suburbs of the Western Cape in South Africa's Fynbos region, which is the endemic provenance of the *A. belladonna* species. The area measures approximately 5.86 km^2, with an estimated terrain elevation of 9 m above sea level. Pinelands, within the greater Cape region, have a Mediterranean-type climate consisting of mild, wet winters and hot, dry summers accompanied by predictably desiccating southeasterly winds (Cowling & Richardson, 1995; Manning *et al.*, 2002; Duncan *et al.*, 2020). Figure 7.1 depicts the Pinelands' monthly average precipitation, temperature, and sunshine hours.

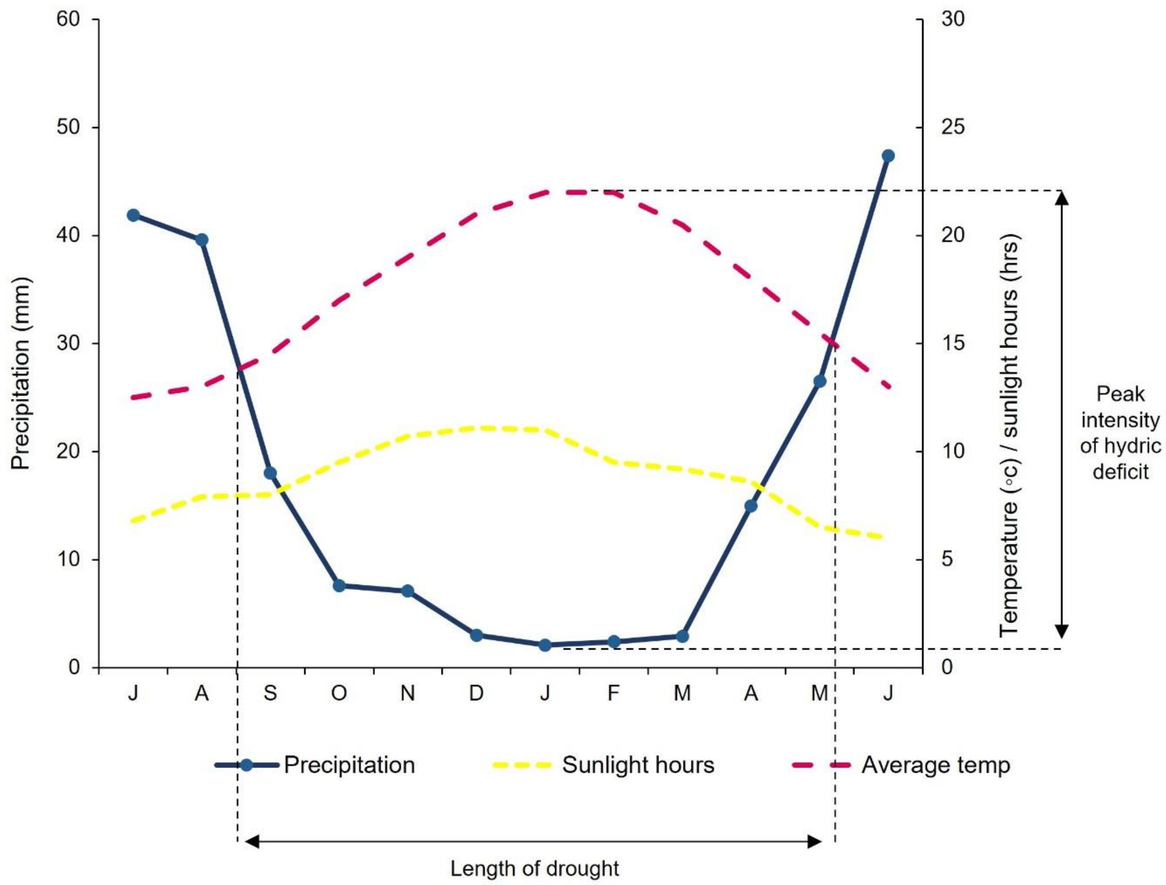

Figure 7.1: Monthly average precipitation levels, temperature, and sunshine hours of Pinelands residential area, Cape Town, South Africa
(Adapted from Filippi (2008) and https://www.timeanddate.com/weather/@3362864/climate)

7.3.2 Study populations

A purposive sampling method was used to identify *A. belladonna* field populations within the study area. Bulb populations were identified within a one-square-kilometre (1 km^2) geospatial area of the first identified population with an inclusion threshold of at least 50 *ex situ* bulbs. In addition, inhabited bulb plantings ought to have naturalised themselves on location for at least 10 years and exhibited signs of flowering. Six field bulb planting populations meeting the qualifying criteria were identified in residential properties during the leafing phase between July and August 2020. These populations were subjectively named A, B, C, D, E, and F (Figure 7.2).

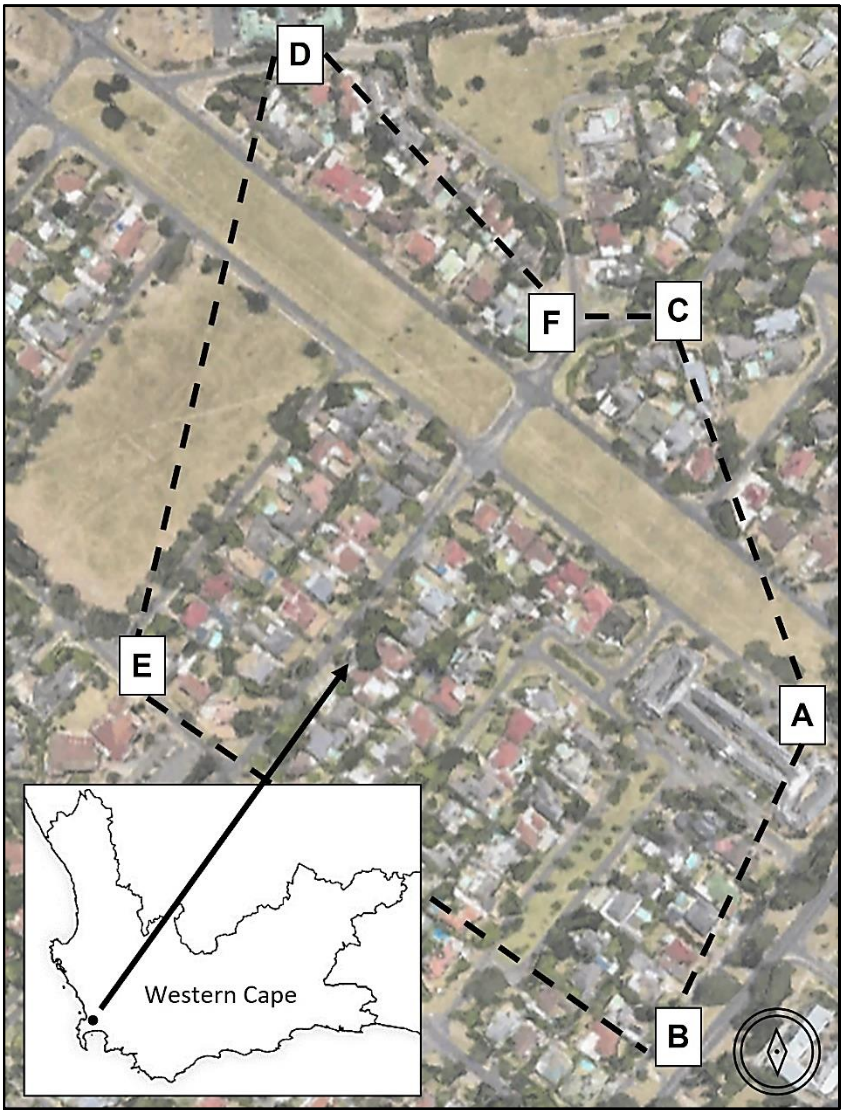

Figure 7.2: Aerial view of study populations A–F in Pinelands, Cape Town, South Africa, observed from 1.78 km above ground (Photo: Google Earth, 2024)

7.3.3 Data collection

Population data were collected in the field during the same season over two years (2020–2022) (January–April for flowering and habitat features and July–September for habitat features). To more accurately represent the established bulb planting age and cultivation practices exercised in each population, additional field data were gathered by enlisting the participation of each landowner in semi-structured interviews. The interviews clarified and prioritised observations to support the triangulation of findings (Kawulich, 2005).

7.3.3.1 Determination of the population attributes

7.3.3.1.1 Population size, structure, and establishment age

A complete count of each field population's bulbs was performed during the leafing phase. Transect lines 0.25 m wide were set up across the breadth of the population to methodically account for each bulb and prevent bulbs from being counted more than once within the area.

The population structure was determined by classifying the bulbs into two categories: mother bulbs and offsets. Mother bulbs were classified as solitary bulbs or linked to offsets, whereas offsets were differentiated as being joined to the outer basal perimeter of the mother bulb (Duncan, 2010; Barnhoorn, 2013). The estimated age of established populations was determined by categorising bulb plantings into age distribution categories of 10+, 20+, 30+, 40+, 50+, or 60+ years. The age was denoted as the inhabited planting age rather than the bulb age, which was unknown.

7.3.3.1.2 Population area, planting density, and bulb positioning

The coverage area for each field bulb population was determined using a 0.25 × 0.25 m grid configuration. The bulb density was calculated by dividing the total bulb number (population size) by the bulb population's coverage area within each location. The population's bulb positioning was determined by examining the exposure and sighting of the bulb necks at or above the soil surface and classified as absent, adequate, or visible.

7.3.3.2 Determination of habitat features

7.3.3.2.1 Associated vegetation species and basal grass cover

Field observations were used to identify associated plant species and basal ground cover within 2 metres of the established bulb population coverage area.

7.3.3.2.2 Aspect and slope

The orientation of each field population was determined using a global positioning system (GPS). Each field population's area of occurrence was visually evaluated and classified into one of three slope categories: none (0°–3°), gentle (3°–8°), and moderate (9°–16°).

7.3.3.2.3 Soil Analysis

Six randomised soil samples were collected at a 15–20 cm depth to identify the soil characteristics from each field population, A to F. The samples were combined to form one representative sample for each population and sent for laboratory soil analysis (Bemlab Pty (Ltd), Strand, Cape Town). The soil samples were analysed for soil type, pH, and soil stone volume percentage.

7.3.3.2.4 Pests

The lily borer caterpillar (*Brithys crini)* was identified in each field population by visual inspection of the bulbs during the flowering season, as infestations of the lily borer are known to affect the *A. belladonna* species negatively (Johnson & Snijman, 1996; Duncan, 2010). The pest occurrence was assigned as present or absent.

7.3.3.3 Determination of cultivation practices

Visual observations were made to establish the species identification and cultivation practices exercised at each field population location over the study period. The aspects of water delivery methods, soil additives and amendments, bulb lifting, division and repositioning, and population maintenance were assessed.

7.3.3.4 Determination of inflorescence morphological features

Morphological data were recorded as markers of inflorescence growth and development using a standard soft cloth metric tape measure (Empisal EMT-001, Builders Warehouse, South Africa) and a stainless-steel ruler (Sealy, Leroy Merlin, South Africa) with a readability of 1500 × 12 mm and 450 × 25 mm, respectively. The characteristics of each inflorescence within each population and season were evaluated to attain maximum variation and minimise the risk of overlooking imperative insights using the following criteria: the percentage of bulbs that produced a flowering inflorescence, the length of the inflorescence stem (scape), and the number of florets per inflorescence. The flowering percentage was calculated by dividing the inflorescence flowering counts by the total number of bulbs in each established population.

7.3.4 Statistical analysis

Data were subjected to a one-way analysis of variance (ANOVA) with statistical data analysis software (Minitab 17, Minitab LLC, Pennsylvania State University, USA) to identify significant differences between populations based on the parameters of population structure, percentage flowering, inflorescence stem length, and floret number. The means were further separated using Fisher's least significant difference (LSD) at a significance threshold of $p \leq 0.05$. Means with different letters differed significantly at the 95% confidence level.

7.4 Results

7.4.1 Population attributes

7.4.1.1 Population size, structure, and establishment age

Across all populations, bulb counts ranged from 52 to 222. The population structures differed significantly ($p \leq 0.05$) between populations (Figure 7.3). In all population groups, mother bulbs accounted for at least 40%. Population D had the most mother bulb constituents (54.8%), followed by B and C, whereas population F had the fewest (40.1%). Bulb offsets accounted for at least 45% of each population, with populations A, E, and F showing the highest offset percentages. The estimated age of established bulb plantings ranged from 20 to 60 years or more across the population groups (Table 7.1 and Figure 7.3).

Table 7.1: Population attributes of *Amaryllis belladonna* populations A–F in the Pinelands study area

Population attributes	Population A	Population B	Population C	Population D	Population E	Population F
Population size (n)	77 bulbs	62 bulbs	52 bulbs	84 bulbs	222 bulbs	202 bulbs
Establishment age	20+ years	30+ year	50+ years	60+ years	40+ years	30+ years
Area coverage (m^2)	2.7 m^2	2.3 m^2	4.5 m^2	5.1 m^2	11.6 m^2	4.9 m^2
Bulb density	31.5 /m^2	26.9 /m^2	11.1 /m^2	16.3 /m^2	19.1 /m^2	41.2 /m^2
Bulb positioning	Absent - adequate	Adequate	Adequate - visible	Adequate - visible	Absent - adequate	Absent - adequate

Table 7.2: Habitat features of *Amaryllis belladonna* populations A-F in the Pinelands study area

Habitat features	Population A	Population B	Population C	Population D	Population E	Population F
Aspect	55˚NE	155˚SE	320˚NW	15˚N	65˚NE	160˚S
Slope	Gentle (3°–8°)	Gentle (3°–8°)	Gentle (3°–8°)	Gentle (3°–8°)	Gentle (3°–8°)	Gentle (3°–8°)
Soil type	Sand	Sand	Sand	Sand	Sand	Sand
Soil pH	7.0	6..5	6.6	6.8	6.6	6.7
Soil stone volume %	1.31%	2.28%	2.74%	2.50%	1.75%	1.43%
Associated vegetation species	*Lavandula dentata & L. angustifolia*	*Brunfelsia pauciflora & Strelitzia reginae*	*Carpobrotus edulis, Rhagodia hastata & Rhaphiolepis indica*	*Aloe arborescens, Portulacaria afra & Vibrnunum sinensis*	*Dietes grandiflora, Euryops virgineus, Salvia chamelaeagnea & S. africana-lutea*	Overhead mature *Schinus molle & Euryops pectinatus*
Basal cover	None	*Stenotaphrum secundatum*	None	None	None	*Cynodon dactylon*
Lily borer caterpillar	Present	Present	Present	Present	Present	Present

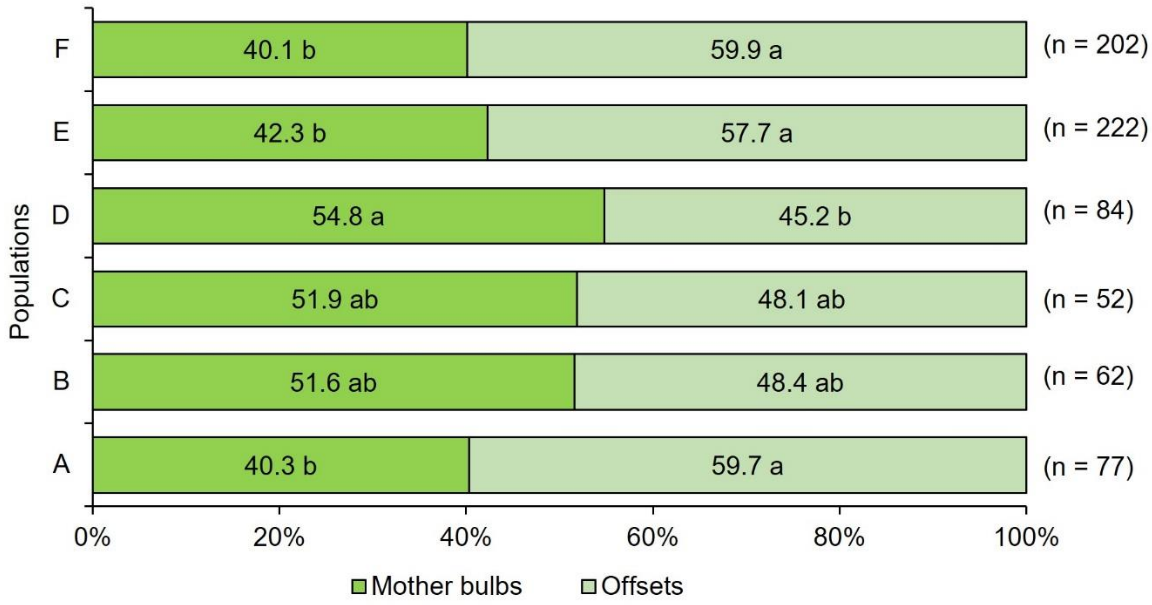

Figure 7.3: Population structure of *A. belladonna* across study populations A–F

7.4.1.2 Population area, planting density, and bulb positioning

The population's bulb coverage area extended from 2.7 to 11.6 m^2. Population F inhabited the largest bulb area, whereas population B occupied the smallest (Table 7.1). The population's bulb densities ranged from 11.1 to 41.2/m^2. Population F had the highest planting density, almost four times that of population C. Many bulbs were difficult to find, especially during dormancy, because their positioning was absent, obscured or ineffectively positioned at or above the surface. Although visibility improved with the larger bulbs and those more densely grown, the bulb locations became more evident during the leafing seasons (Table 7.1).

7.4.2 Habitat features

7.4.2.1 Aspect and slope

Populations A, C, D, and E were generally associated with the northern aspect, whereas populations B and F were associated with the southern aspect. All populations were found to have gentle slopes (3°–-8 °) (Table 7.2).

7.4.2.2 Soil type, pH, and stone volume percentage

All populations were associated with a sand soil type, and the pH levels ranged from slightly acidic to neutral. A soil stone volume of less than 3% was measured across populations. Populations A, E, and F had lower soil stone volume percentages than populations B, D, and D (Table 7.2).

7.4.2.3 Associated vegetation species and basal cover

Most populations were associated with low to medium-growing perennial shrubs and groundcovers up to 1.5 m high comprising indigenous and exotic species. Apart from population F, established beneath a row of mature *Schinus molle* trees, trees had no association with bulb planting populations. Populations B and C were associated with grass basal cover (Table 7.2).

7.4.2.4 Pests

The presence and activity of the lily borer caterpillar in each population group during both flowering seasons were determined (Table 7.2).

7.4.3 Cultivation practices

Most bulbous populations could be identified; however, they were mostly referred to by their common names and not by their scientific vernacular names. All bulb populations received their water from natural precipitation; however, during the warmer and drier summer months, bulb populations B and D received intentional irrigation via periodic hand watering (Table 7.3). Except for population D, during the 2018 summer dormancy period, no bulb populations were lifted, divided, or repositioned. In general, the maintenance of bulb populations was neglected and somewhat absent, with bulbs left to their own devices and unmaintained. Most populations did not follow a seasonal maintenance plan that included the addition of soil additives or amendments, except for populations B and D (Table 7.3). It was found that bulb leaves in most populations detached after the seasonal leafing periods once they had withered entirely and neared dormancy; however, the unsightly senescing leaves in populations B and C were defoliated before this process was completed. All populations' floral stalks were removed once they had been wasted entirely (Table 7.3).

Table 7.3: Habitat features of Amaryllis belladonna populations A–F in the Pinelands study area

Cultivation practices	Population A	Population B	Population C	Population D	Population E	Population F
Water delivery	Natural precipitation	Natural precipitation, Intermittent hand watering in the summer months	Natural precipitation	Natural precipitation, Intermittent hand watering in the summer months	Natural precipitation	Natural precipitation
Soil additives and amendments	No applications	Compost added to soil surface	No applications	Thin layer of bark chip mulch added to the soil surface	No applications	No applications
Bulb lifting, dividing and repositioning	Not exercised	Not exercised	Not exercised	Bulbs were lifted, split & repositioned in December 2018	Not exercised	Not exercised
Population maintenance	Senescent leaves removed post-wilting, Floral stalks removed upon wilting	Defoliation before wilting, Floral stalks removed upon wilting	Defoliation before wilting, Floral stalks removed upon wilting	Senescent leaves removed post-wilting, Floral stalks removed upon wilting	Senescent leaves removed post-wilting, Floral stalks removed upon wilting	Senescent leaves removed post-wilting, Floral stalks removed upon wilting
Species identification & cultivation knowledge	Yes	Yes	Yes	Yes	No	No

7.4.4 Inflorescence morphological features

7.4.4.1 Percentage flowering

A significant variation *($p \leq 0.05$)* in the proportion of flowering bulbs among populations was observed. Percentages ranged from 4.9% to 58.3% within and over both flowering seasons (Figure 7.4). Population D had the highest flowering disposition in both seasons, whereas population F had the lowest. In five of the six populations, bulb flowering performance was less than 30%; nevertheless, flowering exceeded the seasonal total population average in three. The flowering proportion was the same or higher across all populations in 2022 as in the previous year (Figure 7.4).

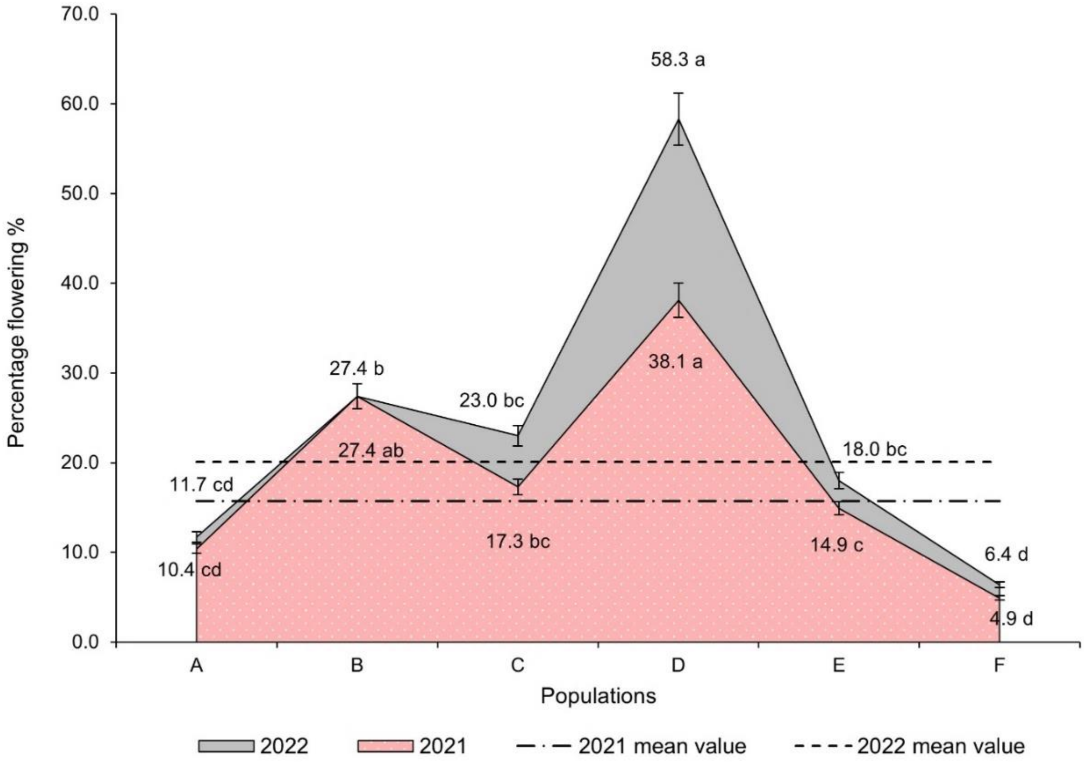

Figure 7.4: Percentage flowering of *A. belladonna* across study populations A–F in 2021 and 2022

7.4.4.2 Inflorescence stem length

Inflorescence stem length varied considerably ($p \leq 0.05$) between the population groups, ranging from 41.9 to 82.2 cm across both flowering seasons (Figure 7.5). Population D had the tallest stems, whereas populations E and F had the shortest. Figure 7.5 illustrates a minimal variation in the average stem length of populations between the two seasons; however, the 2021 flowering season had somewhat taller stems than the 2022 flowering season.

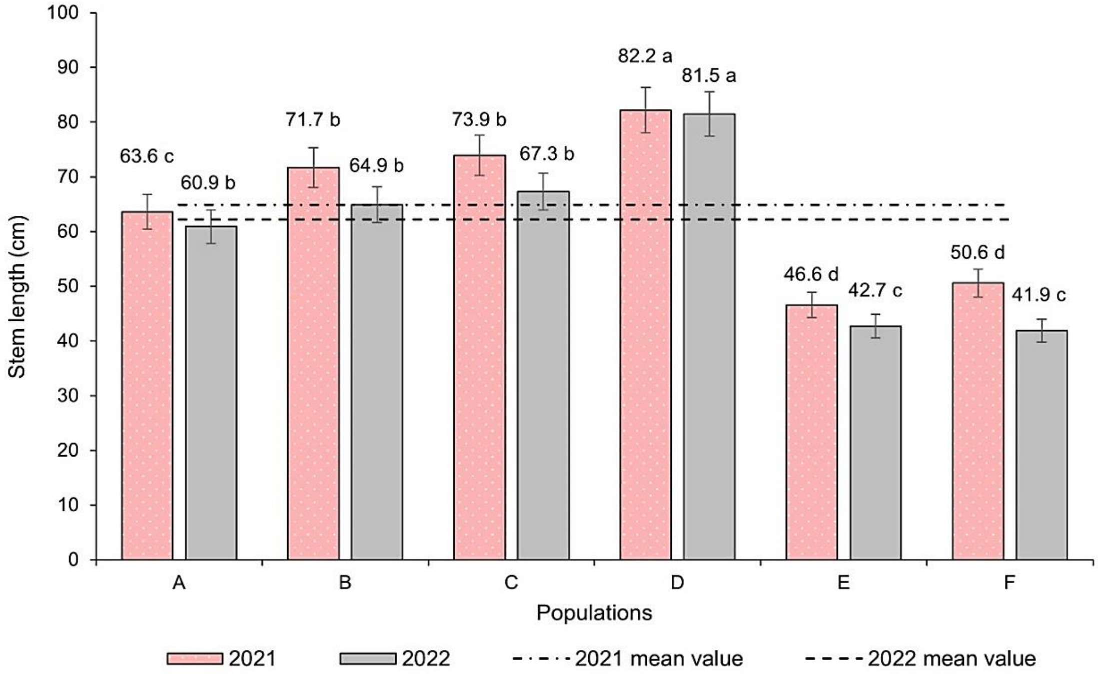

Figure 7.5: Inflorescence stem length of *A. belladonna* across study populations A–F in 2021 and 2022

7.4.4.3 Number of florets

Figure 7.6 shows a significant ($p \leq 0.05$) variation in floret production between population groups. Floret counts ranging from 7.5 to 19.6 were observed across both flowering seasons. Population D had the most florets compared with populations E and F, which had the fewest. As depicted in Figure 7.6, slight heterogeneity was observed in the total inflorescence floret averages between both seasons.

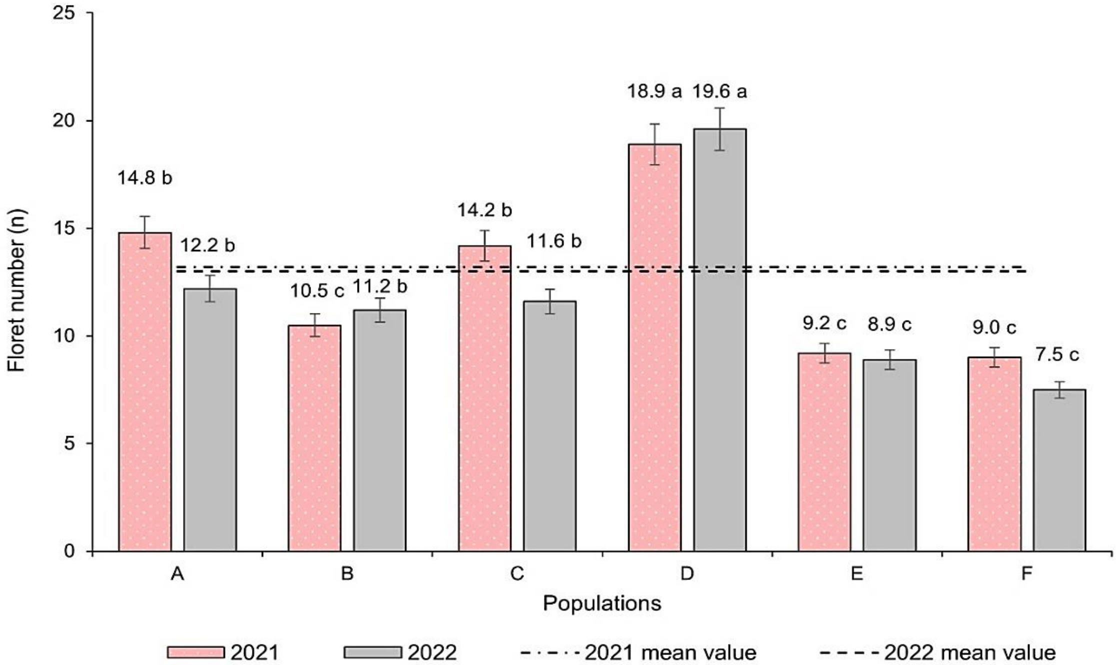

Figure 7.6: Inflorescence floret counts of *A. belladonna* across study populations A–F in 2021 and 2022

7.5 Discussion

Owing to the encounters of mitigating unfavourable conditions in open-field settings and the exposure to several geographical and seasonal biotic and abiotic stresses, studies on *ex situ* bulb cultivation are challenging (Barnhoorn, 2013; Khodorova & Boitel-Conti, 2013); however, they can provide insight into factors that may be frequently overlooked (Manning *et al.*, 2002; Barnhoorn, 2013). This study presented a snapshot account of *A. belladonna*'s established bulb-planting life strategy and flowering propensity under ornamental garden conditions, allowing insights, impacts, and conclusions to be formed. At the outset, the age, size, and bulb quantity initially planted within each population were uncertain compared with their present disposition. However, several interpretations could be drawn from the population's establishment, size, and structural data. The long-term establishment of *A. belladonna* indicates adaptability, tenacity, and long-term survival—all critical traits given the shifting environmental conditions. The species has a slow multiplication capacity, consistent with Theron and De Hertogh (2001) and Duncan (2010). Asexual reproduction of vegetative offsets was the most common strategy of bulb recruitment because seedlings were seldom seen. This anomaly is likely due to the seasonal presence of the lily borer caterpillar in the populations, which devours the flower stalks and recalcitrant seeds, rendering seedling recruitment impossible (Johnson & Snijman, 1996; Duncan, 2010; Barnhoorn, 2013).

The *A. belladonna* populations exhibited significant flowering heterogeneity of between 4.9% and 58.3% within and between seasons. The findings corroborate Wilmot and Laubscher's (2019b) premise that several variables may have influenced the species' flowering propensity and are consistent with other authors' conclusions that numerous factors affect flowering (Rees, 1966; Le Nard & De Hertogh, 1993; Inkham *et al.*, 2019). Besides the flowering anomalies, some parallels were observed. The flowering percentage across all populations was the same or higher in 2022 than in the previous season. Floret counts remained stable, and stem lengths were lower across all populations in 2022 than in 2021. These similarities suggest that broader environmental cues were responsible for commonalities and were strongly associated with regional temperature fluctuations.

Moreover, in both seasons, the populations' precise flowering timeframes, which were not documented in this field study, occurred between mid-February and end-April. However, it was observed that the populations associated with the southern aspect appeared to flower earlier than those related to the northern aspect. According to the study region's climatic data, overall population flowering began after the driest months of January and February, when the hydric deficit intensity peaked, with cumulative temperature differentials at their highest and precipitation levels at their lowest. Temperature is a fundamental factor influencing the physiological and morphological processes that govern floral organ induction and differentiation (Le Nard & De Hertogh, 1993; Roh & Hong, 2007; Horvath, 2009; Khodorova & Boitel-Conti, 2013; Capovilla *et al.*, 2015; Howard *et al.*, 2019; Wang *et al.*, 2021).

Furthermore, a bulb's flowering ability depends on a species-specific cumulative temperature range or cardinal temperature, and deviating from this can compromise anthesis signalling pathways and floral meristematic development (Van Kilsdonk *et al.*, 2002; Dole & Wilkins, 2005; Khodorova & Boitel-Conti, 2013). *Amaryllis belladonna* conforms to an annual warm-cold-warm thermoperiodic cycle, and it is estimated that the species initiates a single inflorescence during the height of summer dormancy, approximately one month ahead of the previous bloom's appearance (Hartsema & Leupen, 1942). These developmental processes rely on the subsurface organ's carbohydrate partitioning, hydration status, and energy supplies, and temperature influences how these components are mobilised and delivered (Wendell *et al.*, 2017; Marković *et al.*, 2021). Ultimately, this may lead to flower abortion, a common occurrence in the *A. belladonna* species (Hartsema & Leupen, 1942; Theron & De Hertogh, 2001). Moreover, Wilmot *et al.* (2023) found that the variables influencing the dormancy period may largely dictate the competitive nature of the *A. belladonna* species' reproductive initiation in the current and subsequent season(s). The developmental plasticity of a plant species is demonstrated by its capacity to continuously monitor environmental cues and adjust its growth to daily and seasonal stimuli through its circadian rhythm (Capovilla *et al.*, 2015). Therefore, climate variables such as temperature, moisture, and light affect all geophytic life cycle phases and influence the degree to which growth, dormancy, development, and flowering occur (Miller, 1992; Le Nard & De Hertogh, 1993; Khodorova & Boitel-Conti, 2013; Capovilla *et al.*, 2015).

During natural production, bulb size affects yield, quality, and flowering efficiency because bulbs serve as a source and sink of internal carbohydrate reserves to attain maturity and flowering competence (Khodorova & Boitel-Conti, 2013; Kapczyńska, 2014; Manimaran *et al.*, 2017). First, the proliferous above-ground leaf growth during the leafing phase provides a potentially disproportionate impression that the flowering capacity is high. Second, the percentage of flowering bulbs compared to population size may appear low; however, a closer look at the population structure indicated that the populations comprised mature bulbs and various stages of bulb juvenility that had not yet achieved flowering maturity. As a result, juvenile bulbs are unreceptive to flower-promoting inductive stimuli (Levy & Dean, 1998; Proietti *et al.*, 2022). The greater blooming performance seen in study populations B, C, and D—where the proportion of mother bulbs was higher—supports this. Despite lower soil stone volume percentages, populations A, E, and F had a higher percentage of juvenile offsets to mother bulbs. In contrast, populations B, C, and D exhibited greater proportions of mother bulbs where larger soil stone volumes were found. These indicate drainage, soil water potential, and nutrient retention factors surrounding the bulb root zone, which are essential during vegetative growth. These findings suggest that the mother bulbs were not providing for the demands of younger bulbs as their soil water-holding capacity was potentially lower; instead, they were reserving their own needs.

According to Seale (1985), Manning *et al.* (2002), Duncan (2010), and Barnhoorn (2013), in addition to temperature, excessive dryness during vegetative leaf production, excessive shade, overshadowing, and premature foliage removal affect flowering. In populations B, C, and F, these characteristics were seen during the growing season(s); thus, inadequate photosynthetic capacity-building may have reduced flowering productivity. This anomaly is further supported by the fact that *A. belladonna* is a perennial hysteranthous taxon in which the leaves and flowers are set apart. Thus, for optimal photosynthetic productivity to generate and maintain sufficient carbohydrate reserves in the species' larger underground storage organs, reliable and longer vegetative leafing seasons are required to sustain them through dormancy and later flowering and fruiting (Dafni *et al.*, 1981; Howard & Cellinese, 2020).

There was a low degree of prominent bulb neck visibility above the soil surface among the established bulb plantings. *Amaryllis belladonna* is a shallow-seated bulb whose necks are best kept elevated at or above the soil surface to support flowering; however, planting it too deeply reduces flowering performance (Seale, 1985; Manning *et al.*, 2002; Duncan, 2010; Barnhoorn, 2013). It is presumed that when the bulbs were planted, their necks were detectable at or above the ground; however, due to soil additions, leaf litter, and bulb retraction to lower depths, visibility progressively faded. The findings that most inhabited bulb populations have remained in the same posture and have not been disturbed for some time—possibly since they were planted—add to the supporting evidence of low visibility and, therefore, a conceivably reduced flowering disposition.

In addition to the findings of long periods of undisturbed bulb plantings, bulb densities differed considerably among population groups. Rees (1975) and Kapczyńska (2013) state that planting density affects crop yield. During the initial years of the established plantings, bulbs may have had ample space, carbohydrate reserves, and additional available resources, making the morphogenic effects of planting densities less noticeable (Rees, 1975). However, as time passes, resources such as sunlight, moisture, and nutrients become scarce, and population densities increase, which may lead to lower productivity and flower production (Rees, 1975; Seale, 1985; Manning *et al.*, 2002; Duncan, 2010). To further substantiate these findings, the *A. belladonna* mother bulb does not wither to create room and opportunity for younger progeny, unlike that found in other geophytic species like *Watsonia* (Thompson *et al.*, 2011); instead, it continues to enlarge whilst producing offsets, resulting in increased and gregarious population densities (Theron & De Hertogh, 2001; Duncan, 2010). This study suggests that increased bulb densities, overcrowding, and resource competition may decrease bulb fitness and flowering yield in established populations of *A. belladonna*. In addition, little to no nutritional supplementation in the form of additives or amendments provided in some populations supports this. Several authors have proposed lifting, splitting, and repositioning bulbs to maximise productivity and prolificacy when reduced flowering performance after long establishment and overcrowding occur (Seale, 1985; Duncan, 2010; Barnhoorn, 2013). The population in which this technique was recorded, population D, showed more pronounced flowering than the other five studied populations in which this approach was not applied. Besides its putative floriferous genetic propensity, this cultivation method most likely contributed to this population's improved productivity and flowering performance. However, flowering was observed to be poor in the year after planting in 2019. An explanation for this delay stems from the fact that bulbs of Amaryllidaceae species resent disturbance due to their sensitive, contractile root systems and the time needed for regeneration, which affects flowering (Manning *et al.*, 2002; Duncan, 2010). According to Duncan (2010) and Warrington *et al.* (2011), established planting interference tactics are purposely used every four to six years in *Nerine* bulb plantings to increase yields and blooming performance when symptoms of degradation appear. Therefore, determining the long-term consequences of disturbances on planting establishment and densities of perennial bulbs is essential, and further investigation is warranted to unravel a better understanding and timeframe of consciously employing these cultivation methods, particularly under *ex situ* conditions, to increase *A. belladonna*'s flowering productivity.

The fitness of *A. belladonna* bulbs is not isolated as, over time, the life strategies of the surrounding vegetation are assumed to have had varying degrees of influence on the populations' establishment and present production levels and competition for resources. Instances found among others may include the growth and expansion of overhanging trees and the planting or removal of other vegetation, resulting in the overshadowing of bulb plantings and curtailing food storage processes. Moreover, although climatic conditions and cultivation practices during the previous season(s) may have influenced *A. belladonna* flowering anomalies, intraspecific heritable variation in morphological traits between populations was anticipated, with some proving more successful than others (Duncan, 2004; Chandel *et al.*, 2023). These traits were observed in bulbs of population D, as despite their high flowering performance, they exhibited the longest inflorescence stems and most florets in both seasons, suggesting a robust genetic disposition.

Lastly, while geophytic flowering is a composite sequence of events synchronised by external environmental signals and endogenous mechanisms (Corbesier & Coupland, 2006; Horvath, 2009; Denay *et al.*, 2017; Proietti *et al.*, 2022), this study recognised that anthropogenic activities and cultivation practices could either favourably or adversely affect the species' energetic demands. Identifying a species and understanding its life cycle and cultural needs are essential for navigating appropriate methods that optimally promote yearly blooming productivity.

7.6 Conclusion

This study has contributed to a greater understanding of the inhabited life strategy and flowering dynamics of *A. belladonna* under garden conditions. The findings revealed that the species has a long lifespan and that vegetative offsets are its most prevalent recruitment strategy. Although flowering heterogeneity ranged from 4.9% to 58.3% within and between seasons, several commonalities were found. These similarities alluded to a broad influence of temperature. Aside from highlighting the need for sufficiently appropriate and sustainable habitat and climatic growing conditions, population attributes (bulb size, structure, positioning, density, and establishment) and cultivation practices (premature defoliation, soil amendments, planting interference and re-establishment) play an equally significant role in synergistically shaping the species flowering behaviours and can cause considerable anomalies. This study recommends further research assessing the species *ex situ* behavioural characteristics, survival strategies and comparative cultivation throughout larger regions. Moreover, research on bulb lifting, dividing, and repositioning methods and timeframes of *ex situ* bulb plantings should be investigated to ensure the species' flower-regulating prolificacy and seasonal continuity.

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CHAPTER 8

STIMULATORY EFFECTS OF AN EXOGENOUSLY APPLIED SEAWEED EXTRACT ON THE MORPHOLOGICAL AND PHYSIOLOGICAL GROWTH AND YIELD IN JUVENILE *AMARYLLIS BELLADONNA* L. BULBS.

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STIMULATORY EFFECTS OF AN EXOGENOUSLY APPLIED SEAWEED EXTRACT ON THE MORPHOLOGICAL AND PHYSIOLOGICAL GROWTH AND YIELD IN JUVENILE *AMARYLLIS BELLADONNA* L. BULBS

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8.1 Abstract

Amaryllis belladonna L. is a hysteranthous bulbous species indigenous to the Cape Floristic Region of South Africa. The species' attractiveness, adaptability, and low-maintenance needs have drawn international interest to its desirable uses in ornamental and landscape applications constrained by the observably slow rate of natural multiplication to reach flowering. A 24-week study was performed to determine the stimulatory effects of a seaweed extract, Kelpak®, on the morphological and physiological responses of *A. belladonna* bulbs cultivated under greenhouse conditions. Juvenile bulbs from five successive age groups were used to evaluate the consistency of observed responses. Treatments consisted of a 0% untreated control and three Kelpak® concentration dilutions at 0.2%, 0.4%, and 1% (*v/v*) administered to five age groups of *A. belladonna* bulbs as a monthly soil drench. The results showed that even at low concentrations, Kelpak® treatments improved the phyto-stimulatory responses of both the bulb aerial and, more substantially, the below-ground storage organs in a concentration-dependent manner. While treatments enhanced the morpho-physiological responses, the consistency of bulb age differed. Higher morphological yields were associated with older bulbs; however, bulbs of *A. belladonna* in years 1 and 2 were deemed the most receptive in circumference, weight coefficients, and chlorophyll content. However, to maximise the efficacy and proliferation rate of the species in a reduced timeframe, a 1% Kelpak® dilution applied at an early developmental stage within the first two years is most beneficial and a priority to elicit rapid, uniform, and healthy bulb growth and development.

Keywords: Amaryllidaceae, cultivation, juvenile bulb, Naked Lady, phytohormones, seaweed biostimulant

8.2 Introduction

Amaryllis belladonna L. (Amaryllidaceae), more commonly known as the "Belladonna Lily", "March Lily", or "Naked Lady", is an endemic drought-tolerant ornamental bulbous geophyte from the Cape Floristic Region (CFR) of South Africa (Manning *et al.*, 2002; Duncan *et al.*, 2020). As a representative of only two species within the genus, it has become a popular plant that has migrated and naturalised in several Mediterranean climatic areas worldwide (Adams, 2001; Duncan, 2004; Duncan *et al.*, 2020). The advent of pink-scented, trumpet-shaped flowers on a single inflorescence from late summer to early autumn signifies the bulb's hysteranthous nature and a species characteristic. The expansion of winter leaf growth subsequently follows this. As the seasonal transition into spring intensifies, bulb resources are preserved by the withering of leaves and the persistence of summer dormancy (Manning *et al.*, 2002; Duncan, 2010; Duncan *et al.*, 2020). The attractiveness, versatility, and low-maintenance requirements of this perennial bulbous species have drawn attention to their valuable and desirable uses in a variety of cultivated floricultural, ornamental, and landscape applications (Reinten *et al.*, 2011; Wilmot & Laubscher, 2019; Gul *et al.*, 2020; Darras, 2021).

Amaryllis belladonna is, however, severely constrained by the observably slow rate of natural multiplication as seedlings, juvenile bulbs (seedlings termed as juvenile bulbs after the first year of seed cultivation), and the division of offsets typically requires several years to attain a critical size competent for reproductive flowering (Theron & De Hertogh 2001; Duncan 2010). In addition, the recalcitrant seeds germinate almost instantaneously and do not survive desiccation; therefore, the seeds need to take advantage of the approaching autumn or winter rains to establish themselves adequately before the upcoming adversities of the summer dormancy period. (Duncan, 2004; Duncan, 2010; Colville, 2017). Currently, the species is propagated primarily by conventional methods, which are the most affordable and simplest options from collected recalcitrant seeds and offsets (also referred to as daughter bulbs or bulblets) (Adams, 2001; Duncan, 2010). *In vitro* tissue culture has been tested (De Bruyn *et al.*, 1992; Veeraballi *et al.*, 2017), yet it is costly in comparison (Zhang *et al.*, 2013). As a result, the timely entry of adequate and economically viable plant material into the horticultural distribution network is hindered. According to Kharrazi *et al.* (2017), Anderson (2019) and Li *et al.* (2023), the hampering juvenile period (lifecycle stages following embryogenesis) of vegetative growth essential in producing a marketable and viable flowering bulb within the commercial propagation framework of geophytes is of concern. There is a continuing prevailing interest in advocating precision cultivation practices to expand the paucity of information and alleviate the challenges of South African indigenous plant species that have shown potential for commercialisation (Reinten *et al.*, 2011; Darras, 2021). Given the foregoing, the practical expansion of *A. belladonna's* cultivation inefficiencies in reducing the truncated lifecycles in a cost-effective, sustainable, and time-saving manner and enhancing their performance in various untapped ornamental and commercial product lines within the horticultural distribution chain, is warranted (Le Nard & De Hertogh, 2002; Anderson, 2006; Darras, 2020).

Alternative and innovative cultivation techniques to support sustainable crop production are paramount, particularly given the insurmountable pressures and peripheral effects of climate change, energy crises, worldwide population growth, the availability of and viability of agricultural land, food security, and pest and pathogen resistance (Khan *et al.* 2009; Wang & Frei 2011; Arioli *et al.* 2015; Kamenetsky-Goldstein 2019; Del Buono 2021). The 'green technology' of naturally based seaweed bioproducts has gained momentum in supporting workable efforts to alleviate these stresses and meet consumer needs (Craigie, 2011; Sharma *et al.*, 2014; Ali *et al.*, 2021a) that were once dominated by the availability of a range of harsh synthetic agrochemicals (Tilman *et al.*, 2002). Whole seaweed extracts consist of a plethora of mainly organic substances applied in low quantities that effectively interact with plant and soil systems in enhancing plant phenotypes, microbial restructuring, nutrient acquisition, pathway regulation, quality products, and abiotic stress tolerance (Calvo *et al.*, 2014; Colla & Rouphael, 2015; Ali *et al.*, 2021a). Moreover, they are at the forefront of the latest trends and sustainable advances in facilitating an inexpensive, environmentally friendly, and safe set of agricultural inputs as part of an integrated system approach for crop production (Caradonia *et al.*, 2019; Souza *et al.*, 2019). As an indication of their consistently proven desirability, effectiveness and relevance, comprehensive research activities of the profitable and experimental products developed from seaweed species (in containerised and field trials) have been extensively investigated (Papenfus *et al.*, 2013; Sharma *et al.*, 2014; Colla & Rouphael, 2015; Ali *et al.*, 2021a; Kisvarga *et al.*, 2022). Furthermore, the ongoing exploration, frequency, mechanisms and modes of action, and profound effects towards the sustainable productivity of a variety of ornamental (Kisvarga *et al.*, 2022) and, more prominently, edible food crops have been appraised (Khan *et al.*, 2009; Colla & Rouphael, 2015; Caradonia *et al.*, 2019).

Kelpak® is a commercial organic seaweed extract (SWE) formulated from a liquid derived from the commonly used, fast-growing giant brown kelp, *Ecklonia maxima* (Osbeck) Papenfuss (Phaeophyceae), that has undergone a patented cold cellular burst process of extraction (Troell *et al.*, 2006; Stirk *et al.*, 2020). This process has excluded chemicals, dehydration, cooling, and heating while emphasising pressure differentials to breach the cell walls in releasing the natural biostimulant (Troell *et al.*, 2006). The extract contains trace levels of macro- and microelements in addition to auxins (11 mg/L), cytokinins (0.031 mg/L), alginates, amino acids, mannitol, and neutral sugars (Stirk *et al.*, 2014; Lötze & Hoffman, 2016). The presence of an increased phytohormone proportional ratio (auxin-to-cytokinin) is ascribed to the several plant-promoting synergistic effects in crops, including but not limited to root system expansion, plant development, nutrient translocation and absorption efficiency, and plant stress tolerance to abiotic influences (Colla & Rouphael, 2015; Lötze & Hoffman, 2016; Kisvarga *et al.*, 2022). Several scientific studies have demonstrated the beneficial effects of Kelpak® applications (Van Staden *et al.*, 1995; Basak, 2008; Papenfus *et al.*, 2013; Makhaye *et al.*, 2021). Additionally, Kelpak®-based research has produced encouraging findings of commercially well-known and valuable indigenous South African species *Erica verticillata* Bergius (Adams *et al.*, 2019) and *Eucomis autumnalis* (Mill.) Chitt (Aremu *et al.*, 2016).

Considering the horticultural prospects of the *A. belladonna* species and the vast agronomic capabilities of seaweed extracts, no information or comprehensive studies have been conducted on the practice of utilising these bio-stimulators as a potentially viable alternative technology and advanced cultivation strategy to augment the early development, juvenile timeframe, and ornamental quality of the bulb. Therefore, the best methods conducive to large-scale propagation and cultivation in accelerating the prolonged juvenile stage by reducing the generation time of this slow-growing indigenous bulb remain to be determined. This study aimed to elucidate the stimulatory effects of exogenous applications of selected concentration dilutions of a seaweed extract, Kelpak®, on the morphological and physiological responses in juvenile *A. belladonna* bulbs cultivated under greenhouse conditions. Furthermore, as it takes the bulb several years to reach flowering maturity, an additional objective was set to evaluate the consistency of any observed responses across five successive age groups. This research anticipates enhancing the knowledge and efficiency of facilitating the species' production processes and life cycle assessment (LCA), as well as providing a proposed continuous long-term, practical, and sustainable horticulture propagation and/or cultivation practice for enhancing the production of geophytes with specialised economic value in the conservation, floriculture, and ornamental sectors.

8.3 Materials and methods

8.3.1 Experimental location

A 24-week study was conducted in the Cape Peninsula University of Technology's Horticultural Sciences research greenhouse facility in Bellville, Cape Town, South Africa (33°55'45" S, 18°38'31" E) from mid-April 2021 to mid-October 2021. The ventilated greenhouse facility with clear polycarbonate rooftop sheeting and a thermostatically automated system (Envirowatch, Envirowatch Solutions, South Africa) ensured a controlled and monitored environment under natural light conditions. Temperature set ranges fluctuated between 18 °C – 26 °C during the day and 10 °C – 18 °C at night, with an average relative humidity (RH) of 60%. The daylight photoperiod coincided with the prevailing conditions between early autumn and late spring (9–12 hours). The photosynthetic photon flux density (PPFD) recorded a daily average of 420 µmol/m^2/s, with the optimal light conditions logged at 1020 µmol/m^2/s. The average soil substrate temperature was 14/20 °C (min/max).

8.3.2 Plant material and preparation

Dormant, juvenile *A. belladonna* bulbs from five successive growing seasons (delineated from one to five years of age), primarily propagated from seed, were sourced from Assegaaibosch Farm on the Agulhas Plain, Western Cape, South Africa in early April 2021 (i.e., mid-autumn). The well-developed bulbs were selectively and sustainably harvested using standard cultural practices, as (Duncan, 2010) described, and graded according to categorical age criteria to ensure sample homogeneity. The bulbs were rinsed of extraneous matter, stripped of senescent leaves, and their desiccated contractile roots removed. Thereafter, the bulbs were immersed for 5 minutes in a 0.1% biocidal solution (Sporekill™, ICA International Chemicals (Pty) Ltd., Stellenbosch, South Africa) (active ingredient: didecyldimethylammonium chloride) removed and adequately air-dried. Before replanting and experimental treatments, the bulbs were conditioned for one week and stored in sealed, breathable crates at a constant ambient temperature of 21°C ± 2°C and RH of 50–70% in a darkened room.

8.3.3 Experimental design and setup

The experimental design comprised four levels of a 0% untreated control and three concentration dilutions at 0.2%, 0.4%, and 1% (*v/v*) of Kelpak® administered to *A. belladonna* bulbs from five consecutive growing seasons (years one through five). Bulbs within each of the five age categories were randomly assigned to each Kelpak® treatment group (Table 8.1). The bulbs were planted in plastic growing trays (15 × 23 × 7.5 cm, with a 5 L volume) using an inert growing medium consisting of pre-rinsed (to remove any impurities and other extraneous materials) silica sand (grade 6/17 Consol®) and fine river sand at a ratio of 1:1 (*v/v*). The trays were supplemented with the remaining media, ensuring each bulb's neck was covered at the surface. The growing trays were labelled and placed on galvanised steel mesh tables (2 × 0.85 m) to obtain a flat, uniform surface height that warranted adequate air and temperature circulation. The bulbs were planted in a randomised block design (RBD) with 50 bulbs per Kelpak® treatment (ten sample replicates per age category from years one through five) (Table 8.1).

Table 8.1: Overview of the randomised experimental setup with duplicate growing trays containing five varying bulb ages placed on four selected Kelpak® concentration (%) treatment tables

Table	1 (control)	2	3	4
Growing tray 1	Y2 + 0% Kelpak® (c)	Y1 + 0.2% Kelpak®	Y4 + 0.4% Kelpak®	Y3 + 1% Kelpak®
Growing tray 2	Y5 + 0% Kelpak® (c)	Y4 + 0.2% Kelpak®	Y2 + 0.4% Kelpak®	Y5 + 1% Kelpak®
Growing tray 3	Y3 + 0% Kelpak® (c)	Y2 + 0.2% Kelpak®	Y5 + 0.4% Kelpak®	Y1 + 1% Kelpak®
Growing tray 4	Y1 + 0% Kelpak® (c)	Y5 + 0.2% Kelpak®	Y3 + 0.4% Kelpak®	Y2 + 1% Kelpak®
Growing tray 5	Y4 + 0% Kelpak® (c)	Y3 + 0.2% Kelpak®	Y1 + 0.4% Kelpak®	Y4 + 1% Kelpak®

(c) = control; (Y1–Y5) = Bulb age from year 1–year 5.

8.3.4 Kelpak® treatments

The SWE (Kelpak®, Kelp Products (Pty) Ltd., Simons Town, South Africa) treatment applications were prepared by diluting the liquid concentrate with reverse osmosis (RO) water to obtain three selected dilutions at 0.2%, 0.4%, and 1% (*v/v*). As inherent South African fynbos species exhibit the need for reduced nutritional requirements (Duncan, 2010), lower dilutions of the recommended manufacturer's dosage were applied. The concentration dilutions were prepared on each treatment day and manually administered as an equally distributed soil drench during the active vegetative growing season, first at planting (0 weeks) and subsequently at 4-week intervals in weeks 4, 8, 12, and 16, while the control was supplemented with RO water (no SWE was applied). Manually irrigated soil drench with municipal tap water was systematically applied weekly to maintain the moisture levels in all bulb treatments between the five SWE applications. Since soil drenching is associated with enhanced absorption of various compounds (Sarkar *et al.*, 2007) and continuous assimilation of plant crops over an extended period (Parkunan *et al.*, 2011), this treatment was recommended. Moreover, because the bulbs were dormant at the onset of experimentation, the delivery of a foliar spray was invariably constrained.

8.3.5 Data collection

8.3.5.1 Determination of vegetative morphological plant growth parameters

Morphological data were collected and captured before, during, and post-harvest as indicators of new growth and development using an electronic laboratory scale (Radwag® PS 4500.R2, Radwag Waagen, Hilden, Germany) with a 0.001 g legibility, standard metric retractable metal tape measure (Stanley Power Lock®, Builders Warehouse, South Africa) and a soft cloth tape measure (Empisal EMT-001, Builders Warehouse, South Africa) with a corresponding 300 × 19 mm and 450 × 25 mm respective readability.

Preliminary pre-plant measurements of initial fresh bulb circumference and weight were measured to ensure sample homogeneity. Twenty weeks after planting, morphological leaf parameters of the number of leaves, leaf length, and width produced by each bulb were recorded. The leaf numbers were quantified manually, whilst the longest established leaf was measured from its base (where it emerged from the bulb) to its apex, and the broadest point of the same leaf was used to determine the leaf width. In addition, the leaf area was determined using the Montgomery equation (ME) as described by Yu *et al.* (2020) and Shi *et al.* (2021).

$$A_{leaf} = \alpha \times L_{leaf} \times W_{leaf}$$

where

A_{leaf} = leaf area; L_{leaf} = leaf length; W_{leaf} = width; α = Montgomery parameter

At 24 weeks, on completion of the treatment period, once natural leaf senescence had occurred, whole bulbs were harvested, rinsed, and air-dried overnight. Thereafter, accumulated post-harvest measurements of fresh bulb circumference, weight, number of roots, and root length were recorded. The root count was obtained manually, whilst the root length was determined as the span from the bulb basal plate to the apex of the longest root. Moreover, the bulb circumference coefficient (the ratio of the fresh bulb circumference at harvest and the initial circumference) and weight coefficient (the ratio of the fresh bulb weight at harvest and the initial weight) were calculated.

$$\text{Circumference coefficient} = \frac{C2}{C1} \qquad \text{Weight coefficient} = \frac{W2}{W1}$$

where

C1 = initial fresh bulb circumference
C2 = harvest fresh bulb circumference
W1 = initial fresh bulb weight
W2 = harvest fresh bulb weight

8.3.5.2 Determination of leaf chlorophyll content

Chlorophyll content (mg/m^2) in the leaf primordia was monitored as a measure of chlorophyll production described by Gitelson *et al.* (1999) using a portable modulated chlorophyll content meter (CCM-300, Opti-Sciences Inc., Hudson, USA). The absorption instrument was calibrated and clipped to three different positions along the leaf blade (top, middle, and bottom) of the 2nd developed outer basal leaf of each sample bulb in a non-destructive manner, and the average relative mean value was recorded. Data readings were logged between 10 a.m. and 2 p.m. at 20 weeks of the experiment, with ten analytical replicate samples performed for each treatment combination.

$$\bar{X} = \frac{(R1+R2+R3)}{3}$$

where

$\bar{X}$ = mean value
R = chlorophyll content reading

8.3.6 Statistical analysis

The morphological and physiological data were computed and statistically analysed using the Minitab analysis software (Minitab 17.0, Minitab LLC, Pennsylvania State University, USA). Experimental results were subjected to a two-way analysis of variance (ANOVA) for factors: Kelpak® concentration dilutions (4 levels) and bulb age (5 levels) and presented as mean values with predicted standard errors (S.E.). Tukey's least significant difference (LSD) was used to determine the main effects and interactions at a $p \leq 0.05$ significance level. Mean values that do not share a letter(s) significantly differ at an α level.

8.4 Results

8.4.1 Effect of Kelpak® treatments and bulb age on morphological bulb growth

8.4.1.1 Pre-plant bulb circumference and circumference coefficient

Pre-plant bulb circumference showed significant differences ($p \leq 0.05$) when the interaction of Kelpak® treatments and bulb age were evaluated. Age-dependently, older bulbs exhibited the highest pre-plant circumference among treatment combinations (Table 8.2). In determining the circumferential coefficient, younger bulbs in years 1 and 2 (1.2–1.5) had significantly higher marked responses to treatment interactions, whereas bulbs in years 3, 4, and 5 maintained their circumferential size with a coefficient of approximately 1.0 (Figure 8.1; Table 8.2). The highest coefficient was observed in the 0.2%–year 1 treatment.

In arriving at a more synthetic conclusion, the bulb circumference coefficient was evaluated irrespective of Kelpak® treatments and bulb age (Figure 8.2; Table 8.2). The findings indicated that the circumference coefficient in Kelpak®-treated bulbs had comparably fewer discernible differences between the 0.2%, 0.4%, and 1% treatments. Nevertheless, the 1% application (1.3) presented the most significant improvement ($p \leq 0.05$) in comparison to the untreated application (1.1) of tap water. Within bulb age, the coefficient decreased significantly with advanced ageing, where the most significant coefficient was observed in bulbs from year 1 (1.4). Expansive bulb growth was either maintained or enhanced, culminating in a circumference coefficient of 1.0 or higher within each of the five years.

Table 8.2: Interactive effects of Kelpak® dilutions and bulb age on the bulb and root characteristics of *A. belladonna* bulbs

Bulb age	Kelpak® treatment	Bulb characteristics				Root characteristics	
		Pre-plant circumference (cm)	Circumference coefficient	Pre-plant fresh weight (g)	Weight coefficient	Number of roots (n)	Root length (cm)
Year 1	0.0% (control)	2.5 ± 0.05 f	1.3 ± 0.04 bcd	0.5 ± 0.02 c	3.2 ± 0.48 e-h	4.9 ± 0.31 bc	6.1 ± 0.38 i
	0.2%	2.4 ± 0.05 f	1.5 ± 0.09 a	0.5 ± 0.01 c	6.7 ± 0.63 ab	5.2 ± 0.25 bc	8.0 ± 0.87 ghi
	0.4%	2.5 ± 0.04 f	1.4 ± 0.04 ab	0.5 ± 0.02 c	6.5 ± 0.66 abc	5.9 ± 0.38 b	7.7 ± 0.54 ghi
	1%	2.5 ± 0.04 f	1.3 ± 0.05 bcd	0.5 ± 0.02 c	6.5 ± 0.67 abc	5.3 ± 0.37 bc	8.7 ± 0.58 ghi
Year 2	0.0% (control)	2.7 ± 0.07 ef	1.2 ± 0.03 b-f	0.7 ± 0.03 c	4.8 ± 0.67 b-e	5.9 ± 0.38 b	7.2 ± 0.44 hi
	0.2%	2.9 ± 0.09 def	1.2 ± 0.06 c-g	0.7 ± 0.03 c	4.0 ± 0.61 d-g	4.5 ± 0.27 bc	6.0 ± 0.62 i
	0.4%	2.8 ± 0.08 def	1.3 ± 0.03 b-e	0.6 ± 0.04 c	6.1 ± 0.38 a-d	5.8 ± 0.36 b	7.6 ± 0.41 ghi
	1%	2.7 ± 0.09 ef	1.3 ± 0.04 abc	0.6 ± 0.04 c	7.2 ± 0.66 a	6.1 ± 0.31 b	9.7 ± 0.62 f-i
Year 3	0.0% (control)	4.0 ± 0.17 d	1.1 ± 0.03 e-h	1.5 ± 0.13 c	2.1 ± 0.30 gh	4.9 ± 0.23 bc	14.3 ± 1.44 d-g
	0.2%	4.0 ± 0.17 de	1.1 ± 0.03 e-h	1.5 ± 0.12 c	3.6 ± 0.33 e-h	4.5 ± 0.22 bc	10.1 ± 0.58 e-i
	0.4%	3.9 ± 0.20 de	1.2 ± 0.06 b-f	1.4 ± 0.12 c	4.5 ± 0.41 c-f	5.2 ± 0.25 bc	10.9 ± 0.82 d-i
	1%	3.9 ± 0.14 de	1.1 ± 0.04 d-h	1.4 ± 0.13 c	4.3 ± 0.36 def	5.3 ± 0.26 bc	13.2 ± 1.16 d-g
Year 4	0.0% (control)	5.3 ± 0.21 c	1.0 ± 0.02 fgh	3.3 ± 0.29 c	2.0 ± 0.15 gh	3.8 ± 0.36 c	16.7 ± 1.94 cde
	0.2%	5.9 ± 0.22 c	1.1 ± 0.01 e-h	3.9 ± 0.40 c	2.5 ± 0.13 fgh	5.3 ± 0.34 bc	15.5 ± 1.33 c-f
	0.4%	5.6 ± 0.35 c	1.1 ± 0.03 d-h	3.6 ± 0.66 c	3.7 ± 0.28 e-h	5.2 ± 0.29 bc	16.7 ± 1.42 cde
	1%	5.9 ± 0.34 c	1.1 ± 0.03 d-h	4.5 ± 0.68 c	2.8 ± 0.15 e-h	6.0 ± 0.49 b	17.1 ± 1.74 cd
Year 5	0.0% (control)	12.7 ± 0.40 a	1.0 ± 0.01 h	34.3 ± 3.30 ab	1.8 ± 0.05 h	9.3 ± 0.47 a	31.4 ± 2.79 a
	0.2%	13.5 ± 0.40 a	1.0 ± 0.01 h	39.7 ± 2.80 a	1.8 ± 0.10 h	9.8 ± 0.39 a	27.9 ± 1.69 a
	0.4%	11.4 ± 0.38 b	1.0 ± 0.02 fgh	28.9 ± 2.38 b	1.9 ± 0.10 gh	8.7 ± 0.65 a	27.1 ± 2.24 ab
	1%	13.5 ± 0.46 a	1.0 ± 0.02 h	38.0 ± 3.53 a	1.7 ± 0.10 h	9.8 ± 0.71 a	21.1 ± 1.34 bc
Two-way ANOVA *F*-Statistic							
Kelpak® treatment		5.06 *	4.78 *	2.70 *	19.38 *	3.71*	1.43 ns
Bulb age		1248.64 *	62.05 *	479.01 *	65.74 *	94.13 *	146.20 *
Kelpak® × Bulb age		3.53 *	2.97 *	2.35 *	4.26 *	2.34 *	3.39 *

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 Tukey's least significant difference test; ns = not significant.

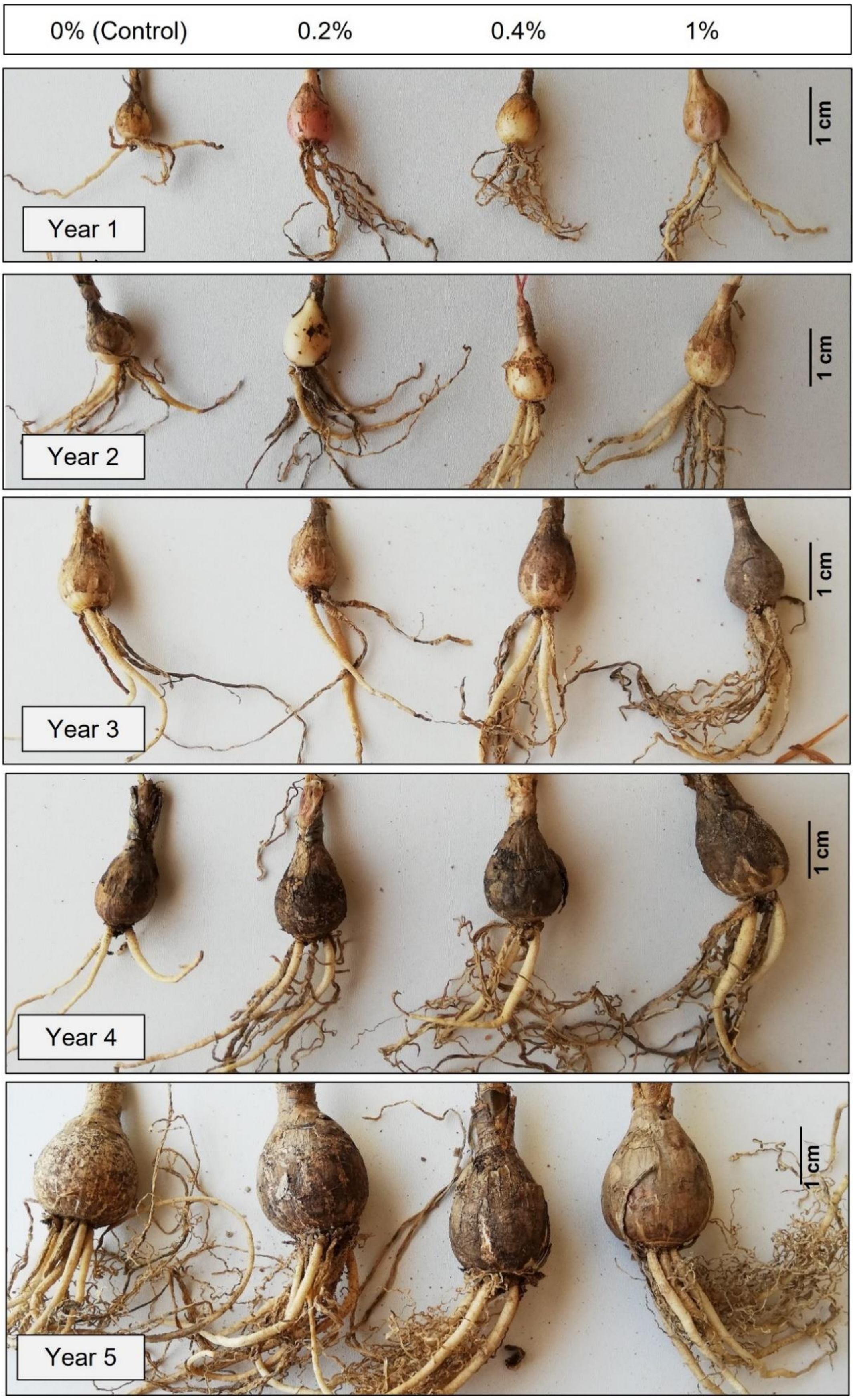

Figure 8.1: The postharvest visible effects of Kelpak® concentration dilutions on bulb growth and development on a series of five growing seasons (age) of *A. belladonna* bulbs after 24 weeks of treatment (Bar = 1cm) (Photo: C Wilmot)

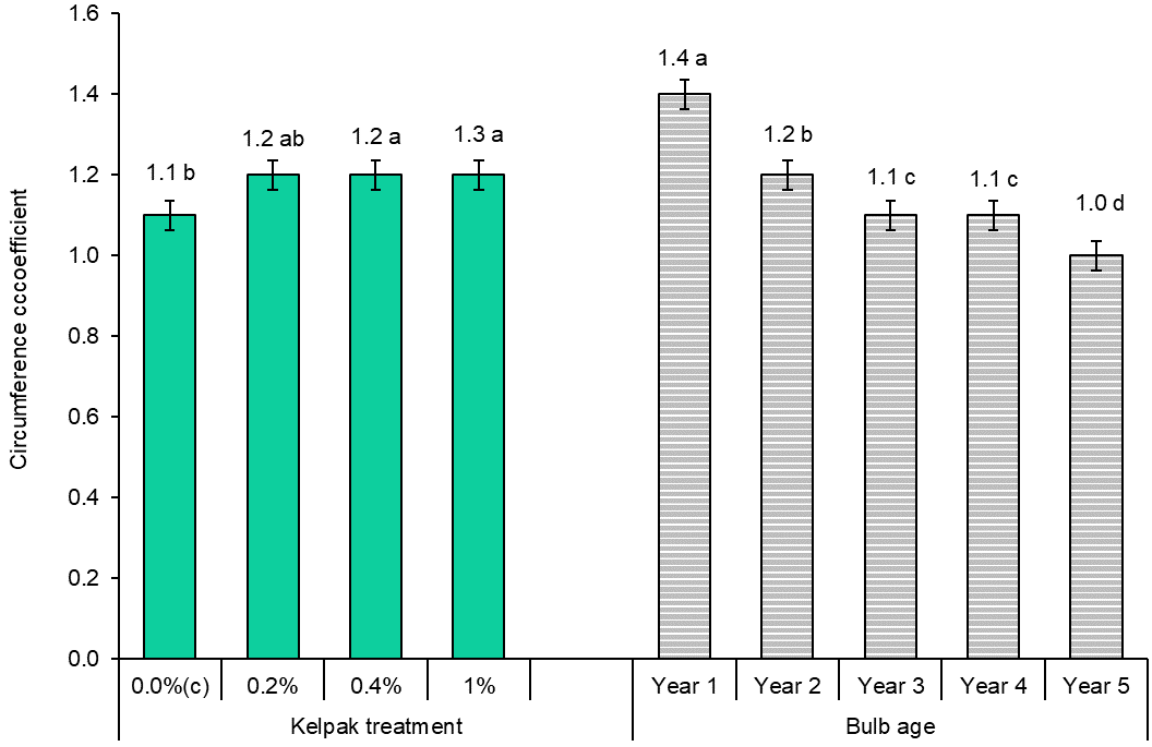

Figure 8.2: The circumference coefficient analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.4.1.2 Pre-plant bulb fresh weight and weight coefficient

Analysis of variance of the factorial interaction of Kelpak® treatments and bulb age demonstrated significantly different ($p \leq 0.05$) responses in the pre-plant bulb fresh weight. The preliminary evaluation found greater biomass in the oldest bulbs from the onset, whereas in bulbs classified in the first four years of cultivation, no statistically marked differences were observed (Table 8.2). The weight coefficient in response to treatment combinations showed a statistically significant similarity of improved growth as bulbs were heavier than their initial accumulated weight. The younger bulbs in years 1 and 2 had the highest coefficient when treated with the higher Kelpak® applications of 0.4 and 1%, respectively. In all treatment combinations, the coefficient was greater than the corresponding control within each year. Moreover, as the age of the bulb increased, an overall decline in the weight coefficient was seen, with the 1% Kelpak®–year 5 treatment presenting the lowest overall value (Figure 8.1; Table 8.2).

As shown in Figure 8.3, the bulb weight coefficient was further assessed unrelated to the Kelpak® treatments and bulb age for a more thorough analysis. A significant increase in bulbs treated with Kelpak® was found with the optimum weight coefficient observed in the 0.4% and 1% (4.5) treatment applications, markedly 1.6 times greater than the 0% (2.8) use of tap water. The weight coefficient decreased significantly as the comparative bulb age increased. Notably, the response was particularly marked for bulbs in year 1 (5.7) with an approximate three times higher coefficient than year 5 (1.8).

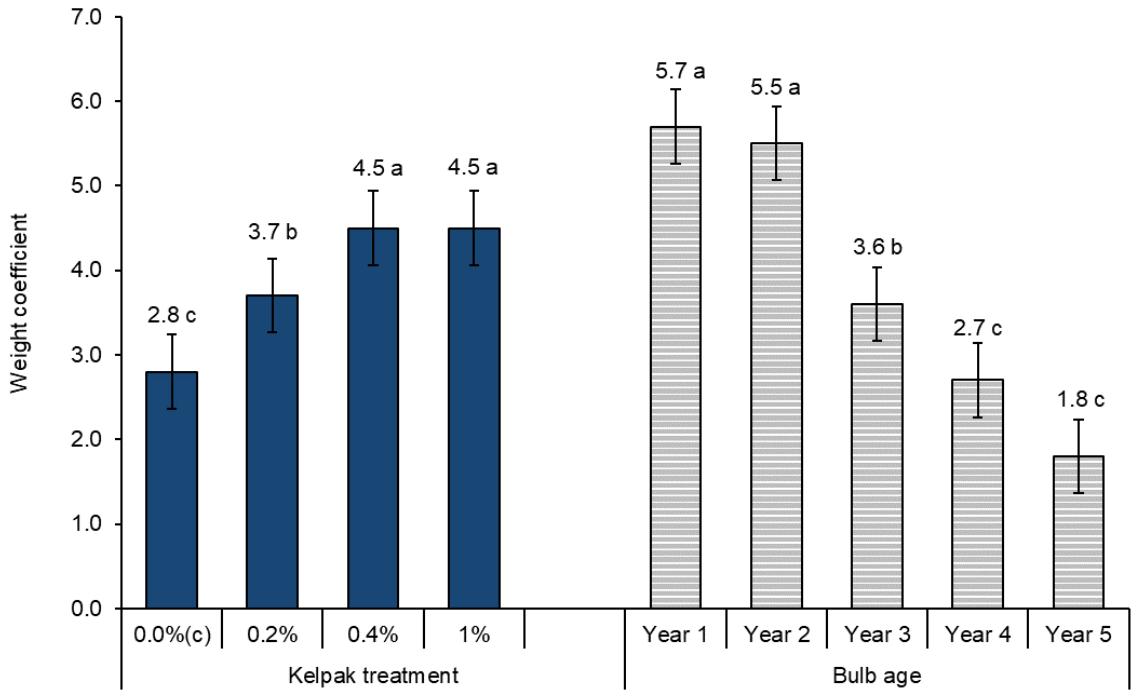

Figure 8.3: The weight coefficient analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.4.1.3 Number of roots

The combination of Kelpak® and bulb age factors found a significantly pronounced difference in the number of contractile roots initiated at a 95% confidence level. Root numbers were highest in Kelpak®-treated bulbs categorised in year 5, whereas minimal statistically marked variations were observed in bulbs from years 1 through 4 (Figure 8.4; Table 8.2).

In establishing a systematic representation, the main effects of Kelpak® treatments and bulb age were independently evaluated (Figure 8.4; Table 8.2). Kelpak® treatment comparisons promoted the induction of significantly more roots, with the higher concentrations of 0.4% and 1% producing 6.2 and 6.5 roots, respectively. The 0% tap water treatment recorded the lowest root formation (5.8); however, it was statistically negligible compared to the 0.2% (5.9) treatment. The results of bulb age displayed a significantly higher number of newly generated roots in the year 5 cultivated bulbs compared to the bulbs in years 1 through 4, which exhibited statistically similar tendencies.

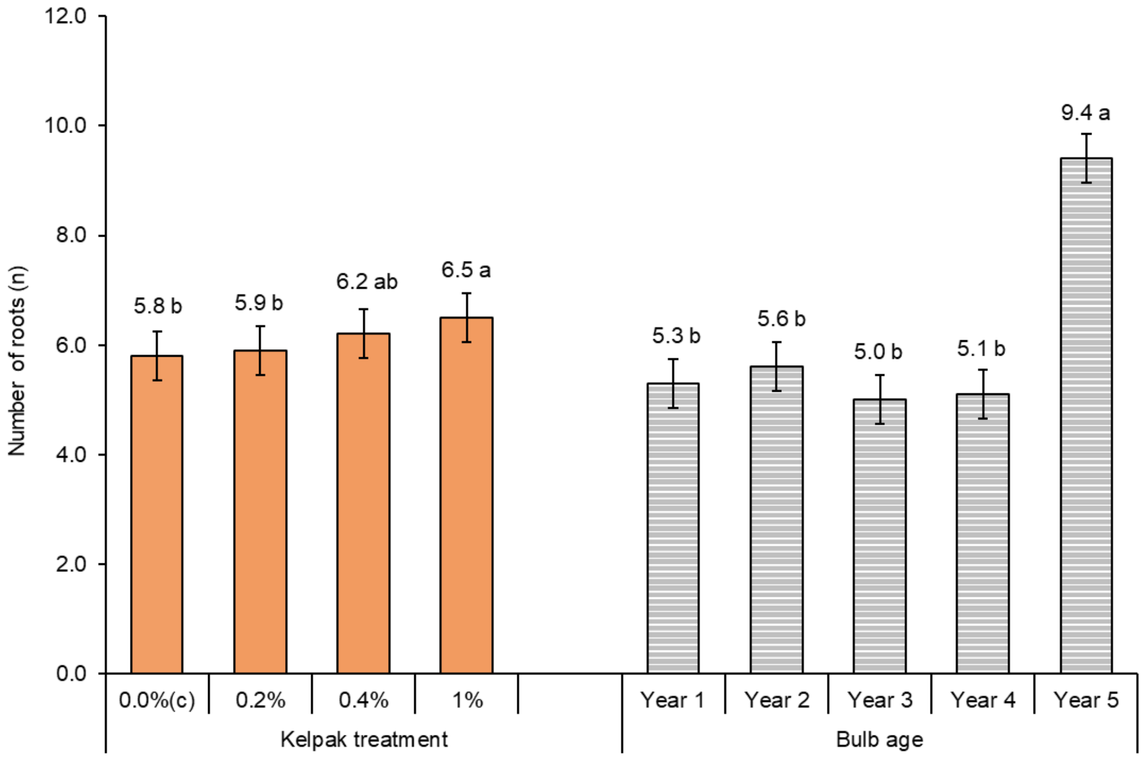

Figure 8.4: The number of roots analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.4.1.4 Root length

Significant variability ($p \leq 0.05$) was observed when the factorial interaction of Kelpak® dilutions and bulb age on the length of bulb roots was evaluated. Newly cultivated and treated bulbs in years 1 and 2 had markedly shorter (6.1–9.7 cm) root lengths compared to the older bulbs in years 3, 4, and 5 (10.1–31.4 cm), with the year 5 bulbs producing the longest roots (Figure 8.4; Table 8.2).

The results of the root length extension, irrespective of Kelpak® treatments and bulb age, as presented in Figure 8.5, showed otherwise. Root length was unaffected ($p > 0.05$) by the dilutions of Kelpak®, and the soil drench applications did not augment this characteristic bulb feature (Figure 8.5; Table 8.2). However, the longest roots were observed in the 0% control application (15.2 cm). In contrast, an age-dependent significant variation was seen in the oldest bulbs in year 5, exhibiting the longest roots (26.9 cm) compared to the shortest ones (7.6 cm) observed in the bulbs from the first two years of cultivation.

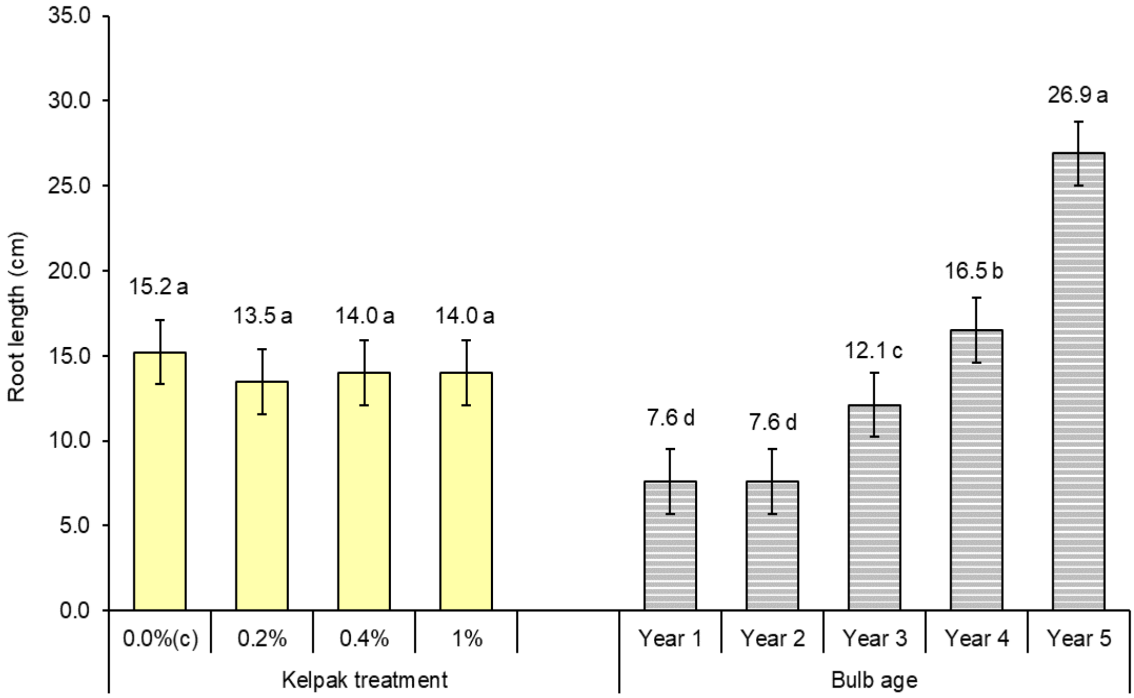

Figure 8.5: The root length analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.4.1.5 Number of leaves

Evaluating the interactive effect of Kelpak® treatments and bulb age, a significant difference was found in the number of leaves formed, where the oldest Kelpak® treated bulbs produced the greatest number of leaves (6.6–7.2) in comparison to those treated from the first year of cultivation (2.6–2.7) (Table 8.3).

Analysis of the autonomous results of the main effects showed that the formation of leaves in Kelpak® treated bulbs significantly increased in a concentration-dependent manner (Figures 8.6 and 8.7; Table 8.3). Compared to the 0% application (3.8), the 1% dosage yielded the most leaves (4.6). The number of leaves increased significantly within bulb age, with the oldest bulbs in year 5 producing more leaves (6.9) than their younger counterparts (2.6–4.5).

Table 8.3: Interactive effects of Kelpak® dilutions and bulb ages on the leaf characteristics and chlorophyll content of *A. belladonna* bulbs

Bulb age	Kelpak® treatment	Leaf characteristics				
		Number of leaves (n)	Leaf length (cm)	Leaf width (cm)	Leaf Area (cm^2)	Chlorophyll content (mg/m^2)
Year 1	0.0% (control)	2.6 ± 0.16 f	29.2 ±1.99 c-g	0.7 ± 0.03 f	19.7 ± 1.79 de	284.6 ± 23.70 cef
	0.2%	2.6 ± 0.16 f	27.4 ± 1.63 d-g	0.7 ± 0.03 f	18.4 ± 1.35 e	218.6 ± 14.30 ef
	0.4%	2.6 ± 0.16 f	9.4 ± 0.96 c-g	0.7 ± 0.03 f	20.2 ± 1.16 de	405.2 ± 5.95 abc
	1%	2.7 ± 0.15 ef	30.7 ± 1.31 b-g	0.7 ± 0.03 f	19.9 ± 1.18 de	393.8 ± 36.20 a-d
Year 2	0.0% (control)	2.8 ± 0.16 def	27.8 ± 1.72 d-g	0.7 ± 0.03 f	18.4 ± 1.94 e	279.6 ± 26.00 def
	0.2%	3.1 ± 0.18 def	29.6 ± 1.72 c-g	0.8 ± 0.04 ef	22.4 ± 1.94 cde	268.0 ± 26.00 ef
	0.4%	3.1 ± 0.14 def	31.3 ± 1.64 a-f	0.7 ± 0.03 f	21.3 ± 1.57 cde	307.4 ± 24.50 b-e
	1%	3.4 ± 0.22 c-f	31.3 ± 1.38 a-f	0.7 ± 0.05 ef	23.3 ± 2.35 cde	420.2 ± 19.30 ab
Year 3	0.0% (control)	3.2 ± 0.13 c-f	23.9 ± 0.67 g	0.9 ± 0.04 def	20.9 ± 2.26 cde	213.4 ± 19.50 ef
	0.2%	3.9 ± 0.23 cd	27.1 ± 1.41 efg	0.9 ± 0.05 def	25.0 ± 1.71 cde	210.8 ± 43.60 ef
	0.4%	3.5 ± 0.22 c-f	31.0 ± 1.06 a-f	1.1 ± 0.04 bcd	34.6 ± 2.25 bcd	240.4 ± 12.00 ef
	1%	4.3 ± 0.21 bc	34.4 ± 1.02 a-d	1.0 ± 0.05 cde	34.6 ± 1.98 bcd	397.6 ± 12.60 a-d
Year 4	0.0% (control)	3.6 ± 0.16 c-f	24.7 ± 1.21 fg	1.0 ± 0.05 cde	25.3 ± 2.21 cde	224.6 ± 4.65 ef
	0.2%	3.8 ± 0.20 cde	28.4 ± 0.89 c-g	1.2 ± 0.07 bc	36.1 ± 1.99 bc	185.6 ± 21.90 f
	0.4%	5.1 ± 0.23 b	33.8 ± 1.27 a-e	1.3 ± 0.07 bc	44.1 ± 3.78 b	246.4 ± 15.50 ef
	1%	5.4 ± 0.16 b	32.5 ± 1.07 a-e	1.3 ± 0.04 b	43.2 ± 2.45 b	429.0 ± 19.10 a
Year 5	0.0% (control)	6.8 ± 0.36 a	37.8 ± 1.69 a	2.2 ± 0.08 a	85.5 ± 6.33 a	208.6 ± 28.00 ef
	0.2%	7.2 ± 0.36 a	33.1 ± 1.24 a-e	2.2 ± 0.13 a	73.32 ± 6.45 a	254.6 ± 25.00 ef
	0.4%	6.6 ± 0.16 a	35.0 ± 1.66 abc	2.1 ± 0.09 a	73.0 ± 4.47 a	250.4 ± 28.00 ef
	1%	7.2 ± 0.33 a	37.2 ± 1.19 ab	2.3 ± 0.07 a	85.8 ± 3.43 a	396.4 ± 22.90 a-d
Two-way ANOVA *F*-Statistic						
Kelpak® treatment		11.49 *	13.03 *	3.58 *	6.38 *	5.86 *
Bulb age		245.48 *	16.89 *	469.41 *	268.01 *	61.32 *
Kelpak® × Bulb age		3.53 *	2.95 *	2.28 *	3.41 *	2.73 *

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 Tukey's least significant difference test; ns = not significant.

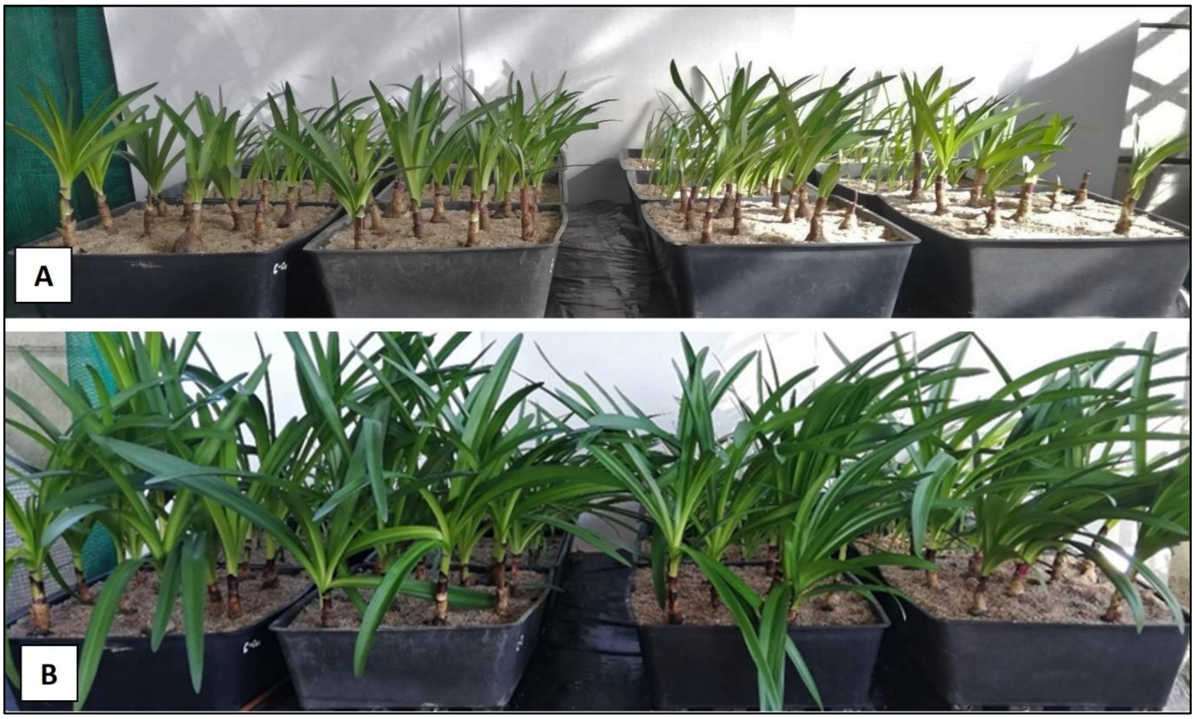

Figure 8.6: The visible effects of Kelpak® concentration dilutions on leaf expansion and development in a series of five growing seasons (age) of *A. belladonna* bulbs after 8 weeks (A) and 13 weeks (B) (Photos: C Wilmot)

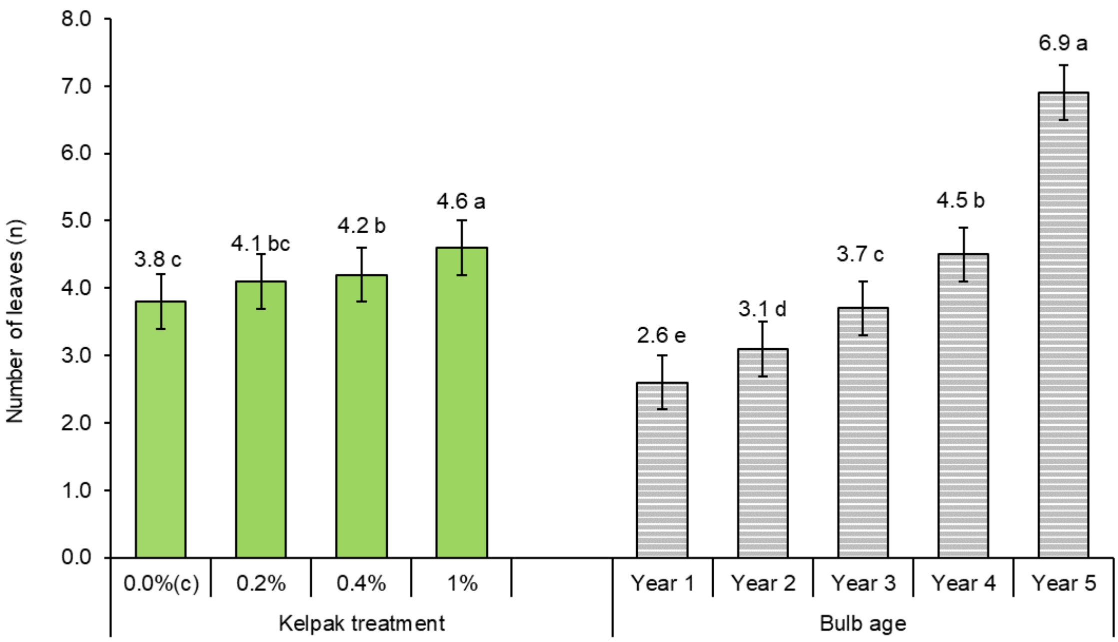

Figure 8.7: The number of leaves analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.4.1.6 Leaf length, leaf width, and leaf area

The extension of leaf length in treated bulbs varied significantly *($p \leq 0.05$)* when the factorial combination of Kelpak® treatments and bulb age was examined. Leaf length across treatment interactions ranged from 24.7 to 37.8 cm. Bulbs treated with 0.4% and 1% Kelpak® dilutions typically performed better (Table 8.3). The interaction of factors significantly enhanced the response of leaf width expansion. Compared to their younger counterparts (years 1 and 2), whose leaves expanded to a maximum width of 0.7 cm, the oldest bulbs in year 5 exhibited the broadest leaf primordia, measuring more than 2 cm when treated with Kelpak® (Table 8.3). Considering the leaf area, a significant interaction between Kelpak® treatments and bulb age was observed, with the older treated bulbs in year 5 (73.0–85.8 cm^2) producing a larger surface area in comparison to the younger cultivated bulbs in years 1 and 2 (18.4–23.3 cm^2) (Table 8.3).

Significant variations were observed in the leaf area when the main effects were evaluated independently (Figures 8.6 and 8.8; Table 8.3). When comparing Kelpak® applications, the lower 0%, 0.2%, and 0.4% concentrations presented smaller numerical values (34.0–38.7 cm^2) than the 1% application (41.4 cm^2). The leaf area decreased significantly as the relative age of the bulbs advanced, with those in years 3, 4, and 5 invariably 1.3–4.0 times greater than those in years 1 and 2, respectively.

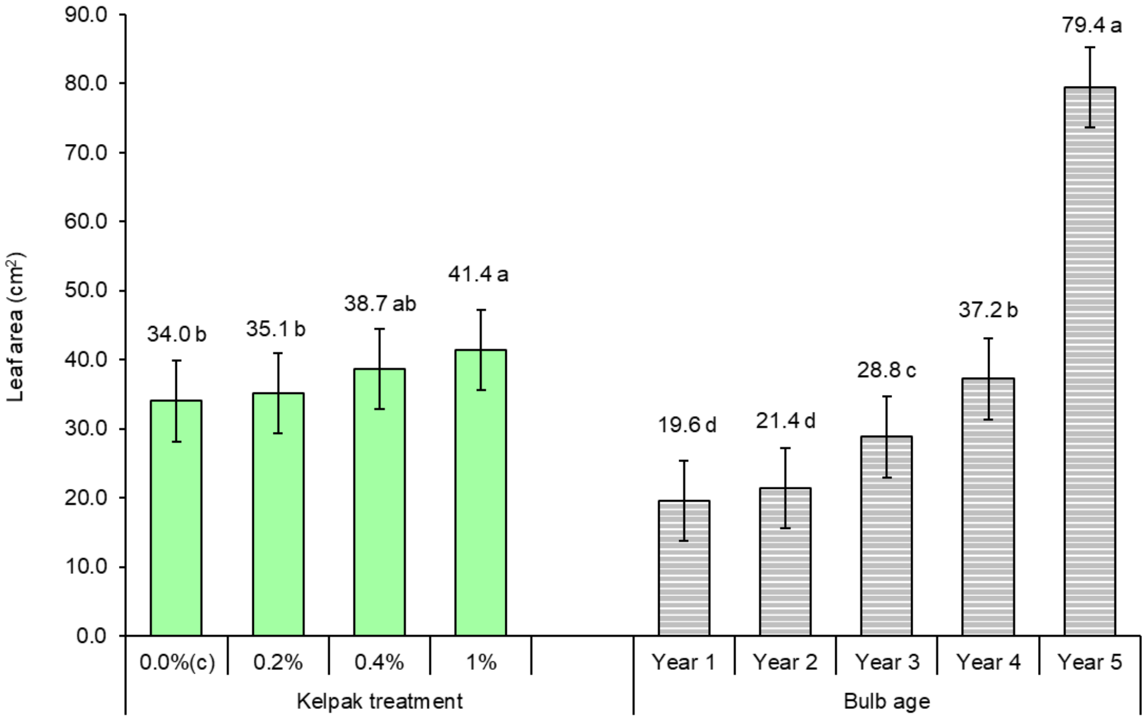

Figure 8.8: The leaf area analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.4.2 Effect of Kelpak® treatments and bulb age on chlorophyll content

8.4.2.1 Chlorophyll content

At a 95% confidence level, the combined effect of Kelpak® and bulb age on the presence of chlorophyll found in the regenerated leaf blades was significantly enhanced. Compared to the untreated bulbs, applying 1% Kelpak® produced a markedly higher chlorophyll content in the leaves in all five bulb age groups (Table 8.3).

Considering the autonomous monitoring of Kelpak® treatment and bulb age, Kelpak® comparisons significantly enhanced the chlorophyll synthesis in bulb leaves in a concentration-dependent manner (Figure 8.9; Table 8.3). The highest Kelpak® dilution application of 1% (407.4 mg/m^2) resulted in an optimal chlorophyll content per unit area, an almost 1.7-fold improvement over the 0% (242.2 mg/m^2) soil drench. With the progressive ageing of the bulbs, the accumulated chlorophyll content in the regenerated leaves significantly decreased. Bulbs in year 1 accumulated the highest concentration (325.6 mg/m^2), which was only marginally greater than the bulbs in year 2 (318.8 mg/m^2). In comparison, the oldest cultivated bulbs in year 5 recorded the lowest chlorophyll value (265.6 mg/m^2) (Figure 8.9).

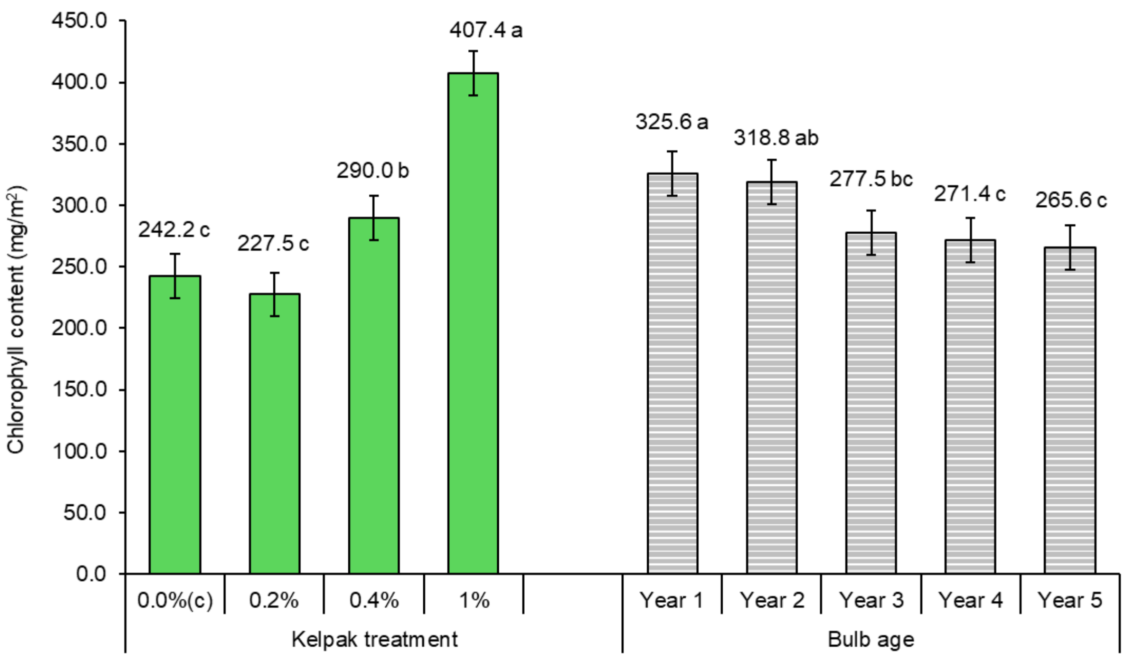

Figure 8.9: The chlorophyll concentration analysed irrespective of bulb age and irrespective of Kelpak® treatment. Bars represented by mean values followed by different letter(s) are significantly different at $p \leq 0.05$ based on Tukey's least significant difference test

8.5 Discussion

Several studies have demonstrated the innumerable, all-round benefits of seaweed extracts and their improvement on nutrient signalling, root system enhancement, crop optimisation, yield, and tolerance to abiotic and biotic stresses in plant systems (Calvo *et al.*, 2014; Battacharyya *et al.*, 2015; Ali *et al.*, 2021a). In addition, improved seed germination yield, reduced seed dormancy, seedling establishment, transplant shock, flowering, fruit palatability and quality, increased chlorophyll production and foliage area, delayed senescence, improved storage ability and resistance to pests and pathogens have been reported (Sharma *et al.*, 2014; Li & Mattson, 2015; Kapur *et al.*, 2018; Ali *et al.*, 2019).

This study observed the beneficial impact of Kelpak® applications in monitoring bulbs' morphological and physiological characteristics from five consecutive seasons (age) and their interactions over 24 weeks. Even at low concentrations, Kelpak® treatments enhanced the responses in both the bulb aerial and, more substantially, the underground storage organs in a concentration-dependent manner. These findings substantiate those of Robertson-Andersson *et al.* (2006), Papenfus *et al.* (2013), and Michalak *et al.* (2017), who found that the concentration of seaweed extracts affected their efficiency, and in most instances, low concentrations augmented plant developmental characteristics. The low concentrations further support Duncan’s (2010) claim that indigenous bulbous species benefit from low Kelpak® application levels.

Contractile roots are an important component of geophytes because, upon contraction, the fleshy roots effectively enable them to lower themselves deeply into the earth and provide support during seasons of overwintering and adversity (Halevy, 1986; Warrington *et al.*, 2011). Furthermore, root formation improves bulb longevity and survival (Kharrazi *et al.*, 2017). Although root length remained unaffected, the contractile roots increased due to treatment applications. Kelpak® was also found to shorten the root length in *Eucalyptus* species (Van Staden *et al.*, 1995) and increase the root density of *Tagetes erecta* (Crouch & Van Staden, 1991). In contrast to these findings, Adams *et al.* (2019) found that Kelpak® treatments enhanced root length while minimising fresh root weight in *E. verticillata*.

The highly active photosynthetic processes in chlorophyll-rich leaves are evidenced by a plant's robust physiological response of increased chlorophyll concentration, visibly enhanced greenness, and observable delays in leaf senescence (Adams & Langton, 2005; Wang *et al.*, 2005). This study found these mechanisms at the higher levels of Kelpak® applications. Furthermore, the increased number of leaves, leaf area, longer duration of vegetative growth, and thus a greater timeframe of carbohydrate accumulation, as demonstrated by the larger bulb circumference and weight coefficients after treatments, support this. Peng *et al.* (1991)

found that faster vegetative development and higher biomass production are the outcomes of improved photosynthetic effectiveness. Similarly, Byczyńska (2018) found that pre-soaking *E. bicolor* bulbs in an SWE before planting improved development, flowering, yield, and increased number of leaves and chlorophyll content upon harvest.

With the advanced ageing of bulbs over five consecutive years, the research findings of treatment applications elicited a culmination of stimulatory, neutral, and inhibitory responses. Considering the natural progressive morphological processes modulated by the indicative age of bulbs and resumed growth each season, bulbs from year 5 habitually had the highest values of pre-plant bulb fresh weight and circumference, root length and number, and leaf length, width, and area and number in comparison to their younger counterparts in an age-dependent manner. These findings support work by Halevy (1990) and Langens-Gerrits *et al.* (2003) that decreased morphological trait values indicate plant age and juvenility. According to De Hertogh & Le Nard (1993) and Kapczyńska (2019), the number of leaves and the relation to plant juvenility are closely linked. Moreover, the duration of the non-flowering juvenile phase to reach a critical bulb size varies by genus, species, and even cultivar (De Hertogh & Le Nard, 1993) and is further influenced by the surrounding environmental growth conditions (Du Toit *et al.*, 2001; Khodorova & Boitel-Conti, 2013; Kapczyńska, 2014; Anderson, 2019).

In further examination of the bulb circumference and weight coefficients to Kelpak® treatments, bulbs in years 1 and 2 were the most responsive. As a species with a tunicate bulb, the dry, papery tunic protects the bulb from desiccation by improving water retention and mechanical damage (Al-Tardeh *et al.*, 2008). These membrane-forming exterior scales shield the continuous lamina of interior fleshy scales that are tightly pressed together (Mishra, 2005). The coefficient gains found in bulbs from years 1 and 2 suggest that the membranous tissues of the younger juvenile bulbs were significantly more permeable, and therefore, more receptive to treatment applications, which presumably explains the stimulatory effect and synthesis of exogenous Kelpak® and the presence of phytohormones in bulb growth and development. However, the weight coefficient produced results with greater dynamics than the circumference coefficient. Seaweed extracts routinely accelerate and promote the growth, differentiation, and synthesis of new proteins in plant cells (El-Sheekh *et al.*, 2016). Similar stimulatory effects of both the aerial and subterranean organs were observed in four-month-old juvenile bulb seedlings of *E. autumnalis* (Aremu *et al.*, 2016). Furthermore, it was found that active surface areas and bulb sizes of species were enhanced by the compounds isolated from the seaweed *E. maxima* (Aremu *et al.*, 2015). The early establishment of strong genotypes from conceivably unknown genetic backgrounds, uniformity, and increased yields are required to meet bulb grading standards for commercial purposes (Anderson, 2006; Barnhoorn, 2013;). The coefficients may support the quantitative expression of these quality attributes as a selection tool for achieving these outcomes. Further evidence of the stimulatory impact and receptivity of younger bulbs to treatment applications emerged from the findings of increased chlorophyll content in proportion to leaf area. The juvenile bulbs in years 1 and 2 had reduced leaf surface areas and higher chlorophyll levels, which was the exact opposite of the older bulbs, which had higher leaf areas and reduced levels of chlorophyll.

Although the circumference and weight coefficients, as well as chlorophyll content, were significantly lower in the older bulbs of years 3, 4, and 5, they were compensated for by the relatively higher root number, root length, leaf number, leaf length, width, and area, which indicated the time and energy required to regenerate new growth and development after replanting. This finding is further supported by visual observations of above-ground leaf development in older bulbs, specifically those in year 5, which were the last to show signs of leaf growth and expansion. According to Stancato *et al.* (1995) and Khodorova and Boitel-Conti (2013), during the initial stages of recommenced growth, bulbs consume stored nutritional reserves in the form of carbohydrates to support the regenerative growth of roots and shoots, which results in a reduction of size, biomass, and firmness; however, once this is attained, the expansion of bulb organs begin to increase due to photosynthetic activities. The regeneration and accumulation of carbohydrates thus determine the precise sequence of dormancy, development, and flowering (Miller, 1992). Similar delayed growth and subsequent development findings were found in replanted bulbs of *Hippeastrum* hybrids (Stancato *et al.*, 1995; Andrade-Rodríguez *et al.*, 2015) and *Nerine sarniensis* (Warrington *et al.*, 2011). The disruption of bulb growth and the time allotted for rejuvenation support Duncan's (2010) recommendations that frequent lifting and replanting of *A. belladonna* bulbs should be limited to avoid disturbing this slow-growing species. Furthermore, the bulb should be cultivated as a perennial crop like that of *N. sarniensis* (Warrington *et al.*, 2011), with lifting performed after 4–6 years or when the bulbs become overcrowded (Duncan 2010).

According to Ali *et al.* (2021b), SWE administration enhanced growth and development at all plant stages, including harvest and post-harvest. The finding supports this study's results, demonstrating enhanced growth in all five age groups. In furthering research, it may be beneficial to investigate whether administering potentially higher concentrations of Kelpak® to older bulbs will result in more effective geophilic structural size and vigour outcomes. Kelpak® dilutions of up to 5% in *E. autumnalis* (Aremu *et al.* 2016) and 10% in three *Eucalyptus* species were efficacious (Van Staden *et al.*, 1995).

The juvenile bulbs, particularly the younger samplings, exhibited improved underground bulbing capabilities and root system architecture following treatment applications. It is, therefore, probable that Kelpak® would not only elicit phyto-stimulatory qualities but also improve the phyto-elicitor activity by inducing responses that would have enabled them to withstand the severe climatic conditions of drought, high temperatures, and salinity during the dormancy period (Battacharyya *et al.* 2015; Drobek *et al.* 2019; Stirk *et al.* 2020; Ali *et al.* 2021a). Van Staden *et al.* (1995) and Aremu *et al.* (2012) advocate investigating propagation and cultivation strategies that promote early plant optimisation and performance that potentially afford them a greater chance of survival and adaptation to circumstances within the environment during acclimatisation and nursery production. Using seaweed extracts facilitates a simple and affordable multipurpose cultivation technique for commercial and small-scale farmers (Van Staden *et al.*, 1995; Aremu *et al.*, 2016; Makhaye *et al.*, 2021). Moreover, plants respond favourably to treatments as early as 10–14 days after administration (Arioli *et al.* 2015).

Before widespread implementation is adopted, it is essential to assess bulbs' susceptibility to treatment regimens (Warrington *et al.*, 2011). Furthermore, since ornamental bulbs have very diverse behaviours and responses to outside influences, it is crucial to understand their specific growth and physiological developmental cycles (Theron & De Hertogh 2001; Kleynhans 2006; Khodorova & Boitel-Conti 2013; Kamenetsky-Goldstein 2019; Kapczyńska & Stodolak 2019). This was evident in the study, in which older bulbs responded differently to treatment applications than their younger counterparts. While the recommendations are commendable, the species responses and the receptive effects of age during cultivation must be evaluated as part of ongoing cultivation efforts and LCA to optimise bulb plant material for sustainable commercial planting and production.

8.6 Conclusion

This study concluded that exogenous applications of Kelpak® given as a soil drench at various ages significantly improved the morphological and physiological responses in juvenile *A. belladonna* bulbs. In a concentration-dependent manner, the low-dosage treatments increased the phyto-stimulatory responses of both the bulb aerial and, more evidently, the below-ground storage organs. The bulb circumference, weight coefficients and chlorophyll content evaluation identified bulbs in years 1 and 2 as the most receptive to treatment applications. Furthermore, this study established the significance of the morpho-physiological responses of the species to Kelpak® treatment and the receptive impact of age during cultivation. A 1% Kelpak® concentration dilution administered during early developmental stages within the first two years is the most advantageous priority for maximising this slow-growing species' proliferation rate. Based on these findings, further investigative research on these aspects is relevant to fully elucidate and broaden the mechanism of action and species receptivity to Kelpak® treatments.

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CHAPTER 9

REGULATED ROOT ZONE WATER TEMPERATURES AND SOILLESS MEDIA IMPROVE BULB YIELD AND OFFSET PRODUCTION OF HYDROPONICALLY CULTIVATED *AMARYLLIS BELLADONNA* L.

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REGULATED ROOT ZONE WATER TEMPERATURES AND SOILLESS MEDIA IMPROVE BULB YIELD AND OFFSET PRODUCTION OF HYDROPONICALLY CULTIVATED *AMARYLLIS BELLADONNA* L.

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9.1 Abstract

The protracted natural bulb growth rate and offset generation constrain the timely expansion of bulbs in Amaryllis belladonna. An 18-month experiment was conducted to determine the efficacy of different root zone water temperatures and soilless media on the bulb yield and offset production of A. belladonna cultivated in a deep water culture hydroponic system. The study comprised dormant juvenile bulbs that were planted in plastic cavity trays filled with soilless media and suspended in heated water reservoirs at different temperatures (16 °C control, 22 °C, 28 °C, and 34 °C). The results found that the autonomous analysis of water temperatures, as opposed to soilless media and the combination, was significant. Warm root zone water temperatures ranging from 16 °C to 28 °C resulted in comparable aerial and subsurface morphological growth and development, promoting the vegetative proliferation of larger juvenile mother bulbs and offset induction. However, an excessively high temperature of 34 °C proved injurious and depleting. The results infer that the intrinsic processes for 'bulbing' were synchronised under inducive extrinsic hydroponic stimuli. A water temperature of 22 °C is recommended for long-term, sustainable production of simultaneously generating optimum reclaimable bulbs and offset generation to abridge the timeous cultivation of continuous A. belladonna vegetative bulb stock.

Keywords: Amaryllidaceae, deep water culture, hydroponics, geophyte, offset induction, water temperature

9.2 Introduction

Geophytes are a diverse classification of flora, and their collective multiplicity is intensifying owing to ubiquitous market changes, competitive demands (Anderson, 2006, 2019; Slezák *et al*., 2020) and the breeding of new cultivars with specialised and desired features (Marasek-Ciolakowska *et al*., 2021). Important scheduling ramifications to advance economic profitability are affected by selected bulb species, tubers and novel cultivars or hybrids with prolonged juvenile phases ranging between 8 to 25 years (Marasek-Ciolakowska *et al*., 2021). Thus, understanding and insight into a geophytic species' behavioural traits are critical to its advancement and provide tools for forecasting and implementing innovative strategies to determine responses under competitive and stringent conditions (Thompson *et al*., 2011; Kamenetsky-Goldstein, 2019; Slezák *et al*., 2020; Marković *et al*., 2021). Present geophytic research initiatives include those centred on vegetative propagation (Marković *et al*., 2021), a progressive decrease of the juvenile period, early selection of desired features (Anderson 2019; Marasek-Ciolakowska *et al*., 2021) and the procurement of indigenous and underutilised species (Reinten & Van Wyk, 2018; De Pascale & Romano, 2019; Darras, 2021).

Global ornamental cultivation practices have greatly revolutionised sophisticated agricultural practices to alleviate adverse conditions during the last three decades (Darras, 2020, 2021). The regulated regimen of hydroponic technology allows for the precise management and use of long-term environmental conditions and inert soilless media transversely over multiple latitudinal regions. This results in widespread year-round production and enhanced crop yields per unit area (Wahome *et al*., 2010; Karagöz *et al*., 2022). Although the initial hydroponic investment is habitually capital-intensive and necessitates skilled personnel and technical expertise, the benefits of quantity and quality assurance, ubiquity, space efficiency, and economic outputs outweigh the costs (Karagöz *et al*., 2022; Velazquez-Gonzalez *et al*., 2022). Likewise, sustainability is realised in a species' life cycle assessment (LCA) with improved cultivation techniques (Darras,2020, 2021). Optimisation of various cereal, condiment, flower, fodder, fruit, medicinal, ornamental, and vegetable crop yields in hydroponic cultivation has been extensively investigated (Fussy & Papenbrock, 2022; Velazquez-Gonzalez *et al*., 2022). However, geophytic optimisation has primarily been used to promote flower-forcing events with little evidence of augmenting vegetative (asexual) plant material. This includes but is not limited to *Crocus, Hippeastrum, Hyacinthus, Leucojum, Lilium, Narcissus* and *Tulipa* species flower-forcing (Miller, 2012; Schroeder *et al*., 2020). In contrast to market quality collections of iterative breeding and flower forcing, hydroponic cultivation may promote the vegetative proliferation of certain geophytic dispositions in readily available cultivars, hybrids, heritage, imperilled, and underutilised species (Wilmot & Laubscher, 2023).

Notwithstanding, in field and greenhouse conditions, the aboveground and subsurface thermoperiodic temperatures are imperative in maintaining a plant species' cardinal range while minimising potential harm from greater or sub-optimal variations affecting the biochemical rate of many morphological and physiological activities of the rhythmic cycles of geophytic cultivation (Du Toit *et al*., 2002; Yan *et al*., 2013; Proietti *et al*., 2022). These activities include but are not limited to, water and nutrient absorption, translocation, transpiration, chlorophyll production and photosynthesis, metabolite accumulation and synthesis (Seiler, 1998; Zobayed *et al*., 2005; Sakamoto & Suzuki, 2015). Among several approaches, the modification of climatic factors is most prevalent. As such, before planting or cultivating a new crop, growers should determine the species' optimal production temperatures that govern plant development (Carlson & Dole, 2015). Substantial research has been undertaken on manipulating root zone temperatures to retain actively developing plant crops outside their precedented life cycle to sustain market needs (Wang *et al*., 2016; Balliu *et al*., 2021; Proietti *et al*., 2022).

Amaryllis belladonna L. (Amaryllidaceae) is an autumn flowering hysteranthous endemic geophyte to the Western Cape, South Africa's fynbos biome (Manning *et al*., 2002; Duncan *et al*., 2020). The species' adaptability, tenacity and attractive beauty have permitted it to be naturalised in several Mediterranean locations, displaying the transient, pink-shaded florets on a seasonal single-harvest inflorescence (Adams 2001; Reinten *et al*., 2011; Wilmot & Laubscher, 2019a; Gul *et al*., 2020). Irrevocably, emphasis and differentiation are placed on its economic significance as containerised flowering potted plants or as fragrant cut flowers lasting up to a week or longer in floral arrangements (Theron & De Hertogh, 2001; Reinten *et al*., 2011; Barnhoorn, 2013; Gul *et al*., 2020; Darras, 2021). The species has likewise garnered scientific attention and use within the pharmacological arena because of its isolated alkaloid constituents, some of which exhibit anti-bacterial, anti-fungal, anti-neoplastic, and anti-parasitic properties (Pettit *et al*., 1984; Evidente *et al*., 2004; Nair *et al*., 2013; Chavarro *et al*., 2020; Evidente, 2023). The hysteranthous species' perennial bulb growth, development and maturation are contingent upon the subterranean storage organs to amass sufficient carbohydrates from seasonal winter aerial growth through summer dormancy to flowering under inductive environmental stimuli (Dafni *et al*., 1981; Howard & Cellinese, 2020). However, encountered in many other geophytes and typified in Amaryllidaceae species (Manning *et al*., 2002; Duncan *et al*., 2020), *A. belladonna* has a prolonged natural juvenile bulb growth rate that necessitates several years to attain a competent adult reproductive flowering size and minimised replication in which the mother bulb divides, inducing offsets (daughter bulbs) (Theron & De Hertogh, 2001; Duncan, 2010). Moreover, premature offset detachment further hinders future development (Duncan, 2010). These traits debilitate the potential and timeous expansion of *A. belladonna* to produce a competent flowering size and continual quality bulb stock material for local and export floriculture and horticultural endeavours.

Considering the preceding, it is plausible to abridge the life cycle of *A. belladonna* and enhance the species' growth and multiplication in a cost-effective, eco-friendly, and timely manner. There has been no research using hydroponic technology to improve the shortcomings of phenotypic vegetative features in the *A. belladonna* species. As a result, the ideal method for increasing the species from the mother bulb material remains unknown as seed propagation produces varied genetic offspring, and traditional bulb cutting is time-consuming and costly (Duncan, 2010; Veeraballi *et al*., 2017). Therefore, to establish a novel method of inducing *A. belladonna* bulb offsets while simultaneously advancing the mother bulb's protracted juvenile phase, the efficacy of regulated root zone water temperatures and soilless media for *A. belladonna* bulbs cultivated in a deep water culture (DWC) hydroponic system was investigated.

9.3 Materials and methods

9.3.1 Experimental location

Experimentation was carried out from April 2020 to October 2022 (eighteen months) in the Cape Peninsula University of Technology's Department of Horticultural Sciences Research Greenhouse in Bellville, Cape Town, South Africa; 33°55'45" S, 18°38'31" E. The ventilated greenhouse was outfitted with a thermostatically controlled Envirowatch system (Envirowatch Solutions, Escourt, South Africa), fans, heaters, evaporative cooling pads, and clear polycarbonate roof sheeting to maintain a controlled and regulated greenhouse environment. Ambient greenhouse temperatures ranged between 16°C and 28°C during the day and 9°C and 14°C at night, with relative humidity (RH) ranging from 59-86%. The average daily photosynthetic photon flux density (PPFD) was 420 mol/m2/s, with an optimal light level of 1020 mol/m2/s recorded under natural light conditions.

9.3.2 Plant material and preparation

Eighty dormant juvenile *A. belladonna* bulbs (10–14 cm circumference, 3–5 cm diameter) were sourced from a commercial flower bulb company (Hadeco® (Pty) Ltd., Maraisburg, South Africa). The bulb and contractile roots were cleaned of any unnecessary debris. After 5 minutes of immersion in a 0.1% biocidal solution (Sporekill™, ICA International Chemicals (Pty) Ltd., Stellenbosch, South Africa) (active ingredient: didecyldimethylammonium chloride), the bulbs were removed and air-dried. Before planting and experimental treatments, the bulbs were stored in breathable crates in a darkened and ventilated room maintained at an ambient temperature of 18 ± 2 °C and RH of 40-60% for a week.

9.3.3 Experimental design and hydroponic setup

The experiment was carried out in a split-plot design with four specified heated water treatments, a control of 16 °C, 22 °C, 28 °C and 34 °C as the main plots, combined with one of two soilless growing media, LECA® (4-10 mm lightweight expanded clay aggregate) and pre-rinsed silica sand (Consol®, grade 6/17) as the sub-plots (Table 9.1 and Figure 9.1). Four identical and separately closed deep water culture (DWC) hydroponic systems were constructed. Each system comprised a 68 L black low-density polyethene (LDPE) plastic rough tote reservoir (620 × 410 × 425 cm, 2.33kg) (Addis 98310BK, Builders Warehouse, Boksburg, South Africa) placed at ground level. A thermostatically adjustable submersible aquarium glass heater (Eheim, Plochinger Str. 54, 733779 Deizisau, Germany) was installed to maintain each system's specified heated water temperatures. In addition, an electromagnetic air compressor (BOYU ACQ-003, Jungle Aquatics, Gauteng, South Africa) linked to two air stones (50 mm) was fitted in each system to increase the aeration of the static nutrient solutions, bubbling air at a rate of 50 L/min. Unlike shallower hydroponic systems, where temperature variations are difficult to mediate, large-volume closed deep water culture (DWC) systems permit error-buffering of solution temperatures in addition to the efficient use of water and fertilisers, reduced waste management contamination and increased recovery (Inden & Torres 2004; Viljoen *et al*. 2021; Velazquez-Gonzalez *et al*. 2022). Bulbs were randomly allocated and planted into individual growing cavities (250 mL) of a plastic cavity tray with one of two different soilless media, leca clay or sand, ensuring the bulb neck was visible at the surface (Duncan, 2010). Leca clay has several advantages, including its lightweight and porous character, capacity to maintain a neutral pH and thermal insulation of the roots (Boudaghpour & Nasir 2008). Sand, despite its high density, poor water retention, and sensitivity to salt build-up, provides the most sustainable and inexpensive plant-supporting medium with good porosity and a low carbon footprint (Olle *et al*., 2012; Fussy & Papenbrock, 2022). The plastic cavity trays were suspended in each tote reservoir and held by 10 mm wooden dowels to ensure the root zone depth (lower portion of the growing tray) remained immersed in the heated nutrient solutions and absent from the bulb basal plates (Figure 9.1). Ten bulb replicates (n=10) for each treatment combination were planted at a density of 20 bulbs per 0.2542 m^2 in the plastic cavity trays suspended in the reservoirs.

Table 9.1: Outline of the split-plot design consisting of eight treatment combinations of heated root zone water temperatures (main plot) and soilless media (sub-plot) in four separate closed deep water culture (DWC) hydroponic systems

	Leca clay (LC)		Silica sand (SS)	
DWC system 16°C (control)	SGT 1	16 °C + LC	SGT 2	16 °C + SS
DWC system 22 °C	SGT 3	22°C + LC	SGT 4	22°C + SS
DWC system 28 °C	SGT 5	28 °C + LC	SGT 6	28 °C + SS
DWC system 34 °C	SGT 7	34 °C + LC	SGT 8	34 °C + SS

DWC = deep water culture system; SGT = suspended growing tray

Figure 9.1: Visual representation of the split-plot experimental setup of juvenile *Amaryllis belladonna* bulbs grown in four identically closed deep water culture hydroponic systems with specified root zone water temperatures and soilless media in the greenhouse (Photo: C. Wilmot)

9.3.4 Nutrient solution preparation and monitoring

A hydroponically formulated granular fertiliser, Nutrifeed™, was prepared by dissolving 10 g/10 L of tap water in a 1:1000 (*w/v*) ratio for each treatment reservoir. The hydro-soluble fertiliser's chemical composition included macro- and micronutrients of N (65 g/kg), P (27 g/kg), K (130 g/kg), Ca (70g/kg), Cu (20 mg/kg), Fe (1500 mg/kg), Mo (10 mg/kg), Mg (22 g/kg), Mn (240 mg/kg), S (75 mg/kg), B (240 mg/kg), Zn (50 mg/kg) (Starke Ayres Pty, Ltd., Gauteng, South Africa). The pH and electrical conductivity (EC) were maintained during the treatment period using a calibrated hand-held digital pH meter (HM Digital PS PH-200) and EC and temperature meter (PS COM-100) (HM Digital Inc., Culver City, CA, USA 90230). The nutritional solution was kept at a pH between 5.5 and 6.5 and an EC between 0.5 and 1.2 mS/cm. The pH was adjusted using either sodium hydroxide (NaOH) to raise the pH or hydrochloric acid (HCl) to reduce the pH. Additional tap water or nutrient solutions were added when the EC fell below or above the required range. To further exclude changes in the nutrient solution due to plant absorption and evapotranspiration, volumes were monitored and maintained at a constant 60 L level in the reservoirs (Velazquez-Gonzalez *et al*., 2022). A waterproof data logger (HOBO MX 2201, Onset, Bourne, Massachusetts, USA) was used to record the water temperatures in all reservoirs at 60-minute intervals. To maintain an aseptic environment, Sporekill™, a biocidal solution containing the active ingredient Didecyldimethylammonium Chloride (ICA International Chemicals (Pty) Ltd., Stellenbosch, South Africa), was added (100 mL/100 L) to each tote reservoir at the commencement of treatments and at each interval when the solutions were renewed. In minimising nutrient concentration build-up and phytotoxicity and guarantee optimal solution productivity, planting trays were flushed, reservoirs were cleaned and sanitised, and aqueous nutrient solutions were replenished monthly (Fussy & Papenbrock, 2022; Velazquez-Gonzalez *et al*., 2022).

9.3.5 Data collection

9.3.5.1 Determination of the morphological parameters

Phenotypic data were recorded before, during and after post-harvest as indicators of bulb growth, development and regeneration using an electronic laboratory scale (Radwag® PS 4500.R2, Radwag Waagen, Hilden, Germany) with a 0.001g readability, a standard soft cloth metric tape measure (Empisal EMT-001, Builders Warehouse, Boksburg, South Africa) (1500 × 12 mm) and a standard metric retractable metal tape measure (Stanley Power Lock®, Builders Warehouse, Boksburg, South Africa) (450 × 25 mm).

Before planting, pre-treatment measurements of the individual mother bulb circumference and fresh weight were recorded to ensure consistency and reliability using the abovementioned measuring apparatus. Various observations and transitional measurements of the number of leaves, leaf length, width, and area were measured 24 weeks after initial leaf growth (2020-planting season and 2021-consecutive planted growth season) to determine the seasonal resumptive vegetative leaf development. Leaf length was measured as the length of the longest leaf from the base of the leaf, where it emerged from the mother bulb to the leaf apex. Leaf width was measured at the broadest mid-section of the same leaf. Leaf area was calculated using the Montgomery equation (ME) described by Yu *et al*. (2020) and Shi *et al*. (2021).

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

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

The treatment period was concluded, and the bulbs were harvested after leaf senescence to allow for natural nutrient reabsorption after the second growth season before bulb dormancy (Duncan, 2010; Barnhoorn, 2013). Before overnight air drying, the roots were gently rinsed with water to eliminate any soilless medium. The post-harvest mother bulb, offsets and roots were separated. The mother bulb circumference, fresh weight, number of offsets, offset fresh weight, and total root fresh weight were measured and recorded using the above measuring apparatus. In addition, calculations were made of the coefficients of mother bulb circumference (the ratio of the post-harvest bulb circumference to pre-plant circumference), mother bulb weight (the ratio of the post-harvest bulb weight to pre-plant weight) and the offset weight (the proportion of the post-harvest offset weight and the pre-plant mother bulb weight). The coefficients were calculated to determine the overall synthesis of bulb growth and development, a practical and supporting selection tool for achieving quantifiable performance standards, variability, and production objectives.

9.3.6 Statistical analysis

Phenotypic data were analysed using the Minitab 17 statistical analysis software (Minitab LLC, Pennsylvania State University, USA). The results were statistically evaluated using a two-way analysis of variance (ANOVA) for the variables, root zone water temperatures (4 levels) and soilless media (2 levels). Data are presented as mean values with standard errors (S.E.s). Tukey's LSD test further separated mean values at a $p \leq 0.05$ significance level.

9.4 Results

9.4.1 Pre-plant and post-harvest mother bulb circumference

The pre-plant mother bulb circumferential response in the elevated water temperatures was significant, according to the analytical findings of factors; however, the post-harvest response was significantly impacted ($p \leq 0.05$) by the interaction of water temperature and soilless media as well as their independent comparative assessments (Table 9.2). The 16 °C–LC treatment had the largest circumference post-harvest, although it was statistically comparable to all other treatment combinations. Greater circumferential dimensions were found in all temperature-treated bulbs other than those grown at 34 °C, where the final circumference was statistically suppressed (Table 9.2). Relative to the comparative reduction of 1.2 cm between the post-harvest and pre-plant circumferential dimensions in the warmest water treatment at 34 °C, a considerably marked improvement of between 6.4–7.1 cm was observed in the three lower heated temperature treatments. Compared to silica sand (16.1 cm), the post-harvest bulb circumference cultivated in Leca clay (17.5 cm) was significantly higher (Table 9.2).

9.4.2 Pre-plant and post-harvest mother bulb fresh weight

In evaluating the factorial analysis of variance of soilless media and interaction with heated water temperatures, the responses of the pre-plant and post-harvest fresh weights of mother bulbs were not statistically different ($p > 0.05$). However, the water temperature responses indicated otherwise (Table 9.2). Statistically, similar post-harvest fresh weights for the lower three temperature treatments were found, with the bulbs grown in the 16 °C treatment exhibiting the highest weight value. In comparison to the pre-plant fresh weights, all temperature-treated mother bulbs increased the post-harvest fresh weight by 62.7–78.6 g, except for those cultivated at 34 °C, where the final comparative weight was suppressed, and an incremental increase of 0.9 g was measured (Table 9.2).

9.4.3 Post-harvest root fresh weight

The total fresh root mass from bulbs grown at different water temperatures differed significantly ($p \leq 0.05$) compared to soilless media and the variable interaction, which were found to be unaffected (Table 9.2). The 22 °C heated water treatment produced the maximum root fresh weight (20.1 g) with the least variability compared to the weights (17.2 g and 14.0 g) in the 16

°C and 28 °C water temperatures, respectively. In bulbs suspended in the 34 °C treatment, the accumulated root fresh weight (4.1 g) was severely inhibited and proved fatal (Table 9.2).

9.4.4 Number of bulb offsets

As shown in Table 9.3, water temperature comparisons exhibited significant differences in the number of bulb offsets initiated at the 95% confidence level; however, soilless media and the variable interaction indicated otherwise. As depicted in Figure 9.2, the bulbs suspended in the 22°C heated water stimulated the production of the most offsets from the mother bulb (2.3) yet, were not significantly different from those produced (2.1 and 1.3) in the 16 °C and 28 °C treatments, respectively. At least one bulb offset was initiated from the mother bulb in each heated water treatment, apart from those in the warmest treatment of 34 °C, which did not evince such an ability (Figure 9.4).

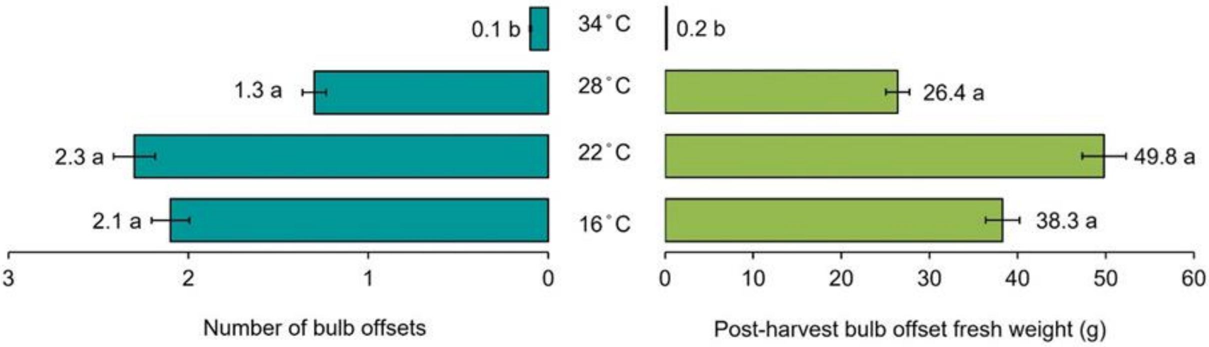
9.4.5 Post-harvest bulb offset fresh weight

The post-harvest fresh weight of bulb offsets grown at various water temperatures differed significantly ($p \leq 0.05$); however, no significant variations were identified in soilless media and their interaction (Figure 9.2). The 22°C water treatment showed the highest accumulated fresh weight (49.8 g) yet did not differ from the 16 °C or 28 °C treatments (38.3 and 26.4 g) (Figure 9.2). The offset weight measured in the 34 °C heated water was negligible (Figure 9.2).

Table 9.2: Effects of root zone water temperatures and soilless media on the characteristics of pre-plant, post-harvest mother bulb circumference and fresh weight and post-harvest root fresh weight of *Amaryllis belladonna* bulbs grown in a deep water culture hydroponic system

Treatment		Mother bulb and root characteristics				
		Mother bulb				Roots
		Pre-plant circumference (cm)	Post-harvest circumference (cm)	Pre-plant fresh weight (g)	Post-harvest fresh weight (g)	Post-harvest fresh weight (g)
		Water Temperature				
16°C (Control)		12.4 ± 0.24 a	19.2 ± 0.59 a	33.4 ± 1.84 ab	112.0 ± 9.16 a	17.2 ± 0.63 a
22°C		10.9 ± 0.30 b	18.0 ± 0.66 a	25.4 ± 1.30 b	88.1 ± 8.32 a	20.1 ± 2.91 a
28 °C		11.8 ± 0.32 ab	18.2 ± 0.50 a	29.5 ± 2.66 ab	105.7 ± 8.01 a	14.0 ± 1.48 a
34 °C		12.9 ± 0.39 a	11.7 ± 0.66 b	34.4 ± 2.69 a	35.3 ± 3.79 b	4.1 ± 0.53 b
		Soilless Media				
Leca clay (LC)		12.3 ± 0.26 a	17.5 ± 0.50 a	32.2 ± 1.64 a	88.0 ± 6.77 a	14.0 ± 1.63 a
Silica sand (SS)		11.7 ± 0.23 a	16.1 ± 0.74 b	29.1 ± 1.60 a	82.6 ± 7.54 a	13.7 ± 1.40 a
		Water Temperature × Soilless Media				
16 °C	× LC	12.6 ± 0.35 ab	19.4 ± 0.76 a	34.5 ± 2.61 a	108.1 ± 15.10 a	17.4 ± 1.12 a
	× SS	12.1 ± 0.32 ab	19.0 ± 0.93 a	32.2 ± 2.69 a	116.0 ± 11.10 a	17.1 ± 0.66 a
22°C	× LC	10.8 ± 0.43 b	18.8 ± 0.91 a	27.4 ± 2.26 a	89.5 ± 12.30 ab	19.7 ± 5.15 a
	× SS	11.1 ± 0.44 b	17.3 ± 0.94 a	23.3 ± 1.01 a	86.8 ± 11.80 ab	20.5 ± 3.01 a
28 °C	× LC	12.3 ± 0.50 ab	18.0 ± 0.68 a	33.0 ± 4.87 a	108.9 ± 9.77 a	13.8 ± 2.54 ab
	× SS	11.2 ± 0.33 b	18.4 ± 0.78 a	26.0 ± 1.84 a	102.5 ± 13.10 a	14.2 ± 1.69 ab
34 °C	× LC	13.3 ± 0.45 a	13.7 ± 0.46 b	33.7 ± 2.72 a	45.4 ± 4.94 bc	5.6 ± 0.59 bc
	× SS	12.4 ± 0.63 ab	9.7 ± 0.83 c	35.1 ± 4.80 a	25.1 ± 3.68 c	2.6 ± 0.60 c
		Two-way ANOVA–F statistic				
Water temperature		7.13 *	36.8 *	3.47 *	20.48 *	16.38 *
Soilless media		3.18 ns	5.79 *	1.89 ns	0.49 ns	0.05 ns
Water temperature × Soilless media		1.05 ns	2.99 *	0.63 ns	0.57 ns	0.26 ns

Mean values ± standard error (S.E.) in the same column with a different letter(s) are significantly different at p ≤ 0.05 (*) based on Tukey's Least significant difference test; ns = not significant



Two-way ANOVA–*F*-statistic

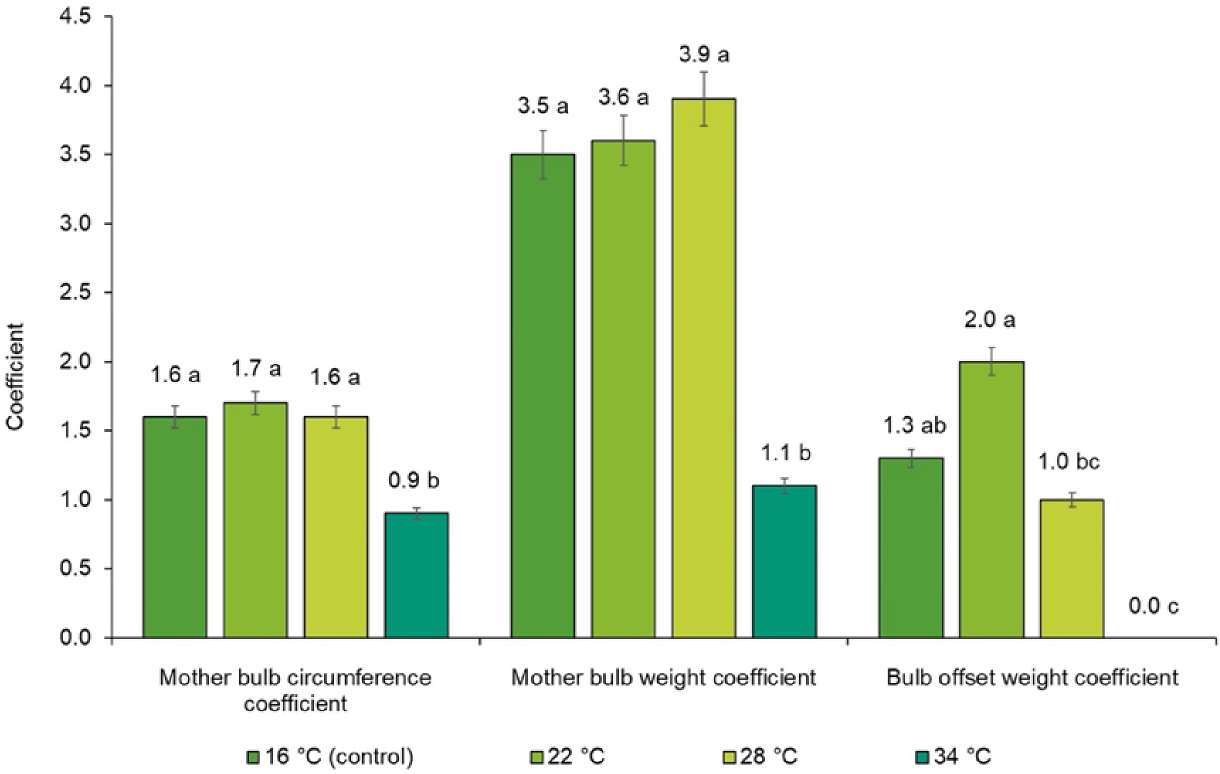
Treatments	Number of bulb offset (n)	Post-harvest bulb offset fresh weight (g)
Water temperature	12.37 *	10.41 *
Soilless media	0.79 ns	0.18 ns
Water temperature × Soilless media	0.52 ns	0.05 ns

Figure 9.2: Effect of root zone water temperatures on the number of bulb offsets and the post-harvest bulb offset fresh weight of *Amaryllis belladonna* grown in a DWC hydroponic system. Bars represented by mean values followed by a different letter are significantly different at $p \leq 0.05$ according to Tukey's least significant difference (L.S.D.), (*) indicates significance at $p \leq 0.05$; ns = not significant

9.4.6 Mother bulb circumference, weight, and offset weight coefficients

The coefficients were used to assess the bulbs' total vegetative productive proliferation and marketability (Figure 9.3). The circumferential coefficient of mother bulbs was considerably improved ($p < 0.05$) by water temperature and the factorial interaction with soilless media. However, the coefficient found in soilless media was unaffected (Figure 9.3). The mother bulbs grown in water temperatures of 16 °C, 22 °C, and 28 °C showed a similar circumference coefficient variability (1.6–1.7). In comparison, those grown under the same conditions at 34 °C showed a significant ($p < 0.05$) decline (0.9). Compared with the interaction with soilless media, the three lower-heated water treatments exhibited the most significant difference in the circumference coefficient. Based on the results in Figure 9.3, the mother bulb weight coefficient was significantly enhanced ($p < 0.05$) by the autonomous analysis of water temperature; however, the response was unaffected ($p > 0.05$) by the soilless media and the interaction of variables. The mother bulb weight coefficient largely reflected the improved statistical differences in the post-harvest fresh weight. The 28 °C water temperature produced the largest and nearly four times greater bulb weight coefficient (3.9). However, it was not statistically better than the coefficients (3.5 and 3.6) in the 16 °C and 22 °C treatments (Figure 9.3). Bulbs in the 34 °C treatment maintained their weight coefficient (1.1) over the study period. The independent analysis of water temperature significantly increased the offset weight coefficient ($p < 0.05$); however, it was not influenced by soilless media or the interaction of variables

(Figure 9.3). The 22 °C heated water yielded the highest offset weight coefficient (2.0), nearly double that of all other treatments (Figure 9.3).



Two-way ANOVA–*F*-statistic

Treatments	Mother bulb circumference coefficient	Mother bulb weight coefficient	Offset weight coefficient
Water temperature	44.3 *	18.13 *	9.16*
Soilless media	1.13 ns	0.55 ns	0.32 ns
Water temperature × Soilless media	3.89 *	0.92 ns	0.05 ns

Figure 9.3: Coefficient outcomes of *A. belladonna* mother bulb circumference, mother bulb weight, and bulb offset weight in response to root zone water temperatures in a DWC hydroponic system. Bars represented by the mean values followed by a different letter(s) are significantly different at $p \leq 0.05$ according to Tukey's least significant difference (L.S.D.), (*) indicates significance at $p \leq 0.05$; ns = not significant

9.4.7 Number of leaves

The number of leaves in the leafing phases was counted in the 2020 (planting) and 2021 (consecutive planted) seasons. The number of leaves of the mother bulbs treated to varied water temperatures was significant ($p \leq 0.05$). In contrast, soilless media and the variable interaction did not affect the number of emerging bulb leaves each season (p > 0.05). In 2020 and 2021, the highest mean number of leaves (10.1 and 9.1) appeared in bulbs grown in the 16 °C water temperature; however, minimal statistical variability was observed compared to the 22 °C and 28 °C treatments. The lowest leaf counts (7.9 and 5.1) were initiated in the warmest water treatment at 34 °C. Noticeable comparative differences in the 2021 cultivation season were found as the quantification of bulb foliage presented differently. They were negatively influenced by all heated water treatments, with an average reduction of 1–2.8 fewer leaves than in the previous season (Table 9.3).

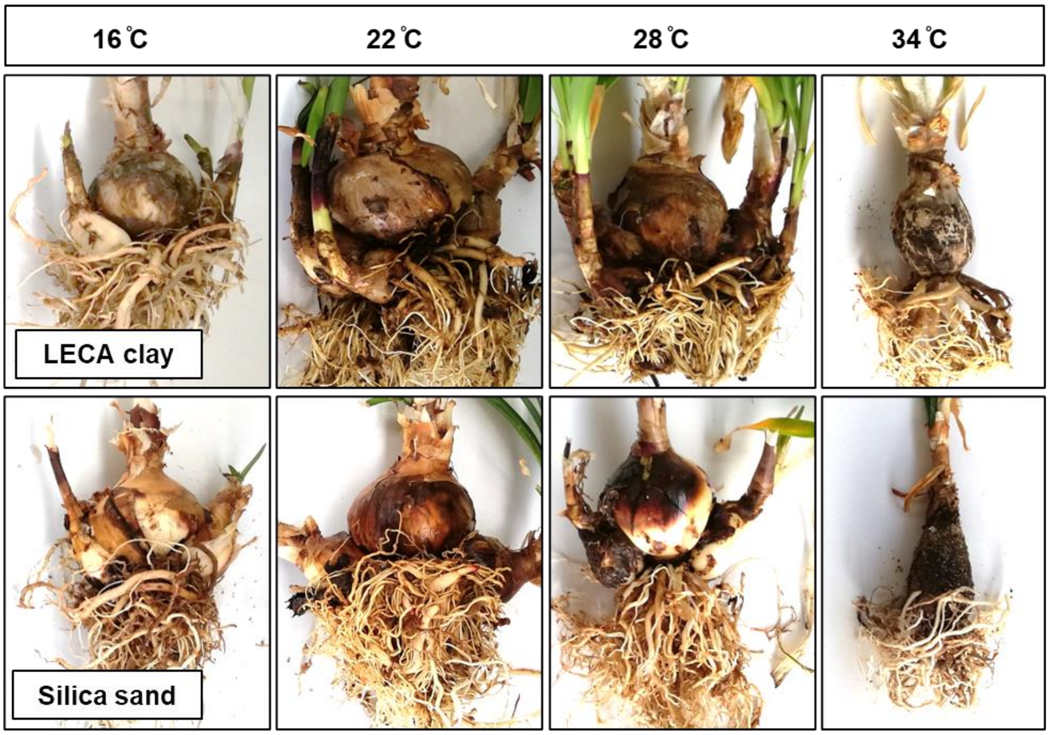


Figure 9.4: Observable effects of root zone temperatures and soilless media on the mother bulb size, offset production, and root architecture of hydroponically grown *Amaryllis belladonna* bulbs (Photographic diagram: C. Wilmot)

9.4.8 Leaf length, leaf width, and leaf area

The resumptive mother bulb foliage parameters of leaf length, width and area were evaluated following 24 weeks in the 2020 planting and 2021 sequential vegetative growth seasons. The independent evaluation of water temperature significantly affected the leaf length ($p < 0.05$). In contrast, the soilless media and the variable interaction had no significance over the two years of cultivation (Table 9.3). In the 2020 and 2021 seasons, statistically similar trends in the extension of bulb leaf blades subjected to temperatures of 16 °C and 22°C were observed. A notable decline was found as temperatures rose, with the 34 °C water-treated bulbs displaying the shortest leaves. The resumptive increase in leaf length in the second year compared to the first ranged between 13.5 and 24.5 cm across all warm water treatments. The expansive leaf width in bulbs showcased similar significant tendencies ($p \leq 0.05$) observed from the autonomous and interactive analysis of the leaf blade extension cultivated in the two seasons (Table 9.3). Compared to the 2020 season, visibly broader leaves in the 2021 treatments were observed, with an increased width between 0.2 and 0.7 cm. The findings of the overall leaf area found that the 16 °C treatment had the highest surface area, but it was not statistically different from the 22°C and 28°C treatments in both seasons (Table 9.3).

Table 9.3: Effects of root zone water temperatures and soilless media on leaf characteristics of the number of leaves, leaf length, width and area of *Amaryllis belladonna* bulbs that were grown in a deep water culture hydroponic system following 24 weeks of the 2020 and 2021 leafing seasons

Treatment		Leaf characteristics							
		2020 season				2021 season			
		Number of leaves (n)	Leaf length (cm)	Leaf width (cm)	Leaf area (cm^2)	Number of leaves (n)	Leaf length (cm)	Leaf width (cm)	Leaf area (cm^2)
Water temperature									
16 °C (Control)		10.1 ± 0.29 a	42.8 ± 1.14 a	1.9 ± 0.06 a	80.8 ± 3.14 a	9.1 ± 0.34 a	55.6 ± 1.55 a	2.6 ± 0.07 a	143.5 ± 5.74 a
22°C		9.6 ± 0.62 a	43.1 ± 1.49 a	1.8 ± 0.07 ab	77.2 ± 4.69 a	8.9 ± 0.50 a	56.6 ± 1.68 a	2.5 ± 0.12 a	140.8 ± 9.21 a
28 °C		10.1 ± 0.45 a	36.2 ± 2.72 a	1.9 ± 0.06 a	68.7 ± 5.22 a	7.8 ± 0.62 a	49.9 ± 1.67 b	2.2 ± 0.15 a	111.9 ± 9.42 b
34 °C		7.9 ± 0.30 b	19.5 ± 1.62 b	1.6 ± 0.07 b	32.3 ± 3.37 b	5.1 ± 0.32 b	44.0 ± 1.03 c	1.8 ± 0.07 b	79.9 ± 3.79 c
Soilless media									
Leca clay (LC)		9.2 ± 0.35 a	34.5 ± 1.90 a	1.8 ± 0.05 a	65.5 ± 4.35 a	7.7 ± 0.35 a	50.8 ± 1.39 a	2.3 ± 0.08 a	120.4 ± 6.51 a
Silica sand (SS)		9.6 ± 0.32 a	36.3 ± 2.09 a	1.8 ± 0.05 a	64.0 ± 4.16 a	7.7 ± 0.50 a	51.2 ± 1.25 a	2.2 ± 1.0 a	117.7 ± 6.74 a
Water temperature × Soilless media									
16°C	× LC	10.1 ± 0.31 ab	41.6 ± 1.24 a	2.0 ± 0.06 a	80.9 ± 2.09 a	8.8 ± 0.51 a	55.2 ±2.34 ab	2.6 ± 0.11 a	143.0 ± 10.20 a
	× SS	10.1 ± 0.50 ab	44.0 ± 1.89 a	1.8 ± 0.10 a	80.8 ± 6.10 a	9.4 ± 0.45 a	56.0 ± 2.15 ab	2.6 ± 0.08 a	143.9 ± 5.82 a
22°C	× LC	8.4 ± 0.96 ab	41.5 ± 2.50 a	1.8 ± 0.11 a	76.2 ± 8.13 a	8.4 ±0.78 a	56.1 ± 2.76 ab	2.4 ± 0.17 a	138.7 ± 15.0 a
	× SS	10.7 ± 0.65 a	44.6 ± 1.62 a	1.8 ± 0.08 a	78.2 ± 5.16 a	9.4 ± 0.64 a	57.1 ± 2.06 a	2.5 ± 0.17 a	142.9 ± 11.50 a
28 °C	× LC	10.4 ± 0.60 ab	34.4 ± 3.81 a	1.9 ± 0.12 a	64.6 ± 7.20 a	8.3 ± 0.54 a	47.5 ± 2.69 bc	2.3 ± 0.18 a	112.1 ± 12.70 ab
	× SS	9.8 ± 0.68 ab	38.0 ± 4.01 a	1.9 ± 0.06 a	72.8 ± 7.72 a	7.2 ± 1.11 ab	51.9 ± 1.84 abc	2.1 ± 0.24 a	111.7 ± 14.60 ab
34 °C	× LC	7.8 ± 0.51 b	20.5 ± 2.75 b	1.6 ± 0.08 a	34.2 ± 5.50 b	5.4 ± 0.40 b	44.2 ± 1.35 c	2.0 ± 0.09 a	87.60 ± 4.62 b
	× SS	7.9 ± 0.35 b	18.4 ± 1.81 b	1.6 ± 0.12 a	30.3 ± 4.10 b	4.8 ± 0.51 b	43.7 ± 1.64 c	1.6 ± 0.07 a	72.2 ± 5.11 b
Two-way ANOVA–F statistic									
Water temperature		6.24 *	35.36 *	4.65 *	27.01 *	15.81 *	14.85 *	10.25 *	14.44 *
Soilless media		1.09 ns	0.90 ns	0.42 ns	0.13 ns	0.0 ns	0.88 ns	1.27 ns	0.13 ns
Water temperature × Soilless media		2.25 ns	0.49 ns	0.37 ns	0.35 ns	1.14 ns	0.49 ns	0.83 ns	0.33 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 Tukey's least significant difference test; ns = not significant.

9.5 Discussion

The all-encompassing findings established that the independent treatment of heated water expressively altered the morphological growth and development responses of *A. belladonna* bulbs. However, soilless media and the combined interaction were insignificant. Warm root zone water temperatures of 16–28 °C were beneficial and comparable; however, a temperature of 34 °C, which was too high, was damaging and depleting. These responses corroborate the enhanced and subdued physiological activity and metrics from the subsurface root zone temperature variations in hydroponically produced crops. *Valerianella locusta,* an annual herb plant grown at low (15 °C) and high (25 °C) root zone temperatures, produced plants that were smaller than those grown at 20 °C (Costa *et al*., 2011). Similarly, He *et al*. (2013) found temperatures of 20 °C over sub-optimal and high temperature-stress responses favoured aeroponic cultivated *Lactuca sativa* growth and development. *Streptocarpus formosus* responded more positively to lower root zone water temperatures of 18 and 22 °C than to temperatures of 26 and 34 °C (Viljoen *et al*., 2021). Similarly, temperatures between 26 and 30°C were more advantageous to *Ornithogalum longibracteatum* bulbs than 34 °C (Nxawe *et al*., 2011). At root zone temperatures ranging from 11 to 34 °C, six Cucurbitaceae species responded inversely for biomass, photosynthesis, and stomatal conductance (Zhang *et al*., 2008).

Increased performance yields may also be ascribed to the year-round continual availability and accessibility of water and nutrients, which are absorbed by the actively searching contractile bulb roots through perpetual immersion in an oxygen-rich hydroponic nutrient solution (Trejo-Téllez & Gómez-Merino, 2012; Barnhoorn, 2013). Similar findings of greater vegetative development and water-holding capacity were found in hydroponically grown Oriental lily hybrids (Ryota *et al*., 2002) and *Eucomis autumnalis* (Ndhlala *et al*., 2012). Asker (2015) found that growing larger Asiatic hybrid lily bulblets and daughter bulbs in an NFT hydroponic system was advantageous. Long-term solution temperatures influence the amount and accessibility of dissolved oxygen, with high temperatures having been demonstrated to diminish oxygen solubility, impede plant performance and root growth, and increase the risk of pests and disease (Gruda, 2005; Falah *et al*., 2010; Thakulla *et al*., 2021). In this study, prolonged root exposure of *A. belladonna* bulbs to 34 °C resulted in hypoxic stress response observations of poor root formation, rotting, and blackening, bulb growth suppression, weight loss, increased respiration, and root ethylene production due to reduced root-oxygen solubility and nutrient absorption (Shaw *et al*., 2013; Sakamoto & Suzuki, 2015; Balliu *et al*., 2021). Apart from the boundaries of restricted root volumes in the hollow plastic cavity trays (Shi *et al*., 2007; Balliu *et al*., 2021), root-oxygen assimilation was optimal at lower temperatures ranging from 16 to 28°C. The dense root architecture, increased biomass, density, and surface area of mother bulbs and offsets for adequate nutrient absorption evidenced this. These important properties determine the definitive operation of the species' contractile root system (Duncan, 2010).

Similarly, to the root performance yields, lower temperatures demonstrated improved aerial growth, development, and parameter metric observations. In contrast, the 34 °C treatment showed poor yields in addition to delayed leaf development at the start of the 2020 and 2021 leafing phases, lower levels of leaf turgor, and early leaf fading. These observations may account for the lack of oxygen in the root zones causing epinastic leaf curvature, stomatal closure, a slowing of leaf growth, turgor and yellowing, all of which are shoot adaptations to compensate for the root system's debilitation and poor shoot-root communication (Jackson, 2002; Shaw *et al*., 2013). Although leaf number may indicate a transition from juvenile to reproductive maturity (Langens-Gerrits *et al*., 2003), all treatments had fewer leaves in the second cultivation season than before. According to Hartsema and Leupen (1942), this may relate to the planting of the bulbs in the previous season, affecting the leaf formation and resulting in decline. However, the lower temperature treatment differentials were notably counterbalanced by the greater leaf length and width parameter values in the second season. The enlarged surface area is suggested to have maximised the photosynthetic activity to amass sufficient photosynthates while reducing the barriers to obtaining nutrients and water within the warm water hydroponic system (Nxawe *et al*., 2009; Anderson, 2019).

Soilless media is currently one of the fastest-growing areas, offering unlimited potential within the horticultural sector (Balliu *et al*., 2021; Karagöz *et al*., 2022;). *Fritillaria imperialis* growing in a soilless culture (sand medium) (Kahraman & Özzambak, 2006) and *Gladiolus grandiflorus* in a hydroponic bag culture (Wahome *et al*., 2010) procured the highest vegetative growth, bulblet and flower formation and quality attributes. Soilless media had no significant impact on the study's morphological bulb traits; however, the findings suggest that different soilless substrates could be evaluated, or the soil media substituted entirely with reusable LDPE plastic aqua prick trays (Schroeder *et al*., 2020). This suggestion is under careful evaluation in support of input resource factors, cultivation and LCA (Darras, 2020; Fussy & Papenbrock, 2022) associated with the *A. belladonna* species.

In elucidating the study's coefficients, the juvenile *A. belladonna* mother bulb circumference and weight coefficients were comparable and significant at 16 °C, 22 °C, and 28 °C. However, the weight coefficient indicated a more significant dynamism than the circumference. The largest induced offset weight coefficient was found at 22 °C due to more significant offset generation. Thus, at lower heated root zone water temperatures, particularly at 22 °C, juvenile mother bulbs simultaneously generated larger, heavier bulbs and maximum offset capacity without early separation. According to Khodorova and Boitel-Conti (2013), Kapczyńska (2014) and Manimaran *et al*. (2017), bulb size impacts output quality, yield, and flowering productivity during natural production since bulbs function as a source and sink of internal carbohydrate reserves to reach competency. It is suggested in this study, and supported by Miller (1992), Thompson *et al*. (2011), Wu *et al*. (2012) and Andrade-Rodríguez *et al*. (2015), that the variables related to bulb root zone temperatures improved the efficiency of carbohydrate absorption and mobilisation, leading to higher yields. Intriguingly, the 22 °C water treatment marginally lowered the mother bulb weight; however, this was compensated for by a greater offset weight than the 16 °C and 28 °C treatments. These findings infer that the vegetative processes under the role of phytohormones and inductively mediated extrinsic hydroponic conditions were competing and synchronised, governing the intrinsic provision of accumulated biomass and 'bulbing' (Thompson *et al*., 2011; Atif *et al*., 2020). Furthermore, offsets are suggested as possible sinks for regulating the allocation of excess assimilates in the developing *A. belladonna* bulb, owing to the insensitive juvenility, meristem inability, and unresponsiveness to inductive cues that promote flowering (Levy & Dean, 1998; Proietti *et al*., 2022). Similarly, under favourable external circumstances, Thompson *et al*. (2011) found improved seasonal corm and cormlet production responses in unsuccessfully flowered *Watsonia* species.

Offset induction was neither vast, vigorous, nor uniform; however, visual observations of up to 5 formed offsets suggested that some *A. belladonna* bulbs, which were not homogenous, were more proliferous, signifying a potentially robust genetic disposition (Chandel *et al*., 2023). According to Kharrazi *et al*. (2017), offset division in species of *Hippeastrum* is promoted in those bulbs that produce a minimum of 3 bulblets per year. However, in most cases, propagation is accomplished by other conventional techniques. Notching, sectioning, scooping, twin scaling, and, more recently, tissue culture depletes the mother bulb, which cannot be reused (Barnhoorn, 2013; Hartmann *et al*., 2017). Moreover, conventional vegetative methods are not always economically practical due to the slow replication rate, ineffective techniques, meticulous labour practices, stringent hygiene standards, and survival rates that rely on fresh bulb development and sprouting (Kharrazi *et al*., 2017; Kapczyńska, 2019). In contrast, this study demonstrated that hydroponic cultivation promoted the vegetative multiplication of *A. belladonna* through offset induction and development without premature separation while establishing the size and longevity of the reclaimable clonal juvenile mother bulb.

This study supports the fundamental role of subterranean temperature stimuli in geophytic cultivation. Moreover, it reveals that plant species may navigate environmental and seasonal variations as a climate-smart functional and survival strategy by innovative or passive tactical adaptations to strengthen asexual propagation viability at different periods (Atif *et al*., 2020). The enhanced hydroponic performance activity from juvenile *A. belladonna* bulbs indicates a favourable multimodal propagation and cultivation technique that promotes extended growth beyond dormancy, which is crucial for economic efficiency. It may be a precursor to supporting growers and retailers with intriguing and remedial opportunities in fulfilling long-term commercial horticultural demands and conservation efforts of small, incompetent bulbs. Similarly, this study established that with systematic and thorough research and the timely adoption of treatment routines, greater cultivation product outcomes can be calibrated in the *A. belladonna* species, as previously published in Wilmot and Laubscher (2019b), Gul *et al*. (2020) and Wilmot *et al*. (2023; 2024).

9.6 Conclusion

In summary, the independent treatment of heated root zone water temperatures other than soilless media and the collective interaction significantly increased the *Amaryllis belladonna* vegetative bulb production under deep water hydroponic cultivation. Warm water temperatures of 16 °C–28°C resulted in comparable and optimistic quantitative and qualitative growth and development of the aerial and subsurface organs. However, a high temperature of 34 °C impacted negatively through increased injury and depletion. This study established that juvenile mother bulb growth and offset generation were promoted via competing and simultaneous assimilation processes in response to inducive exogenous controlled hydroponic stimuli. The authors recommend a 22 °C water temperature optimal for contemporaneously proliferating larger, heavier juvenile mother bulbs and offset capacity while minimising energy resource inputs (intensity and duration) for *A. belladonna*'s long-term ecoculture, production and LCA. The authors advocate further research to unravel the practicality and viability of various geophytes, bulb sizes, and soilless substrates that may advance definitive protocols and agronomic efficiency for continuous duplication of vegetative bulb stock, ultimately leading to flower production goals.

9.7 Acknowledgements

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CHAPTER 10

WARM BULB STORAGE OPTIMISES FLOWERING ATTRIBUTES AND FOLIAGE CHARACTERISTICS IN *AMARYLLIS BELLADONNA* L.

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WARM BULB STORAGE OPTIMISES FLOWERING ATTRIBUTES AND FOLIAGE GROWTH IN *AMARYLLIS BELLADONNA* L.

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10.1 Abstract

Amaryllis belladonna is an autumn-flowering bulbous geophyte endemic to the Western Cape, South Africa. The species' erratic floral 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 period 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. 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 after planting for this seasonal single-harvest species.

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

10.2 Introduction

Cut flowers and potted plants are among the most extensively produced and marketed ornamentals in the leading and competitive traditional floriculture sector and are a multibillion-dollar international export-oriented industry (Sharma, 2019; Anumala & Kumar, 2021). 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 (Barnhoorn, 2013; Darras, 2021). However, recent awareness of ornamental horticulture has rekindled the interest in features of production sustainability as a selection criterion (Darras, 2020; Thörning *et al.*, 2022). 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 (Ingram *et al.*, 2019; Darras, 2020; Thörning *et al.*, 2022). 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 (Darras, 2020; Thörning *et al.*, 2022). 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 (Lee & Miller, 2015; Miller, 2017a; Darras, 2020). 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 (Darras, 2021). 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 (De Pascale & Romano, 2019; Darras, 2021; Thörning *et al.*, 2022).

Amaryllis belladonna L. is an inimitable autumn-flowering bulbous geophyte endemic to the botanically diverse fynbos biome of South Africa's Cape Floristic Region (Adams, 2001; Theron & De Hertogh, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020). Formerly, *A. belladonna* was classified as a monotypic genus of the Amaryllidaceae family (Campos-Rocha *et al.*, 2017). The species is cultivated and has naturalised in Mediterranean regions worldwide, where hot, dry summers alternate with mild, wet winters (Adams, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020). *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 10.1a). Its strapshaped leaves unfurl actively at the onset of cooler autumn temperatures and winter rains. When late spring transcends and seasonal temperatures rise, the leaves wither, initiating the bulb's summer dormancy (Adams, 2001; Theron & De Hertogh, 2001; Manning *et al.*, 2002; Duncan *et al.*, 2020).

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 (Reinten *et al.*, 2011; Barnhoorn, 2013; Wilmot & Laubscher, 2019a; Gul *et al.*, 2020; Darras, 2021). 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 (Theron & De Hertogh, 2001; Duncan, 2004; Duncan *et al.*, 2020), limiting its marketable application as an influential cut flower and potted plant under the tight parameters of the traditional floriculture trade (Figures 10.1a and 10.1b).

Flowering is a multifaceted complexity of sequential events governed by endogenous mechanisms and extrinsic environmental signals (Corbesier & Coupland, 2006; Horvath, 2009; Denay *et al.*, 2017). 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 (De Hertogh & Le Nard, 1993; Roh & Hong, 2007; Horvath, 2009; Khodorova & Boitel-Conti, 2013; Capovilla *et al.*, 2015; Howard *et al.*, 2019; Wang *et al.*, 2021). Temperature regulation during dormancy is crucial to regulate bulbs' reproductive forcing, qualities and timing intended to produce timely high-quality flowers (Le Nard & De Hertogh, 1993; Miller, 2017b; Darras, 2020). 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 (Rees, 1966). Depending on their natural phenological growth conditions, different taxa require different successive temperature regimes to pass through certain developmental stages to flowering (Theron & De Hertogh, 2001; Khodorova & Boitel-Conti, 2013; Kamenetsky-Goldstein, 2019). Mediterranean geophytes' annual rhythmic cycles typically follow a warm-cold-warm cycle.

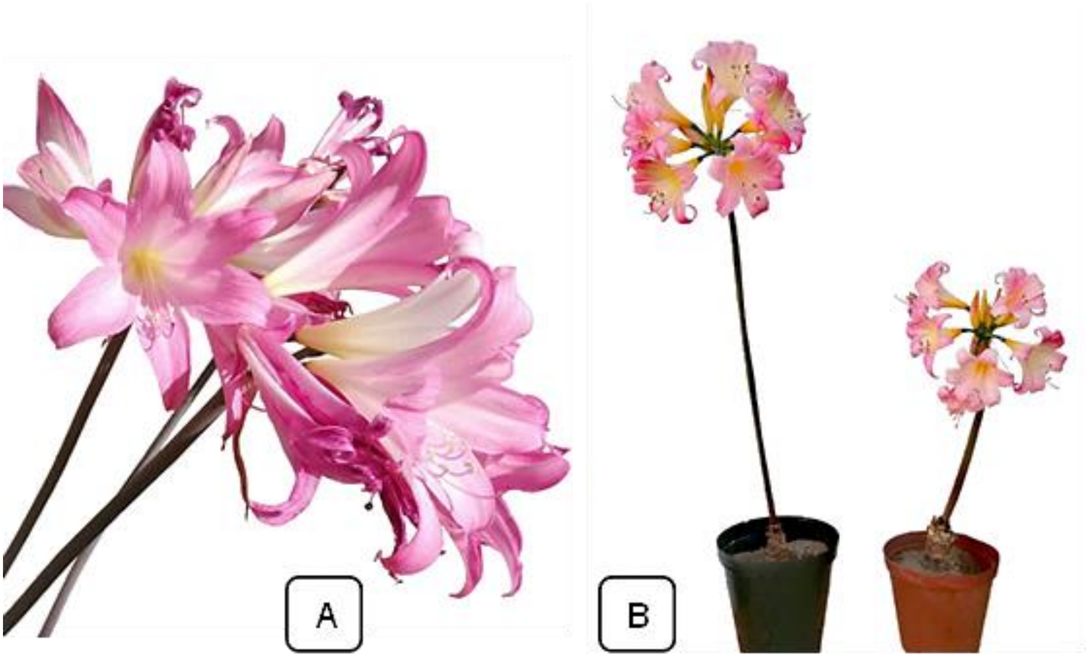

Figure 10.1: *Amaryllis belladonna* in full anthesis as a cut flower (a) or potted plant (b) (Photos: C. Wilmot)

According to Wilmot and Laubscher (2019b), 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 (Manning *et al.*, 2002). 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 (Roh & Hong, 2007). Similarly, when subjected to consistently higher storage temperatures immediately after leaf wilting, saffron (*Crocus sativus* L.) bulbs flowered earlier (Molina *et al.*, 2005). Storage temperatures up to 25 °C promoted healthy vegetative development, inflorescence maturity and flower bud opening in *Watsonia* corms (Thompson *et al.*, 2011). Storage significantly impacted the flower diameter and number of days before flowering in *Hippeastrum* (Inkham *et al.*, 2019) and accelerated flowering in *Eucomis* species (Carlson & Dole, 2015). Other Amaryllidaceae genera that flourish in hot, dry summer areas and respond to warm storage techniques include *Narcissus* species, *Nerine flexuosa*, and *N. sarniensis* (Warrington *et al.*, 2011). According to Roh and Hong (2007), standardised forcing protocols make 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 specialised cultivation technologies and adaptations to overcome obstacles in furthering our understanding of indigenous and underutilised plant species (Reinten *et al.*, 2011; De Pascale & Romano, 2019; Viljoen *et al.*, 2021). Progress cannot advance without thorough scientific investigation and the awareness that ornamental geophytes' intrinsic genetic variation and composition are increasingly valued (Kamenetsky & Miller, 2010; Reinten *et al.*, 2011; Marasek-Ciolakowska *et al.*, 2021), and research is needed to encourage growers to cultivate and reintroduce these species to the industry (Loyola *et al.*, 2019; Salachna *et al.*, 2020). 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 (Rees, 1966; Kapczyńska, 2014; Slezák *et al.*, 2020). 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, resilient indigenous, 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 (Wilmot & Laubscher, 2019b). 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.

10.3 Materials and methods

10.3.1 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 included a thermostatically regulated system and a transparent polycarbonate roof sheet (Envirowatch, Envirowatch Solutions, 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. Relative humidity (RH) averaged 60%. Under natural light conditions, the daily average photosynthetic photon flux density (PPFD) was 420 µmol/m^2/s with an intensity peaking at 1020 µmol/m^2/s. The photoperiod corresponded to the prevailing conditions between late spring and early winter (9–12 hours).

10.3.2 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 Duncan (2010) 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.

10.3.3 Experimental design and treatment setup

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 10.1). 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 and that proposed by Duncan (2010). 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 10.1). 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 (Duncan, 2010). 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 10.1: 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 = duration; (c) = control

10.3.4 Data collection

10.3.4.1 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 10.2). 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.

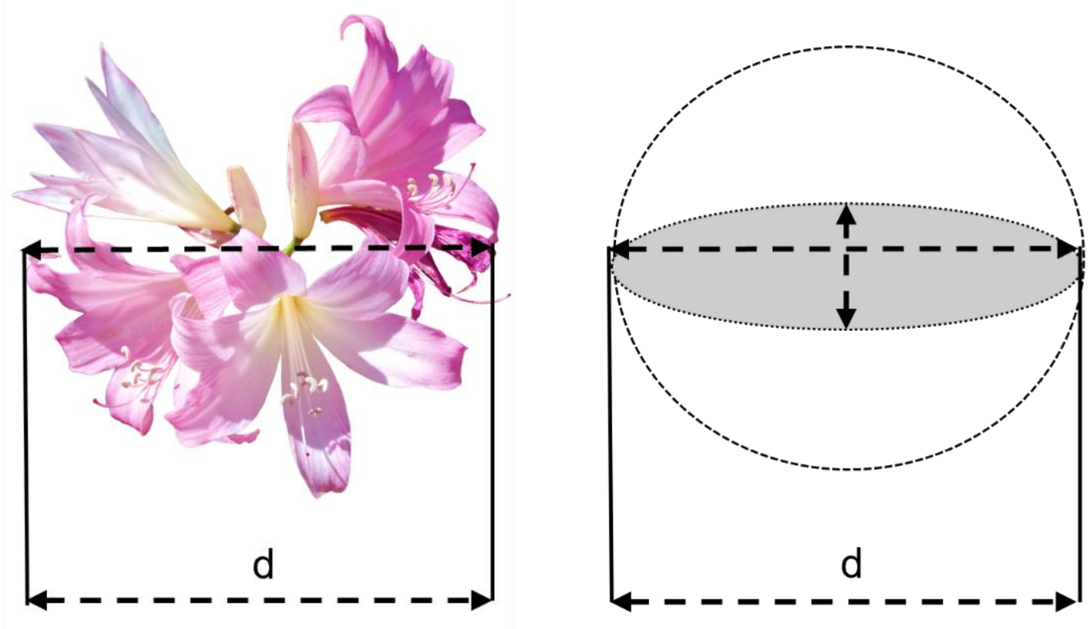

Figure 10.2: Determination of the relative average inflorescence crown diameter (d) of *Amaryllis belladonna*, measured from one side of the circumferential edge through the centre of the umbel arrangement to the other side and at a 90° horizontal rotation (Photo and diagram: C. Wilmot)

10.3.4.2 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.

10.3.4.3 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 defined 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 Yu *et al.* (2020) and Shi *et al.* (2021) was used to calculate leaf area.

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

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

10.3.5 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.

10.4 Results

10.4.1 Effect of warm bulb storage period on inflorescence morphological development

10.4.1.1 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 10.3, 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%).

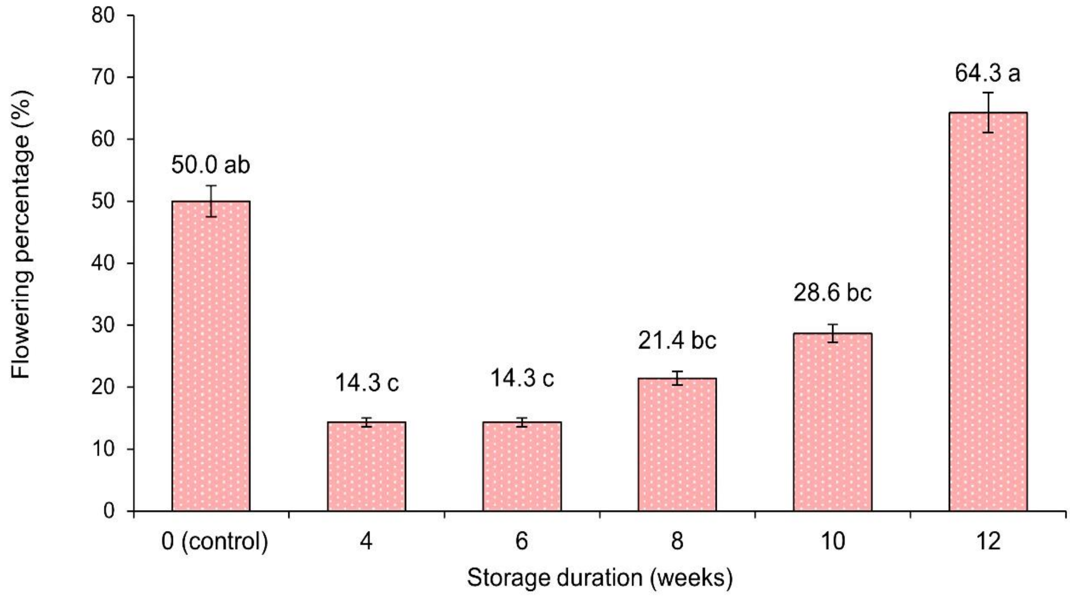

Figure 10.3: Effect of warm bulb storage duration on flowering percentage, as defined by successful inflorescence maturation of *Amaryllis belladonna*. Bars represented by mean values followed by a different letter(s) are significantly different at $p \leq 0.05$, according to Fisher's least significant difference (L.S.D)

10.4.1.2 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 10.1b). 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 10.2). 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.

10.4.1.3 Number of florets

The analysis showed that the storage treatments had a significant ($p \leq 0.05$) effect on the number of florets produced by each inflorescence, as shown in Table 10.2. 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.

10.4.1.4 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 10.2.

10.4.1.5 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 10.2 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).

10.4.1.6 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 10.2 ($p \leq 0.05$). 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 10.2). 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.

Table 10.2: 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.

10.4.1.7 Inflorescence longevity

The data presented in Figure 10.4 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).

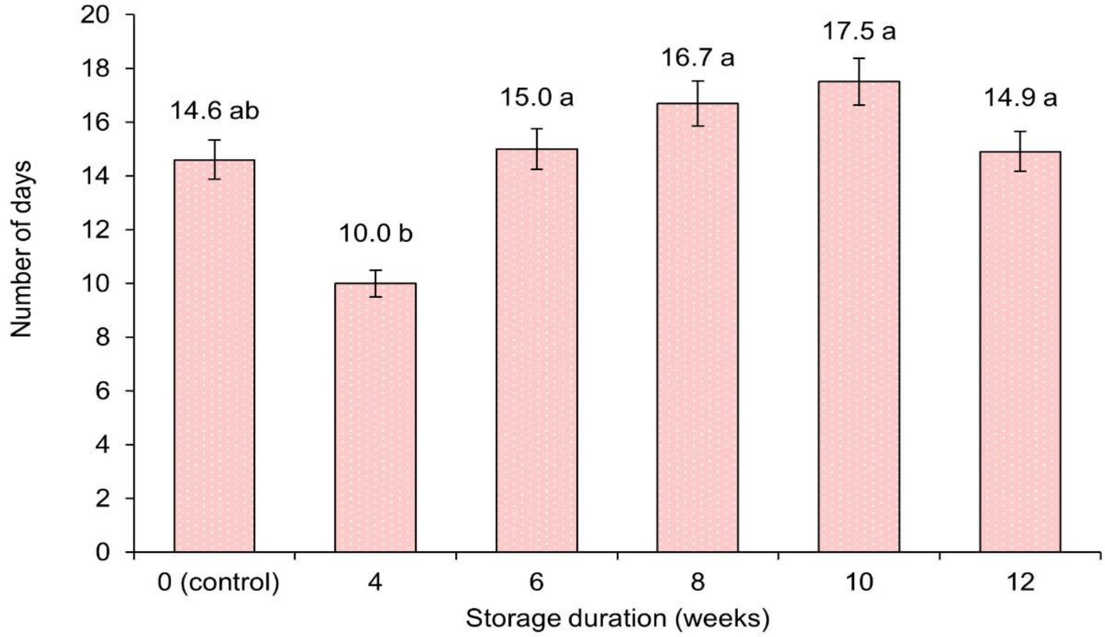

Figure 10.4: Effect of warm bulb storage duration on *Amaryllis belladonna* bulbs inflorescence potted longevity. Bars represented by mean values followed by a different letter(s) are significantly different at $p \leq 0.05$, according to Fisher's least significant difference (L.S.D)

10.4.2 Effect of warm bulb storage period on flowering time course

10.4.2.1 Visible flower buds, anthesis, opening of 50% florets and complete floral senescence

The results in Figure 10.5 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 that were 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 10.5). 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.

The influence of the 50% floret opening on inflorescence showed similar trends to the effect of the storage treatments on anthesis compared to the control. Figure 10.5 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 10.5). 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.

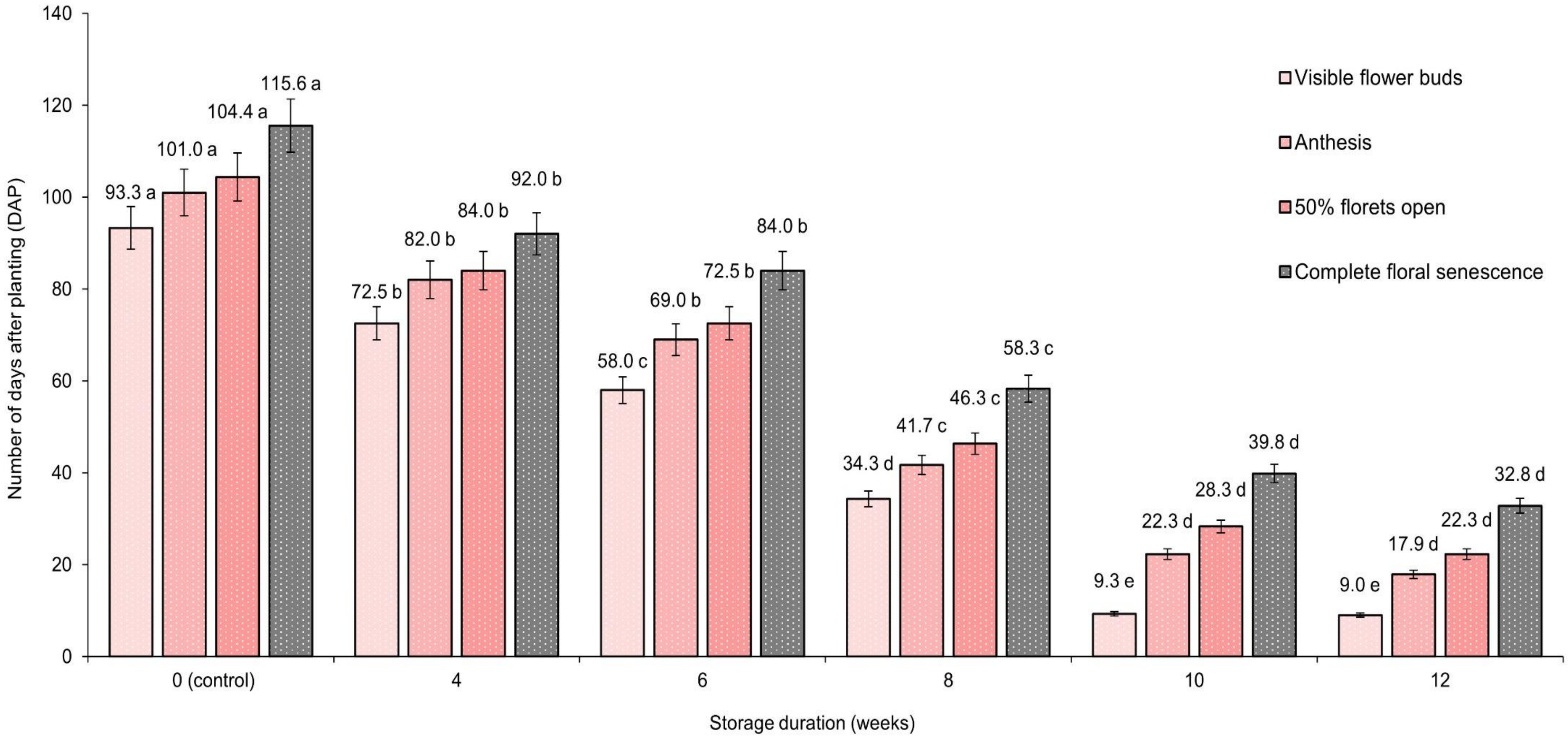

Figure 10.5: Effect of warm bulb storage duration on the number of days till the emergence of visible flower buds, anthesis, the opening of 50% florets and complete floral senescence of *Amaryllis belladonna* after planting. Bars represented by mean values followed by a different letter(s) are significantly different at $p \leq 0.05$, according to Fisher's least significant difference (L.S.D)

10.4.3 Effect of warm bulb storage period on leaf morphological growth

10.4.3.1 Number of leaves

As shown in Table 10.3, there was no significant difference ($p > 0.05$) in the number of leaves after the storage treatments and subsequent planting 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.

10.4.3.2 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 10.3. 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.

Table 10.3: 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

10.5 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

(Hartsema & Leupen, 1942; Theron & De Hertogh, 2001) and seen in other bulbous species of *Hippeastrum*, *Iris*, *Lachenalia*, and *Nerine*, where an after-storage planting resulted in the cessation of flower development (Rees, 1966; Van Kilsdonk *et al.*, 2002; Kapczyńska, 2012). 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 (Duncan, 2010). According to Du Toit *et al.* (2002) and Thompson *et al.* (2011), 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 Du Toit *et al.* (2002), Roh (2005) and Kapczyńska (2014) 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 (Warrington *et al.*, 2011; Capovilla *et al.*, 2015; Carlson & Dole, 2015). 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 (Capovilla *et al.*, 2015). 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 Rees (1966) and (1992), 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* (Warrington *et al.*, 2011) and *Lachenialia* species (Kapczyńska, 2012) 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 (Dole & Wilkins, 2005; Khodorova & Boitel-Conti, 2013). This finding validates the research that the capacity for a bulb to flower depends on the key storage intervals; straying from these threshold parameters increases the risk of inflorescence abortion (Van Kilsdonk *et al.*, 2002). According to this study's findings, the timing, length, and variety of subsequent temperature regimes affected the flowering response, aligning with those of Du Toit *et al.*, 2002; Kim & Oh, 2021. 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 (Rees, 1966). Hartsema and Leupen (1942) 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 (Warrington *et al.*, 2011). As a result, factors affecting the dormant period define the competitive character of the commencement of reproductive activities in the species.

Flowering periodicity, productivity, and market quality depend not 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 (Rees, 1966; De Hertogh & Le Nard, 1993; Inkham *et al.*, 2019). 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 (Wendell *et al.*, 2017; Marković *et al.*, 2021). 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 (Dafni *et al.*, 1981; Howard & Cellinese, 2020). 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 (Hartsema & Leupen, 1942; Theron & De Hertogh, 2001). 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 (Miller, 1992; Roh, 2005; Capovilla *et al.*, 2015).

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 Kapczyńska (2012), 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 (Kapczyńska & Kidawska, 2016). The quantity of flowers on an ornamental plant greatly reflects its aesthetic value and impacts its qualitative characteristics, according to Chen *et al.* (2019). Other key factors influencing decorative quality include crown diameter (Zhao *et al.*, 2022) and fullness ratio (Kapczyńska & Stodolak, 2019). 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 (Chandel *et al.*, 2023) and carbohydrate assimilation (Miller, 1992; Kim & Oh, 2021).

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 (Gul *et al.* 2020). 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, although insignificant, the minimum stem length was 37 cm, 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 (Wendell *et al.*, 2017; Marković *et al.*, 2021). Similar results were obtained in *Lachenalia* species (Kapczyńska & Kidawska, 2016), *Nerine sarniensis* (Warrington *et al.*, 2011), and *Ornithogalum dubium* (Luria *et al.*, 2002).

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 quicker sprouting of Asiatic lily cv. “Royal Trinity” (Malik *et al.*, 2017) and accelerated growth and flowering of *Ornithogalum thyrsoides* hybrids (Roh & Hong, 2007). 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 (Duncan, 2010; Barnhoorn, 2013).

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, Rees (1966) 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 Van Doorn and Woltering (2008) and Zhang *et al.* (2021), 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 propensity 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 (Reinten & Van Wyk, 2018; Darras, 2021; Thörning *et* *al.*, 2022). By 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 (De Pascale & Romano, 2019; Darras, 2021). Along with Reinten *et al.* (2011) and Darras (2021), this study demonstrates the potential of *A. belladonna* as a seasonal 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.

10.6 Conclusion

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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CHAPTER 11

CONCLUSIONS AND RECOMMENDATIONS

CONCLUSIONS AND RECOMMENDATIONS

11.1 Conclusions and recommendations

The South African flowering *Amaryllis belladonna* L. is a well-known hysteranthous bulbous species of the horticultural and floricultural industries. However, the species faces development constraints due to protracted bulb juvenility, offset generation for competent flowering size, and inconsistent and transient flowering behaviours upon reproductive bulb maturity. Likewise, there is a lack of scientific research and quantitative empirical data on cultivation methods, from planting to flowering, harbouring indubitable potential. Therefore, this study investigated the cultivation practices and environmental conditions of *A. belladonna* at different stages of bulb development and explicitly explored the effects of various abiotic factors on bulb growth and seasonal flowering. In advancing the theoretical, practical, and scientific proficiency of the *A. belladonna* species within the textual mandate of this thesis, it presented visual depictions and interpretations across chapters to support the cognitive association found within the study's written scholarship findings.

Chapter 2 of the literature review elucidated *A. belladonna*'s in-depth character, identified the myriad design uses, concepts, and horticultural traits, and emphasised the economic value, life cycle assessment challenges, constraints, and potential opportunities for cultivation research. Although this genus has proven to be a valuable and distinctive-indigenous taxon and resource of the Cape flora, this review found that the bulbous species is limited by a lack of scientifically based and quantifiable empirical data on practical cultivation approaches for various stages of bulb growth, from planting to seasonal flowering, which has irrefutable economic potential. This review concludes that numerous variables related to bulb yield, dormancy, temperature stimuli, water and nutrient availability, cultural practices, and seasonal fires synergistically shape the growth, development and flowering disposition of *A. belladonna*. This chapter contributes to a deeper understanding of and dispensation towards improving *A. belladonna* cultivation scheduling ramifications, economic potential, and viability. This review recommends addressing these fundamental factors to strengthen a species' prominence and capacity for competitive economic differentiation in the local and international flower bulb and cut flower sectors.

Chapter 3 presented the factors influencing flower initiation in *A. belladonna*. Preliminary data indicated that various factors stimulate flower initiation in the species. Findings of bulb size, age, dormancy, planting establishment, cultivation methods, bulb disturbance, and environmental factors of temperature, hydration, day length, and seasonal fire are associated with the initiation of flowering in the species. Moreover, this revealed that knowledge pertinent to the elicitors is varied and not adequately described. This chapter contributes to an improved understanding of the fundamental factors and dynamics facilitating *A. belladonna* flower initiation proficiency. This review recommends additional studies from planting to flowering to overtly examine the dynamic role and complexities of factors influencing the species' flower initiation, which could lead to the development of flower-forcing techniques, extending the short-lived flowering period and enhancing the economic potential.

Chapter 4 determined the horticultural and floricultural market potential of *A. belladonna*. Findings established that the species has attracted international interest because of its adaptability, attractiveness, drought resilience, and fire-stimulated flowering attributes. In continuum, it alluded to the variety of applications and design uses of the species within the broader fringes of the floriculture and horticulture arena. This chapter contributes towards augmenting the ornamental functional design of *A. belladonna* in gravel, grass, and rock garden landscapes, naturalistic and roadside plantings, among others, and its use in packaged retail flower bulbs, potted plants, and scented cut flowers for local and international markets. This review recommends that further studies focus on species' potential markets rather than predetermined product-based strategies.

Chapter 5 evaluated the hydroponic cultivation capacity of ornamental bulbous species. Findings revealed that the literature has primarily documented flower-forcing techniques associated with hydroponic cultivation, and the variety of such species is limited. Considerably little information is available on hydroponic cultivation employed in vegetation induction and bulb regeneration to expand bulb size and yield, and offset production. Specialised equipment, such as innovative prick/pin trays, can facilitate new experimental research methodologies and adaptations. Moreover, its comprehensive integration to alleviate adverse conditions can provide a profitable and sustainable management approach for enhancing bulb development, offset production, and flowering potential in a changing climate. This chapter contributes towards trialling a wider variety of bulbous geophytes and enhancing a greater capacity for bulb development and flowering productivity by facilitating *A. belladonna,* among other species, to attain maturity, size, and reproductive fitness sooner for local and international horticultural distribution chains. This review recommends further experimental studies to confirm the feasibility and practicality of recalibrating cultivation by maximising favourable growth conditions and product outcomes for a broader range of bulbous geophytes using a skilled hydroponic regimen.

Chapter 6 established the impacts of fire-stimulated flowering on South African geophytic biodiversity. Geophytic flowering is most prevalent during the first post-fire period, with certain species remaining dormant for several years and relying solely on fire for long-term survival. The findings of initiated flowering and regenerative growth of selected geophytic taxa, which inhabit different regions and vegetation habitats of South Africa following wildfires, are documented; however, these are primarily denoted in the species' natural habitats, with little account for those under cultivation. Moreover, the variables that drive this phenomenon are poorly defined, and additional and more quantifiable information is required to broaden the understanding of plant-environment interactions. This information may indicate a potential strategy for using fire to address the ramifications and reveal characteristics that strengthen species' capacity for biodiversity, cultivation fitness, and recruitment in fire-dependent ecosystems and under cultivation. This chapter contributes to a deeper understanding of how fire and its peripheral effects can modify the flowering proficiency of *A. belladonna* and other South African bulbous geophytes and draws attention to its distinctive role in preserving plant species richness and biodiversity, ecotourism, and the survival and well-being of natural above- and below-ground ecosystems. This review recommends further studies and experimentation to systematically pursue a deeper intellectual and practical comprehension of the degree of direct and indirect proximal variables of fire and their interplay on species-specific geophytic flowering fitness patterns, responses, and recruitment for future natural and experimental field settings. These findings may enhance conservation and horticultural efforts for botanically endangered, rare, and underutilised geophytic species in a changing climate.

Chapter 7 assessed the inhabited bulb planting life strategy and flowering dynamics of *A. belladonna* under *ex situ* garden conditions. Findings revealed that the species has a long lifespan and is recruited primarily through vegetative offsets. Although flowering heterogeneity ranged from 4.9% to 58.3% within and between seasons, commonalities alluded to a broad influence of temperature. Aside from highlighting the need for sufficiently appropriate and sustainable habitats and climatic growing conditions, the study concludes that population attributes (bulb size, structure, positioning, density, and establishment) and cultivation practices (premature defoliation, soil amendments, planting interference and re-establishment) were significant synergistic constituents of flowering behaviour and proficiency. This chapter contributes to a deeper understanding of *A. belladonna*'s *ex situ* life strategy and disposition towards cultivating commercial plantings by augmenting bulb populations' recruitment, development, and reproductive maturity for seasonal cut flower production and fitness continuity for selected markets. This study recommends further studies on the species' *ex situ* behavioural characteristics, survival strategies, and comparative cultivation throughout larger regions. Moreover, advancing cultivation studies on bulb lifting, division, and repositioning methods and timeframes of *ex situ* bulb planting should be conducted to ensure species flower-regulating prolificacy and seasonal continuity.

Chapter 8 demonstrated that an exogenous application of the seaweed extract Kelpak® significantly improves the morphological and physiological responses in juvenile *A. belladonna* bulbs when administered as a monthly soil drench to five bulb age groups. In a concentration-dependent manner, low-dose treatments increased the phyto-stimulatory responses of bulb aerial and, more evidently, below-ground storage organs. The bulb circumference, weight coefficients, and chlorophyll content showed that 1- and 2-year-old bulbs were most receptive to treatment. This study also emphasised the importance of the species' morphophysiological responses and age-receptive impact during cultivation. This study concludes that a 1% Kelpak® concentration dilution administered during the early developmental stages within the first two years is the most advantageous strategy for maximising the efficiency and proliferation rate of the species. This chapter contributes towards cultivating juvenile *A. belladonna* bulbs by optimising their capacity for early growth, development, and vigour, strengthening their adaptation and survival to environmental conditions for *ex situ* bulb planting acclimatisation and nursery production. This study recommends further studies to elucidate the mechanisms of activity and species receptivity to Kelpak® during cultivation.

Chapter 9 established that the autonomous treatment of regulated root zone water temperatures, other than soilless media and collective interactions, significantly increased *A. belladonna* vegetative bulb production under deep water hydroponic cultivation. Warm water temperatures from 16 °C to 28 °C improved the growth and development of aerial and subsurface organs, whereas excessively high temperatures of 34 °C negatively affected and depleted bulbs. Competing assimilation processes promote juvenile mother bulb growth and offset generation in response to inducive exogenous controlled hydroponic stimuli. This study concludes that an optimal water temperature of 22 °C is most beneficial for contemporaneously proliferating reclaimable juvenile mother bulbs and offset capacity while minimising energy resource inputs (intensity and duration) for long-term sustainable production and life cycle assessment of *A. belladonna*. This chapter contributes towards cultivating and producing a greater capacity and timely supply of *A. belladonna* bulb stock materials (reclaimable mother bulbs and offsets) and undersized, incompetent bulbs for commercial flower bulb markets. In the long term, this strategy anticipates facilitating seasonal flowering competence and production by actively promoting species to reach earlier bulb maturity, size, and reproductive fitness for the commercial bulb and flowering potted plant markets. This study recommends further studies to unravel the species' large-scale practical viability under alternative hydroponic technology to advance a new paradigm of definitive cultivation protocols and the agronomic efficiency of continuous duplication of vegetative bulb stock that may extend to more sophisticated flower production goals.

Chapter 10 showed that warm bulb storage after lifting affects flowering production, flowering time, and flower quality attributes but not foliage growth in *A. belladonna*. In addition to promoting higher flowering capacity and shorter intervals under greenhouse cultivation after planting, extended warm bulb storage did not stereotypically advance the flowering time.

Irrespective of bulb storage, inflorescence abortion occurred. The cumulative temperature range during bulb dormancy supports the inflorescence maturity's energy demands and the opening of floret buds. If not adequately maintained, *A. belladonna's* flowering ability is compromised. This study concludes that bulbs should be stored at an elevated temperature for 8–10 weeks after harvest to achieve the highest floret quality 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 most profitable for this seasonal single-harvest species. This chapter contributes to the viability of seasonal cultivation and flowering production of uplifted, flower-sized *A. belladonna* bulbs by facilitating and enhancing flowering competence, yield and quality attributes for commercial potted plant and cut flower markets. This study recommends further studies on a broader range of storage temperatures, durations, and initial lifting dates during dormancy to identify patterns and develop more precise cultivation protocols to improve flowering competency and attributes, potentially prolonging the season.

While this thesis's preceding chapters alluded to their specific findings, conclusions, recommendations, and contributions to scientific knowledge, they perpetuated the overall insights, interpretations, and suggestions to be formed. With the premise that specific South African fynbos species, such as *A. belladonna*, claim not to require special treatment and flourish in neglected and harsh conditions, while this may be true in the wild, attempts to foster their economic development under such conditions in cultivation are unlikely to be effective; therefore, modifications of abiotic parameters under cultivation that promote growth, development, and flowering are critically valued. This study supported this proposition based on the quantifiable statistical findings of *A. belladonna* field observations and cultivation experimentation in chapters 7, 8, 9, and 10. Moreover, cultivation elicitors for the bulb development and flowering of *A. belladonna* were selected not solely for their reported positive effects but for their ease of application, affordability, minimal time-consuming and rigorous regimen within sustainable cultivation frameworks suitable for commercial production endeavours and those of small-scale growers. Similarly, this study demonstrated that by dividing the complex and fundamental cultivation scheduling ramifications of *A. belladonna* bulb juvenility, offset production and flowering behaviour into smaller, feasible, and timely cultivation treatment activities and regimens, the species' innate characteristic capacity and competency outcomes can be recalibrated and optimised for potential flower bulb and niche cut flower and flowering potted plant markets.

In addition, since this study implemented cultivation approaches at various phases of bulb development (age), this stratagem is cognisant, with indications of sensitivity and receptivity evident as early as the first year of bulb development. Considering the overall life strategy and working within seasonal *A. belladonna* hysteranthous life cycle constraints, selecting treatment regimen techniques, bulb age, and receptivity that promote timely growth and development rather than inhibit development due to untimely implementation and insufficient preparation is crucial. These fundamental principles were learned from this study, resulting in the loss of growing and flowering season/s and/or plant material. As a result, more studies recommend prescribed treatment applications at different bulb ages (sizes) as part of *A. belladonna*'s ongoing cultivation methodology and LCA to identify trends and definitive protocols to expand cultivation practices for specific developmental phases and large-scale production. Such research is particularly pertinent during the flowering phase of the impending inflorescence initiation and the emergence of imminent inflorescence in reproductively mature bulbs to ensure seasonal flowering continuity. Likewise, as this study focused on the extrinsic morphological responses of *A. belladonna* to extrapolated treatments and environmental conditions, and due to the availability of time and budget constraints, future studies may examine the intrinsic morphophysiological trajectories during crucial developmental stages through species dissection to substantiate the extrinsic responses and contributions to the cultivation methodology found in this study.

While the present study achieved its research objectives, one initial study objective was to investigate the flowering disposition and prolificacy following a summer fynbos fire in an inhabitable *in-situ* natural (wild) setting. This investigation was conducted during a natural summer fynbos fire in January- February 2020 at the Koegelberg Nature Reserve, Western Cape. However, due to unforeseen events, extreme restrictions, and mobility constraints imposed on countries globally due to the COVID-19 pandemic beginning in mid-March- April 2020, this field study could not proceed. Although an impediment, a substantial and observable natural, inhabitable *A. belladonna* population and an opportunity co-exist for future study into the region's likelihood and incidence of another fynbos fire. This research may provide a deeper understanding of the species' fire-stimulated flowering mechanisms, responses, and patterns that may contribute to improving future naturalistic plantings and experimental studies.

In South Africa, efforts are ongoing to explore new techniques for developing underutilised indigenous crops and to recognise fynbos as an indigenous economic resource that requires interdisciplinary research. Moreover, sustainable cultivation, propagation, and postharvest management improvements are imperative to make South African plant species more accessible. This study has contributed to such requests by esteeming the indigenous bulbous species *A. belladonna*, which has not received adequate time and fortitude in earnest of integrative cultivation study as promoted and prominent among other Amaryllidaceae species, alluding to greater insight into the distinct and unique characteristic dispensation, limitations, and systematic approaches to overcome challenges. Likewise, since it was challenging to acquire cultivated *A. belladonna* plant material in significant quantities at wholesale or retail nurseries within the species-endemic Western Cape area and growers' collections were insufficient, not of adequate size (age), and not offered for purchase, this study emphasises and reinforces the value of this research and its contribution to enriching the species' practical cultivation. This study thus contributes to further research studies that may seek to recalibrate similar cultivation constraints of underutilised indigenous geophytic species and dispense more comprehensive theoretical, technological and practical knowledge to support commercial growers, conservationists, landowners, breeders and users in practice.

In theory and tangible practice, the current study's comprehensive research findings, conclusions, recommendations, and potential of *A. belladonna* are apparent. It is believed that this study's applied results in practice contribute valuable and novel material to developing and advancing cultivation practices at various stages of bulb development, thereby perpetuating prospects of enhanced economic value, quality, and reproducible commercial production for the competitive differentiation of *A. belladonna* in floricultural and horticultural markets.

CHAPTER 12

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APPENDICES

Appendix A: Publication of the manuscript "Flowering initiation in *Amaryllis belladonna*"

Flowering initiation in *Amaryllis belladonna*

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Abstract

An understanding of initiation and influencing factors are necessary to develop forcing techniques for flowering plants. The March lily (*Amaryllis belladonna*) is a late summer flowering bulbous plant of South Africa. The inflorescence bears 2-12 soft pink fragrant funnel-shaped flowers on 'naked' (leafless) stems. It makes an excellent potted plant and fresh cut flower lasting up to a week in a bouquet. Preliminary data of the aspects influencing the morphological changes to promote flower-bud initiation are discussed. These include physical traits of bulb size, age and dormancy; planting establishment with relevance to methods and bulb disturbance and the environmental factors of temperature, watering, day length and seasonal fire. This review is aimed to encourage further research and popularization to enhance the year-round growing of *A. belladonna* to expand its economic and commercial potential.

Keywords: naked ladies, cut flower, *Amaryllidaceae*, initiation, hysteranthous bulb

INTRODUCTION

Flowering of *Amaryllis belladonna* occurs in late summer which is different to many other flowering bulbous species, which flower in autumn, winter, spring and early summer. *A. belladonna* exhibits active growth in winter with the senescence of their leaves at the beginning of summer before the bulb goes dormant. As several environmental factors can affect bulb development and play a major role in flower development (De Hertogh and Le Nard, 1993) it remains unclear which are the contributing factors to initiate flower development in *A. belladonna.*

The family *Amaryllidaceae* consist of 59 genera and about 850 species with the biggest diversity in South America (28 genera), South Africa (18 genera), Mediterranean region (8 genera) and Australia (3 genera) (Adams, 2001; Snijman, 2004). Amaryllidaceae bulbs such as *Galanthus*, *Leucojum* and *Narcissus* are more adaptable to cooler temperate climates while *Amaryllis, Clivia, Hippeastrum, Nerine* and *Zephyranthes* are more suitable for warm temperate and subtropical climates (Snijman, 2004). Southern Africa has 210 endemic species consisting of 111 species in Namaqualand and the Cape Region with 77% of these found nowhere else in the world (Snijman, 2004). Most species in South Africa are well adapted and dependant to the occurrences of natural wildfires for their flowering and reproductive phases. Unfortunately, due to habitat loss, 59 species have become endangered and or vulnerable and 58 species are near threatened due to their habitat loss. Habitats consist mainly of ephemeral pools, river banks, seasonally dry places and the understorey of rainforests (Snijman, 2004). Species such as *Clivia, Cryptostephanus* and *Scadoxus*, have rhizomes while most other *Amaryllidaceae* have bulbous storage organs which grow well below ground (Snijman, 2004). While most *Amaryllidaceae* species have ornamental economic value many are traded as Traditional African Medicines. Most bulbs are highly toxic in large dosages and were mainly used for their psychoactive effects, *Amaryllis* which was used as arrow poison by Khoi and San tribes (Snijman, 2004; Duncan, 2010; Solomon, 2018).

This mini review is aimed at exploring factors which effect morphological changes in flowering initiation of *A. belladonna* to expand future research in improving flowering for economic and commercial potential.

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Appendix B: Publication of the manuscript "*Amaryllis belladonna*: A potential urban landscape wonder"

Amaryllis belladonna: a potential urban landscape wonder

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Abstract

***Amaryllis belladonna* is an indigenous bulb endemic to the southwestern Cape of South Africa and one of two members of the Cape genus. It is closely linked to the *Brunsvigia* and *Nerine* bulbous species. This bulb has a hysteranthous nature of showcasing the arrival of white to different shades of pink scented trumpet-shaped flowers in late summer to early autumn. By losing its leaves and going into dormancy in the height of summer, it conserves its resources making it a drought-tolerant summer blooming perennial found in nutrient-poor soils. In the wild the specie is well adapted to the fire-prone fynbos environment only after which it sends out blooms in abundance. In cultivation it requires minimum attention and considered to be an impressive and reliable garden landscape and rocky roadside ornamental. *A. belladonna* has proven to be a popular plant that has become naturalized in Mediterranean climates throughout the world. This review could enhance the use and design of *A. belladonna* in the urban landscape.**

Keywords: hysteranthy, fynbos, endemic, bulbous ornamental, Mediterranean

INTRODUCTION

South Africa boasts an abundant array and diversity of over 2700 indigenous bulbous species suitable to different climatic conditions. Countless genera endemic to the country have been popularized both locally and internationally for a variety of ornamental purposes (Manning et al., 2002; Barnhoorn, 2013). Many of these evergreen bulbs are much loved and are familiar plants in many garden landscapes however; the deciduous species are much less cultivated. These deciduous bulbs add an interest of colour and detail to areas for a short time and then go into dormancy; vanishing but surviving underground (Honig, 2014). Changes in temperature and seasonal rainfall are fundamental to a bulbs success in any landscape environment. An understanding of how a bulb reacts in and out of season requires patience. This is necessary to improve the plant and to overcome the problems especially associated with relocation and adaption of the plants between the different hemisphere climatic conditions (Reinten et al., 2011). Some South African plants have not been well researched in all basic aspects, thus remaining questions relating to the propagation, cultivation, natural behaviour and often the landscape use and design are absent. These factors are all required in order to fully understand the plants full marketable potential (Seale, 1985; Manning, 2007; Reinten et al., 2011; Barnhoorn, 2013). The aim of this review paper is to explore the use and design potential of *Amaryllis belladonna* L. (*Amaryllidaceae*) in the urban landscape.

AMARYLLIS BELLADONNA L. DESCRIPTION

Botanical description

A. belladonna is a South African indigenous deciduous true bulb more commonly known as the "Belladonna lily", "March lily" locally or the "Naked lady", "Madonna lily" or "Jersey lily" internationally. *A. belladonna* was for over more than two centuries considered the only species. In 1997, a second species, *A. paradisicola,* an equally beautiful specimen

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Appendix C: Publication of the manuscript "Evaluating hydroponic cultivation for ornamental bulbous species to enhance flowering and bulb production in a changing climate"

Evaluating hydroponic cultivation for ornamental bulbous species to enhance flowering and bulb production in a changing climate

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Abstract

The annual rhythmic cycle of ornamental bulbous species is highly dependent and tightly regulated by numerous abiotic signals for effective bulb formation and flower production. A flower bulb's developmental and seasonal cycle, capacity, and timeframe to reach a critical flowering maturation stage, multiplication and growing climatic regions is extremely diverse and is contingent on the species. The utilization of controlled, monitored, and flexible mechanisms with emphasis on hydroponic systems in maximising favorable growing conditions can potentially increase the knowledge-demanding and sustainable production and yield of these geophytes. Records of scientific studies on the variety of species cultivated in these conditions is limiting. This paper aims to assess the prospective possibilities of research, development, and innovative approaches to enhance the commercial production and flowering of a range of bulbous species as a climate-smart crop within a hydroponic setting.

Keywords: bulb development, controlled environment, flower bulb, nutrient solution, soilless substrates

INTRODUCTION

Global climate change and the adverse effects have created challenges to the demand and supply of specialized horticultural crops within different climatic regions around the world. The negative impacts of climate change have impacted on the growth and development of geophytes. The annual rhythmic cycle of ornamental bulbous species is highly dependent and tightly regulated by numerous environmental signals for effective bulb formation and flower production. A flower bulb's developmental and seasonal cycle, capacity, and timeframe to reach a critical flowering maturation stage, multiplication and growing climatic regions is extremely diverse and is contingent on the species. With the aim toward re-establishing, realigning, and overcoming these obstacles affecting bulbous geophytes, modern technological and inventive advances need to be researched and integrated to improve and enhance their commercial production. Hydroponics is a well-known alternative and innovative technology that has gained momentum and shown successful results in agricultural and ornamental crop cultivation. Hydroponic cultivation of geophytes has been documented with success through hydroponic forcing for the main intention of flower production however, the literature on a wider variety of species and specific developmental product target outcomes are limited.

This paper aims to seek the prospective possibilities of research, development, and benefits of growing a wider range of bulbous species and their floricultural product types as an environmentally friendly and sustainable crop using precision smart hydroponic techniques in a changing climate.

EFFECT OF CLIMATE CHANGE INFLUENCES ON BULB DEVELOPMENT

Climate change is a global phenomenon that has been researched extensively and the

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Appendix D: Full-text acceptance of the manuscript "Fire-stimulated flowering among South African geophytes: implications for biodiversity in a changing climate" to *Acta Horticulturae*

Zimbra **mail103560@telkomsa.net**

Acta Horticulturae - fulltext accepted : Fire-stimulated...

From : symposiacontributions@ishs.org Wed, Dec 04, 2024 08:20 PM
Subject : Acta Horticulturae - fulltext accepted : Fire-stimulated...
To : wilmot@telkomsa.net

Dear author,

This is to confirm that your article:
Fire-stimulated flowering among South African geophytes: implications for biodiversity in a changing climate
has been reviewed and is accepted by the editorial board of:
III International Symposium on Greener Cities: Improving Ecosystem Services in a Climate-Changing World (GreenCities2024)
for publication in Acta Horticulturae

Presenting Author: Ms. Carolyn Wilmot wilmot@telkomsa.net

Symposium details + contact information are available from:
https://www.ishs.org/symposium/808

Appendix E: Submitted manuscript “Flowering prolificacy of *Amaryllis belladonna* L. under ornamental garden conditions: The influence of population attributes, habitat features, and cultivation practices” to *Horticulture, Environment, and Biotechnology*

---------- Forwarded message ---------
From: **Horticulture, Environment, and Biotechnology Editorial Office** <em@editorialmanager.com>
Date: Sat, 20 Apr 2024, 7:40 am
Subject: HEAB-D-24-00217 - Submission Confirmation
To: Muhali Jimoh <moajay006@gmail.com>

Dear Dr Jimoh,

Thank you for submitting your manuscript,
"Flowering prolificacy of Amaryllis belladonna L. under ornamental garden conditions: The influence of population attributes, habitat features, and cultivation practices", to Horticulture, Environment, and Biotechnology

The submission id is: HEAB-D-24-00217
Please refer to this number in any future correspondence.

During the review process, you can keep track of the status of your manuscript.

Your username is: muhalijimoh
If you forgot your password, you can click the 'Send Login Details' link on the EM Login page at https://www.editorialmanager.com/heab/.

With kind regards,

Journals Editorial Office HEAB
Springer

Appendix F: Publication of the manuscript "Stimulatory effects of an exogenously applied seaweed extract on the morphological and physiological growth and yield in juvenile *Amaryllis belladonna* L. bulbs"

THE EGYPTIAN JOURNAL OF BOTANY (EJBO)

Stimulatory effects of an exogenously applied seaweed extract on the morphological and physiological growth and yield in juvenile *Amaryllis belladonna* L. bulbs

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[2]*Department of Plant Science, Olabisi Onabanjo University, P.M.B. 2002, Ago-Iwoye, Ogun State, Nigeria*

Amaryllis belladonna L. is a hysteranthous bulbous species indigenous to the Cape Floristic Region of South Africa. The species' attractiveness, adaptability, and low-maintenance needs have drawn international interest to its desirable uses in ornamental and landscape applications constrained by the observably slow rate of natural multiplication to reach flowering. A 24-week study was performed to determine the stimulatory effects of a seaweed extract, Kelpak®, on the morphological and physiological responses of *A. belladonna* bulbs cultivated under greenhouse conditions. Juvenile bulbs from five successive age groups were used to evaluate the consistency of observed responses. Treatments consisted of a 0% untreated control and three Kelpak® concentration dilutions at 0.2%, 0.4%, and 1% (v/v) administered to five age groups of *A. belladonna* bulbs as a monthly soil drench. The results showed that even at low concentrations, Kelpak® treatments improved the phyto-stimulatory responses of both the bulb aerial and, more substantially, the below-ground storage organs in a concentration-dependent manner. While treatments enhanced the morpho-physiological responses, the consistency of bulb age differed. Higher morphological yields were associated with older bulbs; however, bulbs of *A. belladonna* in years 1 and 2 were deemed the most receptive in circumference, weight coefficients, and chlorophyll content. However, to maximize the efficacy and proliferation rate of the species in a reduced timeframe, a 1% Kelpak® dilution applied at an early developmental stage within the first two years is most beneficial and a priority to elicit rapid, uniform, and healthy bulb growth and development.

Keywords: Amaryllidaceae, cultivation, juvenile bulb, Naked Lady, phytohormones, seaweed biostimulant

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INTRODUCTION

Amaryllis belladonna L. (Amaryllidaceae) more commonly known as the "Belladonna Lily", "March Lily" or "Naked Lady", is an endemic drought-tolerant ornamental bulbous geophyte from the Cape Floristic Region (CFR) of South Africa (Manning et al. 2002; Duncan et al. 2020). As a representative of only two species within the genus, it has become a popular plant that has migrated and naturalised in several Mediterranean climatic areas worldwide (Adams 2001; Duncan 2004; Duncan et al. 2020). The advent of pink-scented, trumpet-shaped flowers on a single inflorescence from late summer to early autumn signifies the bulb's hysteranthous nature and a species characteristic. The expansion of winter leaf growth subsequently follows this. As the seasonal transition into spring intensifies, bulb resources are preserved by the withering of leaves and the persistence of summer dormancy (Manning et al., 2002; Duncan, 2010; Duncan et al., 2020). The attractiveness, versatility, and low-maintenance requirements of this perennial bulbous species have drawn attention to their valuable and desirable uses in a variety of cultivated floricultural, ornamental, and landscape applications (Reinten et al. 2011; Wilmot and Laubscher 2019; Gul et al. 2020; Darras 2021).

Amaryllis belladonna is, however, severely constrained by the observably slow rate of natural multiplication as seedlings, juvenile bulbs (seedlings termed as juvenile bulbs after the first year of seed cultivation), and the division of offsets typically requires several years to attain a critical size competent for reproductive flowering (Theron and de Hertogh 2001; Duncan 2010). In addition, the recalcitrant seeds germinate almost instantaneously and do not survive desiccation; therefore, the seeds need to take advantage of the approaching autumn or winter rains to establish themselves adequately before the upcoming adversities of the summer dormancy period. (Duncan 2004; Duncan 2010; Colville 2017). Currently, the species is propagated primarily by conventional methods, which are the most affordable and simplest options from collected recalcitrant seeds and offsets (also referred to as daughter bulbs or bulblets) (Adams 2001; Duncan 2010). *In vitro* tissue culture has been tested (De Bruyn et al., 1992; Veeraballi et al., 2017), yet costly in comparison (Zhang et al., 2013). As a result, the timely entry of adequate and economically viable plant material into the horticultural distribution network is hindered. According to Kharrazi et al. (2017), Anderson (2019) and Li et al. (2023), the hampering juvenile period (lifecycle stages following

Appendix G: Publication of the manuscript “Regulated root zone water temperatures and soilless media improve bulb yield and offset production of hydroponically cultivated *Amaryllis belladonna* L.”

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Research Paper

Regulated root zone water temperatures and soilless media improve bulb yield and offset production of hydroponically cultivated *Amaryllis belladonna* L.

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ARTICLE INFO

Keywords:
Amaryllidaceae
Deep water culture
Hydroponics
Geophyte
Offset induction
Water temperature

ABSTRACT

The protracted natural bulb growth rate and offset generation constrain the timely expansion of bulbs in *Amaryllis belladonna*. An 18-month experiment was conducted to determine the efficacy of different root zone water temperatures and soilless media on the bulb yield and offset production of *A. belladonna* cultivated in a deep water culture hydroponic system. The study comprised dormant juvenile bulbs that were planted in plastic cavity trays filled with soilless media and suspended in heated water reservoirs at different temperatures (16 °C control, 22 °C, 28 °C, and 34 °C). The results found that the autonomous analysis of water temperatures, as opposed to soilless media and the combination, was significant. Warm root zone water temperatures ranging from 16 °C to 28 °C resulted in comparable aerial and subsurface morphological growth and development, promoting the vegetative proliferation of larger juvenile mother bulbs and offset induction. However, an excessively high temperature of 34 °C proved injurious and depleting. The results infer that the intrinsic processes for 'bulbing' were synchronized under inducive extrinsic hydroponic stimuli. A water temperature of 22 °C is recommended for long-term, sustainable production of simultaneously generating optimum reclaimable bulbs and offset generation to abridge the timeous cultivation of continuous A. belladonna vegetative bulb stock. A water temperature of 22 °C is recommended for long-term, sustainable production of simultaneously generating optimum bulbs and offset generation to abridge the timeous cultivation of continuous A. belladonna vegetative bulb stock.

1. Introduction

Geophytes are a diverse classification of flora, and their collective multiplicity is intensifying owing to ubiquitous market changes, competitive demands (Anderson 2006, 2019; Slezák et al., 2020) and the breeding of new cultivars with specialized and desired features (Marasek-Ciolakowska et al., 2021). Important scheduling ramifications to advance economic profitability are affected by selected bulb species, tubers and novel cultivars or hybrids with prolonged juvenile phases ranging between 8 and 25 years (Marasek-Ciolakowska et al., 2021). Thus, understanding and insight into a geophytic species' behavioural traits are critical to its advancement and provide tools for forecasting and implementing innovative strategies to determine responses under competitive and stringent conditions (Thompson et al., 2011; Kamenetsky-Goldstein, 2019; Slezák et al., 2020; Marković et al., 2021). Present geophytic research initiatives include those centred on vegetative propagation (Marković et al., 2021), a progressive decrease of the juvenile period, early selection of desired features (Anderson 2019; Marasek-Ciolakowska et al., 2021) and the procurement of indigenous and underutilized species (Reinten and Van Wyk, 2018; De Pascale and Romano, 2019; Darras, 2021).

Global ornamental cultivation practices have greatly revolutionized sophisticated agricultural practices to alleviate adverse conditions during the last three decades (Darras 2020, 2021). The regulated regimen of hydroponic technology allows for the precise management and use of long-term environmental conditions and inert soilless media transversely over multiple latitudinal regions. This results in widespread year-round production and enhanced crop yields per unit area (Wahome et al., 2010; Karagöz et al., 2022). Although the initial hydroponic investment is habitually capital-intensive and necessitates skilled

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Appendix H: Publication of the manuscript "Warm bulb storage optimises flowering attributes and foliage growth in *Amaryllis belladonna* L."

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Article

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,*]

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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].

Appendix I: Editors' Choice Article award for the publication title "Warm bulb storage optimises flowering attributes and foliage growth in *Amaryllis belladonna* L."


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CERTIFICATE OF PUBLICATION

EDITOR'S CHOICE ARTICLES

The certificate of publication for the article titled:

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

Authored by:

Carolyn Margaret Wilmot; Muhali Olaide Jimoh; Charles Petrus Laubscher

Published in:

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Appendix J: Declaration of doctoral candidate and co-authors' roles and contributions to each chapter/manuscript

Authors:	**C.M.W. – Carolyn Margaret Wilmot** **M.O.J. – Muhali Olaide Jimoh** **C.P.L. – Charles Petrus Laubscher**
Chapter 2:	Conceptualisation, C.M.W., M.O.J. and C.P.L.; methodology, C.M.W. and C.P.L.; validation, C.P.L. and M.O.J.; investigation, C.M.W. and C.P.L.; resources, C.M.W., C.P.L.; writing-original draft preparation, C.M.W.; writing, review and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 3:	Conceptualisation, C.M.W., and C.P.L.; methodology, C.M.W. and C.P.L.; validation, C.P.L.; resources, C.M.W., C.P.L.; writing-original draft preparation, C.M.W., C.P.L; writing, review and editing, C.M.W., C.P.L.; supervision, C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 4:	Conceptualisation, C.M.W., and C.P.L.; methodology, C.M.W. and C.P.L.; validation, C.P.L.; resources, C.M.W., C.P.L.; writing-original draft preparation, C.M.W., C.P.L; writing, review and editing, C.M.W., and C.P.L.; supervision, C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 5:	Conceptualisation, C.M.W., and C.P.L.; methodology, C.M.W. and C.P.L.; validation, C.P.L. and M.O.J.; resources, C.M.W., C.P.L.; writing-original draft preparation, C.M.W.; writing, review and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 6:	Conceptualisation, C.M.W., and C.P.L.; methodology, C.M.W. and C.P.L.; validation, C.P.L. and M.O.J.; resources, C.M.W., C.P.L.; writing-original draft preparation, C.M.W.; writing, review and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 7:	Conceptualisation, C.M.W., and C.P.L.; methodology, C.M.W. and C.P.L.; software, M.O.J. and C.M.W.; validation, C.P.L. and M.O.J.; formal analysis, C.M.W. and M.O.J.; investigation, C.M.W. and C.P.L.; resources, C.M.W., C.P.L.; data curation, M.O.J. and C.M.W.; writing-original draft preparation, C.M.W.; writing, review, and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 8:	Conceptualisation, C.M.W., M.O.J. and C.P.L.; methodology, C.M.W. and C.P.L.; software, M.O.J. and C.M.W.; validation, C.P.L. and M.O.J.; formal analysis, C.M.W. and M.O.J.; investigation, C.M.W. and C.P.L.; resources, C.M.W., C.P.L.; data curation, M.O.J. and C.M.W.; writing-original draft preparation, C.M.W.; writing, review, and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 9:	Conceptualisation, C.M.W., M.O.J. and C.P.L.; methodology, C.M.W. and C.P.L.; software, M.O.J. and C.M.W.; validation, C.P.L. and M.O.J.; formal analysis, C.M.W. and M.O.J.; investigation, C.M.W. and C.P.L.; resources, C.M.W., C.P.L.; data curation, M.O.J. and C.M.W.; writing-original draft preparation, C.M.W.; writing, review, and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.
Chapter 10:	Conceptualisation, C.M.W., M.O.J. and C.P.L.; methodology, C.M.W. and C.P.L.; software, M.O.J. and C.M.W.; validation, C.P.L. and M.O.J.; formal analysis, C.M.W. and M.O.J.; investigation, C.M.W. and C.P.L.; resources, C.M.W., C.P.L.; data curation, M.O.J. and C.M.W.; writing-original draft preparation, C.M.W.; writing, review and editing, C.M.W., M.O.J., and C.P.L.; supervision, M.O.J. and C.P.L.; project administration, C.P.L.; funding acquisition, C.P.L.

All authors read and agreed to the final version of each manuscript and the contributions made.