

TEMPERATURE EFFECTS ON BULB GROWTH AND INFLORESCENCE

DEVELOPMENT OF LACHENALIA cv. Ronina

by

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Abstract

Lachenalia cv. Ronina, a new flower bulb variety developed by the ARC-Roodeplaat Vegetable and Ornamental Plant Institute, has excellent characteristics as a flowering pot plant, but information on cultivation practices is limited. Temperature is the most important environmental factor regulating the growth cycle of this flower bulb, therefore three temperature regimes, representing a cool, moderate and warm winter climate, were chosen to manipulate floral development. During this study the bulb structure, development and growth were determined during the bulb preparation phase (year 1) and subsequently the morphology of the bulb was evaluated during the pot plant phase (year 2).

Regarding the bulb structure and development, cultivar Ronina has a typical rhythmic, sympodial, modular growth. Bulb growth and module formation is affected by temperature. The low (LTR) and moderate (MTR) temperature regime, which represent the cool and moderate winter climate in South Africa were found to be the best temperature regimes for bulb production. The high (HTR) temperature regime caused bulbs to develop faster, but flower abortion occurred. At the end of the bulb preparation phase, daughter bulbs were observed in the axils of the leaf bases in bulbs of all three temperature regime treatments. Additional inflorescences from underdeveloped growth modules were detected in the axils



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of the inner leaf bases of bulbs of the high temperature regime. The bulbs as well as the roots are the main sinks for the carbohydrates, whereas the inflorescence and especially the leaves are the main source for soluble sugars.

Due to the more stable temperature that was applied in the growth cabinets, the flowering date of bulbs in all three treatments flowered two months earlier than plants growing in the open. During this production phase, simultaneous flowering occurred more within bulbs that were subjected to the LTR during the bulb preparation phase. These bulbs also produced broader leaves with more spots on and better quality inflorescences with a longer keeping ability than those of the higher temperature regimes. A correlation was found between the leaf number and the number of inflorescences of plants in the pot plant phase, grown from LTR treated bulbs. The bulb fresh mass / size at the end of the bulb preparation phase cannot be used as a reliable criterion to predict the quality of the pot plant. By examining the bulb structure at the end of the bulb preparation phase, the quality of the pot plant can be predicted.

Keywords: Hyacinthaceae, bulb structure, pot plant, keeping ability



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CHAPTER 1

INTRODUCTION

Lachenalia pot plant production is a fairly new industry in South Africa and in the world and therefore a brief survey of the taxonomy, morphology and ecology will help the reader to obtain a better understanding of the rest of this thesis. Furthermore, the research program and production system, which is currently managed by the ARC - Roodeplaat Vegetable and Ornamental Plant Institute in South Africa, will be described. Finally, the importance of temperature in bulb growth and development will briefly be discussed.

1.1 Taxonomy

The genus *Lachenalia* Jacq.f. ex Murray belongs to the family Hyacinthaceae (Duncan, 1988) which was previously part of the family Liliaceae, *sensu lato* (Dahlgren, Clifford and Yeo, 1985). It is the largest genus in the family consisting of approximately 110 species (Duncan, 1988). According to Duncan (1992) a high degree of morphological variation, which exists within several species and the existence of many intermediate forms between related species, as well as the difficulty of identifying distinguishing characteristics that can be applied to delimit these species, has resulted in problematic taxonomy. A certain amount on the cytological aspects have brought to light a remarkably variable chromosome number amongst the species and it is thought by Duncan (1992) that further research in this area will be of great importance in accurately classifying this diverse group of geophytic plants.

The cultivar Ronina dealt with in this thesis is a hybrid between *L. aloides* (L.f.) Engl. and *L. reflexa* Thunb. (Hancke and Coertze, 1988). *Lachenalia aloides* is easily recognized by its lanceolate, usually heavily marked leaves and its inflorescence of pendulous, cylindrical flowers in which the inner perianth segments protrude conspicuously. *Lachenalia reflexa*,



is a dwarf species with one or two bright green leaves, which vary from lanceolate to lorate, usually reflexed and can be plain or heavily spotted on the upper surface. The leaf margins are often thickened and usually undulate. The peduncle is usually short and almost completely embraced by the leaf bases. The greenish-yellow, cylindrical-ventricose flowers are borne in an upright position, the outer perianth segments have green or greenish-yellow gibbosities and the inner segments protrude. Flowers fade to dull red as they mature (Duncan, 1988). This cultivar was considered as one of the best varieties for commercial use as a pot plant and this is why this plant was used in this study (Coertze *et al.*, 1992).

1.2 Description

The *Lachenalia* plant is a small bulbous geophyte. The storage organ is a true bulb with dry membranous tunics, which protect it from drying out and from physical injury. The genus exhibits a variety in leaf number per plant. In some species, the mature bulb produces one to two leaves, while others may produce up to eight leaves. Even in leaf shape the species differ from robust and broad to short and cylindrical. The colour, spotting and banding patterns as well as texture vary within the genus. The foliage can also grow into an upright or spreading position. In certain species, it also has been observed that leaves lie flat on the ground or in a rosette at ground level. Three different types of inflorescences are encountered in the genus, namely spicate, sub- spicate and racemose. A wide spectrum of flower colours exists in the genus from blue, green to yellow and red. Three flower shapes occur, namely horizontal pipes, hanging bells and hyacinth shapes. Some species even exhibit a pleasant odour. All these characteristics contribute to the attractiveness of the plant (Duncan, 1988).

1.3 Distribution and Habitat

Lachenalia is endemic to Southern Africa where it has a wide distribution from the south-

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western region of Namibia, south through-out the Cape Province of South Africa to as far inland as the south-western Free State, from where its probable boundary makes an arc to the south-east down to the Eastern Cape to the east coast. The genus is mainly concentrated in the north-western, western and south-western parts of the Cape province which experiences a mediterranean -type climate with winter rainfall and the overwhelming majority of the species follow a winter growth cycle (Duncan, 1988).

Due to its wide distribution, the genus is encountered in a very wide range of habitats, such as semi-desert conditions in deep sand, rocky outcrops in humus-rich soil, seasonally inundated flats and marshes and high rainfall montane conditions (Duncan, 1992).

1.4 Establishment of the Lachenalia research program

Floriculture is emerging as a high-value industry in many Sub-Saharan economies, where it contributes to creating employment and generating foreign exchange (World Bank, 1996). The flower bulb industry as a sector of the floriculture industry comprises two sub-sectors, namely dry bulb sales directly for the public and bulbs for the so-called 'forcing sector' (production of cut-flowers and potted bulbs under controlled conditions). Because flower bulbs have an important share in the floriculture industry and the world wide demand for cut-flowers and potted plants rises by about 3-5 percent annually, forcing of bulbs became an important industry (Kleijn and Heybroek, 1992). *Lachenalia* varieties can be used in the floriculture industry for potted plants and cut flowers as well as garden bulbs for the following valuable characteristics (Hancke, 1991):

- Large variation in appearance exists within the genus.
- The genus has a long flowering period from May to September.
- The flowers of the inflorescence are long lasting, from 4 to 6 weeks.
- The plants can be propagated vegetatively without problems. This can be done by means of bulblet production from leaf cuttings, spontaneous daughter bulb and

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bulblet formation from active growing bulb and tissue culture.

The plants have a low temperature and light requirement during the active growing season. It thus has a low energy requirement thereby reducing production costs.

In addition to Hanke's (1991) list of characters, the fact that the bulbs can be taken out from the substrate and stored, makes post harvest handling and physiological manipulation much easier for the grower.

Based on the mentioned characteristics, the *Lachenalia* research program at ARC-Roodeplaat started in 1965 and has gone through several evolutionary phases (Niederwieser *et al.*, 1998), namely:

- From 1965-1972, the focus was on developing procedures and techniques for maintenance and storage of bulbs, growing conditions, hybridization, pollen storage, seed germination, seedling growth, as well as the propagation of *Lachenalia*.
- From 1972-1982, the major emphasis of the program was on the production of hybrids.
- From 1983-1991, less emphasis was directed to breeding, but more effort was put on the initiation of trials abroad and the establishment of an international network to introduce *Lachenalia* to the international flower bulb market. The most significant achievement during this period was the development of tissue culture techniques for producing virus-free planting material.

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From 1992 to date, a multi-disciplinary research program was established to intensify efforts to commercialize the *Lachenalia* production. Priorities were focussed on flower manipulation studies, optimal temperature for pot plant cultivation, elimination of the virus infected plants, developing hybrid evaluation systems, production of propagation materials and trials on vegetative propagation



methods.

1.5 **Production system**

Lachenalia varieties are mainly produced in the summer rainfall area where winters are more severe than in natural habitats, although these plants have seldom been lost during cold spells. This production situation developed primarily due to the breeding program that was conducted at ARC - Roodeplaat, which is situated in the proximity of the majority of flower and bulb growers in South Africa. The production of bulbs is done under shade net and plants are grown in a composted bark mixture. At present, the production of *Lachenalia* consists of four phases (Figure 1.1) that differ distinctly, namely:

- (1) Bulblet production from cuttings followed by a dormant phase
- (2) Bulb enlargement followed by a dormant phase
- (3) Bulb preparation followed by a dormant phase
- (4) Pot plant production

The objective of phase 1 is to propagate disease-free bulbs by means of leaf cuttings under out door conditions and in tissue culture. Bulbs obtained from phase 1, that are too small for the bulb preparation phase (phase 3), are grown for another season (phase 2) to reach a bulb size of 4-5 cm in circumference (\pm 1g). The objective of phase 3 is to obtain a maximum bulb size of 5-6 to \geq 9 cm in circumference, coupled with a good keeping quality to ensure that high quality pot plants will be obtained during the next season (phase 4), following an extended dormant period. The objective of phase 4 is to produce a uniform, high quality crop with a good shelf life within the shortest possible period with the lowest inputs. After this phase the mother bulb tend to decrease in size or break up in daughter bulbs, whilst the daughter bulbs grow independently into different sizes. Normally the bulbs of these pot plants, which are sold to the consumer, are planted in their gardens. If not sold, these bulbs are then taken up in the production system and grouped into different production phases according to their size.



During storage periods the dormant bulbs are cleaned, stored in flat trays and stacked in well ventilated rooms at a relative humidity (RH) of 60-70%. Storage temperatures vary according to the ultimate use of the bulbs (Figure 1.1). Phase1 and 2 bulbs are stored at 25°C until planting for the next phase and phase 3 bulbs, which have been prepared for the pot plant phase (phase 4), are stored at different temperatures. Soon after harvest, phase 3 bulbs are stored at 35° C for ± 14 days to ensure a uniform crop the next season (phase 4) (Louw, 1991). After this high temperature storage, the bulbs are stored at 25° C until required stage for flower differentiation and then they are stored at 13° C for two weeks to enhance flower development before planting (Louw, 1991; Niederwieser *et al.* 1997).

1.6 Influence of temperature on bulb growth and development

In order to verify the temperature whereby a newly bred plant is cultivated, the environmental conditions of their natural habitat must be understood. *Lachenalia* species naturally occur in winter rainfall areas where the winter season is regarded as mild. These bulbs survive the mild to hot dry summers in the form of a resting bulb (Duncan, 1988; Hancke, 1991).

According to Louw (1991) the monthly mean, maximum and minimum temperatures are surprisingly uniform for all the *Lachenalia* growth regions in comparison with other environmental factors. From this it can be deduced that temperature plays an important role in the physiology of *Lachenalia*. In the winter the temperatures are seldom lower than 5°C, with a mean of 12°C and a maximum of 18°C. In the summer the temperatures are seldom higher than 30°C with a mean of 22°C and a minimum of 18°C (Louw, 1991).

Temperature plays an important role in plant growth during greenhouse forcing. For example, in Dutch irises, the prevailing temperature, after planting, is one of main factors affecting plant growth. For instance, temperatures only above 6°C lead to faster plant growth (Fortanier and Zevenbergen, 1973), however, a high soil temperature after planting

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may result in short stems. This effect might be due to pre-mature anthesis, which occurs separately from stem extension (De Hertogh and Le Nard, 1993). In *Lilium longiflorum* temperature affects all aspects of greenhouse forcing including shoot emergence, leaf unfolding and flower development (Smith and Langhans, 1962). According to Smith and Langhans (1962) warmer temperatures tended to produce taller plants and increased flower abortion. Nevertheless, Roh and Wilkins (1973) reported that the response to temperature is not linear and temperatures above 21° C have little additional effect in accelerating plant development in *L. longiflorum*. In addition, De Hertogh *et al.* (1976) showed that at 13° C, raised primary flowers of *L. longiflorum* were increased and secondary flowers inhibited. The opposite was true at 21° C, where secondary flower formation was stimulated and raised primaries repressed.

For *Tulipa*, greenhouse temperatures for precooled bulbs are generally maintained at a maximum of 16-18°C. A lower temperature during the first days after planting enhances rooting. If the temperature remains low, flowering is delayed but an increase in stem length at anthesis is observed (De Hertogh and Le Nard, 1993). In addition, Dosser and Larson (1981) observed that forcing temperatures of 26°C day / 22°C night led to a lower flower percentage. Even in *Hyacinthus*, greenhouse temperatures are controlled for rapid flowering. First the temperature is held at 10-13°C for a few days, then followed by 23°C until the first signs of colour development (De Hertogh and Le Nard, 1993). In above mentioned bulb, higher temperatures immediately after the cold treatment may result in the detachment of the inflorescence, this is known as 'Spitting' (Bergman, 1983).

Nevertheless, there is no published information available on the effect the growing temperature during the bulb preparation phase might have on the performance of *Lachenalia* (as a pot plant) during the pot plant phase (Figure 1.1, Phase 4). Louw (1991) was the first researcher who studied the effect of different storage temperatures on inflorescence initiation, differentiation and subsequently development in a *Lachenalia* bulb. However, the focus was on cultivar Romelia. Afterwards, similar articles on storage temperatures were published by Roh *et al.* (1995). Therefore, this study will unfold many

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problem areas in the production system.

1.7 The aim of this study

Development of a new crop includes a combination of superior plant material, production technology and marketing strategies. Regarding production technology, research results are limited and accurate information on the temperature to be used for optimal bulb production as well as for the cultivation of high quality pot plants is not available. The aim of this study therefore was:

- To make a proper study of the bulb structure and architecture during the growth phases
- To manipulate plants during the different growth phases to determine the effect on flower production and quality using different temperature regimes
- To determine carbohydrate partitioning in the different plant parts and relate this to the plant's performance

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PHASE 1

Bulblet production from cuttings



STORAGE (25°C)

PHASE 2

Bulb enlargement: Showing bulbs at end of phase 2



STORAGE (25°C)

PHASE 3

Bulb preparation: Showing bulb at end of phase 3



STORAGE (25°C+13°C)

PHASE 4

Pot plant production



Figure 1.1 Schematic illustration of four production phases of Lachenalia.



CHAPTER 2

BULB GROWTH AND STRUCTURE

2.1 Summary

The annual growth cycle of most *Lachenalia* species is characterised by active leaf growth during autumn, flowering during winter, followed by leaf senescence and a dormant period during the hot dry summer (Duncan, 1988). Being a fairly new introduction to the flower market, there is a demand for high quality, marketable size bulbs, but due to the lack of information regarding bulb growth and structure, there is a great need for further research.

The plants normally have a typical rhythmic, sympodial, modular growth. At the time of planting the bulbs consisted of a swollen bulb scale (cataphyll) and two swollen leaf bases (euphyll) of the previous module, surrounding the initials of the new module consisting of two cataphylls, two euphyll primordia and an inflorescence primordium. No 'supernumery bulblets' were observed in this cultivar, but at the end of the growing cycle, daughter bulbs were detected in the axils of the swollen leaf bases.

2.2 Introduction

The annual life cycle of *Lachenalia* is characterised by active leaf growth during autumn, a long flowering period from winter to spring, followed by leaf senescence and a dormant period during the hot dry summer (Duncan, 1988). This kind of growth cycle, with a definite dormant phase, is one of the main reasons why *Lachenalia* bulbs show great potential during dull winter seasons as an ornamental to be used as pot plants, cut flowers or as garden plants massed in formal beds and borders.



Information on the onset and duration of various stages of bulb growth and development for a quality end-product is not yet available for *Lachenalia* commercialization. Manipulation of bulb growth is dependant on an understanding of bulb construction and growth habitat. Most bulbs are constructed by a series of morphologically equal, consecutive units or modules and are therefore described as modular (Bell, 1991). Each bulb of *Lachenalia* is a sympodium (Roodbol and Niederwieser, 1998), which means that it consists of a series of units which are determinate due to the consumption of the apical bud during inflorescence development (Bell, 1991). The bulb structure of cultivar Romelia was described by Roodbol and Niederwieser (1998), but some additional details are still required for a clear understanding of the phenological changes of the plant during the growing season and storage of bulbs.

The objectives of this study were to determine the effect of different temperature treatments on the development of bulb units (growth modules) up to a marketable size and to describe the annual growth cycle of cultivar Ronina plants during this period.

2.3 Materials and Methods

Sixteen- months- old bulbs (± 1 g), 4 cm in circumference, were selected after a first growing season (phase 2 in Figure 1.1). Temperature, day length and light intensity throughout the phase 2 followed a natural, seasonal pattern characteristic for the Pretoria region. At the end of the growing season in early summer, the bulbs were collected and stored dry at 25°C until autumn of the following year (phase 3 in Figure 1.1). When this experiment started, a temperature regime representing the monthly average minimum and maximum temperature for the Pretoria region, was chosen for growing these phase 3 bulbs to a flowering export quality size (± 8 g).

Four hundred bulbs were individually planted in 9 cm plastic pots containing sterilised composted bark mixture as growth medium and grown in a temperature controlled cabinet



(Model PGW - 36, Conviron, Canada) at $22^{\circ}/10^{\circ}$ C day/night, with 14 hours illumination at $\pm 200 \mu$ mol.m².s⁻¹ PAR. Bulbs were watered three times a week to field capacity, but from mid-August (22 weeks after planting) watering frequencies were gradually decreased and temperatures were increased to $32^{\circ}/20^{\circ}$ C until mid-October (30 weeks after planting) when no water was applied and day-night temperatures were raised to a constant 35° C to force bulbs into a dormant stage before harvesting and storage. During the growing season, ten bulbs were randomly collected at 2 week intervals until the end of the experiment when remaining bulbs were harvested on the 15^{th} of November.

Every fourth week the dry weight and circumference of the sampled bulbs were measured. Since growth was mainly the result of morphological changes in the bulb, it was also necessary to look at bulb structure. Morphological studies were therefore conducted on these bulbs by means of serial hand sections, ± 1 mm thick, made at planes perpendicular and parallel to the bulb axis. Sections were stained with toluidine blue (O'Brien and McCully, 1981) and studied, using a dissection microscope. Bulbs were also taken apart by removing single scales from outside to the centre to supplement the observations on the sections.

2.4 Results and Discussion

2.4.1 Bulb growth

Figure 2.1 illustrates the sigmoidal growth pattern of the bulbs expressed in terms of circumference and dry mass. During the first 14 weeks after planting, bulbs showed little change in their dry mass and circumference (Figure 2.1), probably due to the root system that developed extensively during water uptake and the reduction in bulb size which will be discussed under 'Bulb structure'. After anthesis (\pm 16 weeks after planting), the bulb size increased markedly reaching an average of 8.83 cm during August. From mid-August (\pm 22 weeks after planting) to mid-November (at harvest) bulb dry mass decreased, probably due to the reduced watering frequency, deterioration of inflorescence parts as well as the



cataphyll (bulb scale) becoming more tunicate.

2.4.2 Bulb structure

At the time of planting (Figure 2.2) the bulb consisted of two modules, namely the new module (module x1) situated inside the previous year's module (module x). Similar development was described in cultivar Romelia (Roodbol and Niederwieser, 1998), but during this study differences in the modular growth pattern, as well as in plant parts described, were observed within bulbs of cultivar Ronina. In Figure 2.2 a it is shown that a bulb module consists of a dry papery tunic which was the 2^{nd} cataphyll (MxC2) in the old module (Year I) and two thickened leaf bases (MxL1;MxL2) from the discarded leaf laminas of the previous module (module x). The new module (module x1) comprised two cataphylls (Mx1C1;Mx1C2) and two green leaves (Mx1L1;Mx1L2) enclosing the differentiating terminal inflorescence (Mx1Inf) for Year II. At this stage the root primordia were already present around the periphery of the basal plate.

The cataphylls are neotenic leaves (reaching maturity in the primordial stage) and are mainly devoid of chlorophyll, even above the soil, therefore typical bracts which will usually not grow out of the bulb to produce a lamina, but play an important role in protecting the young apical bud (Bell, 1991).

Two weeks after planting, the leaves (Mx1L1;Mx1L2 in Figure 2.2) and their 2nd cataphyll were visible above the substrate. This bulb scale (Mx1C2) enclosing the leaves extend its semi-transparent membranous distal part above the substrate during this period, but hardly ever produces a lamina and could not possibly have a leaf scar (Rees, 1969). At the end of the growing season this scale becomes mainly tunicate. According to Roodbol and Niederwieser (1998) this cataphyll is called a thin bract and in cultivar Romelia it was visible above the soil within four weeks after planting.



Approximately six weeks after planting the young bud of the next module (module x1) was fully developed and clearly visible inside the bulbs (Figure 2.2 a and 2.3 a). The 1st cataphyll of the new module (Mx1C1), enclosing the second cataphyll (Mx1C2), the leaves (Mx1L1;Mx1L2) and the differentiating inflorescence (Mx1Inf) when young, never grew out with the leaves, but instead was reduced in size to become a small bract at anthesis and disintegrated during senescence of aerial parts with the result that it was often missed or was even absent at the time of bulb inspection. This bract is morphologically the true prophyll which is the leaf at the first (proximal) node on a shoot (Bell, 1991). Roodbol and Niederwieser (1998) used the term bulb scale for this cataphyll in describing the bulb structure, however, in cultivar Romelia, apart from the one prophyll, mainly observed, up to three may be present.

During the period of ± 6 weeks after planting, no adventitious supernumery bulbs, as described in cultivar Romelia (Roodbol and Niederwieser, 1998), were observed in the axillary meristem of the cataphylls or leaf bases of module x1 (Figure 2.3 a). The thickened leaf bases (MxL1;MxL2) of the old module continued reducing in size, probably due to the loss of carbohydrates being translocated to the aerial parts (see Chapter 5 for confirmation).

After 10 weeks (mid-May), floral emergence occurred in the bulbs and a new lateral apical bud (module x2) was observed on the basal plate of the sampled bulbs (Figure 2.3 b) where the abaxial side of the prophyll (Mx2C1) was facing the inflorescence (Mx1Inf) of the previous module (inflorescence of the current season) (Figure 2.3 c). This bud continued to develop to become the new module with the terminal inflorescence after the flowering of the previous module. A new lateral bud proximal to it will develop and continue to repeat the whole process again.

Approximately two weeks after floral emergence (± 12 weeks after planting), the plants were in full-bloom (anthesis). The inflorescence (Mx2Inf) of the newest module did not develop or emerge after the primary one, but was already preformed for the next season. No additional inflorescences were observed in the axils of the leaf bases. However, in cultivar



Romelia a secondary inflorescence was observed in 20% of the bulbs dissected (Roodbol and Niederwieser, 1998). In this report these inflorescences were not diagrammatically described nor discussed, therefore one cannot verify from where they initiated within the bulb. Twenty six weeks after planting during mid-September, the current season's inflorescence (Mx1Inf) started to die off in preparation towards the dormant phase (absence of visible external growth). By mid-October (\pm 30 weeks after planting) all primordia of module 3 were visible inside the bulb and the rest of the aerial parts of the bulbs died-off before entering the dormant phase.

By mid-November (± 34 weeks after planting), flower differentiation occurred in Mx2Inf and the leaves (Mx2L1;Mx2L2) as well as the two cataphylls (Mx2C1;Mx2C2) of module x2 in the bulbs were visible (Figure 2.3 c). During this period the most resent lateral bud (module x3) was observed.

Two new modules (module x2 and x3) were therefore formed at the end of the growing season. These modules will, under favourable conditions, probably continue to develop after harvesting, during the dormant phase, meaning that inflorescence initiation is spontaneous and before dormancy. These results are in contradiction with those of Louw (1991) and Roh *et al.* (1995) who stated that *Lachenalia* inflorescences are only initiated during dormancy. The inflorescence is in fact the product of the apical meristem of each module, but flower differentiation does occur during dormancy.

Daughter bulbs were also visible from this stage in $\pm 40\%$ of the bulbs dissected. Figure 2.3 c illustrates that these daughter bulbs (Db) were formed close to the remnants of the of the inflorescence scape (Mx1Inf1), mainly in the axil of the outer swollen leaf base (Mx1L1). Between the inner leaf bases (Mx1L2) daughter bulbs were also observed in a few bulbs dissected.

2.5 Conclusion



In this chapter the bulb architecture was interpreted and described for the first time in terms of modular, sympodial growth by applying existing botanical terminology and principles. This description can form the basis for future work on bulb manipulation in *Lachenalia*. It was also shown in this experiment that inflorescence differentiation occurred before dormancy concurrently with modular formation and not during dormancy, as previously described by Roodbol and Niederwieser (1998) on cultivar Romelia.

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Figure 2.1 Sigmoidal growth pattern of bulbs in terms of circumference (cm) and dry mass (g) from planting to harvesting.





a.) Cross section of a bulb illustrating the development of a new apical bud (module) at the planting stage.



b.) Diagram of the construction of a modular structure.

Figure 2.2 Illustration of the modular growth pattern at the stage of planting.

Inf - inflorescence	Db -
L1 - leaf	Mx -
L2 - second leaf	Ab -
C1 - cataphyll (bract)	inflo
C2 - cataphyll (true bulb scale)	

Db - daughter bulbs Mx - Module Ab - Apical bud (containing C1,C2, L1, L2 & inflorescence, thus a new growth module)



a) Cross section of a bulb, \pm six weeks after planting



b) Longitudinal section of a bulb, ± 10 weeks after planting



c) Cross section of a bulb, at harvest (± 34 weeks after planting)

Figure 2.3 Developmental stages of the bulb during the growing season.

Inf - inflorescence

- L1 leaf
- L2 second leaf
- C1 cataphyll (bract)
- C2 cataphyll (true bulb scale)

Db - daughter bulbs Mx - Module Ab - Apical bud (containing C1,C2, L1, L2 & inflorescence, thus a new growth module)

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CHAPTER 3

TEMPERATURE EFFECT ON THE PLANT GROWTH DURING THE BULB PREPARATION PHASE

3.1 Summary

The effect of three temperature regimes on the growth of small bulbs of cultivar Ronina to flowering size $(\pm 7 \text{ g})$ was studied. Potted bulbs were grown in three temperature controlled cabinets with temperature regimes chosen to represent a cool, a moderate and a warm winter. Plants were destructively harvested to investigate environmental effects on plant morphology and additionally flowering, anthesis and flower senescence were monitored.

Under all three temperature regimes bulb growth followed a typical sigmoidal curve. In general root growth does not support optimal bulb size under the different temperature regimes. Leaf growth in plants under the moderate temperature regime was more vigorous and foliage had a healthier appearance than under the low and high temperature regime treatments. Inflorescence emergence was earlier under the low and moderate temperature regime. At the end of the growing season, bulbs grown under the high temperature treatment formed additional inflorescences. The best temperature regimes for *Lachenalia* bulb production during the bulb preparation phase were the low and moderate temperature regime, which represented the cool and moderate winter climate in South Africa.

3.2 Introduction

Lachenalia cv. Ronina is a variety with excellent characteristics as a flowering pot plant (Coertze *et al.*, 1997; Niederwieser *et al.*, 1997). Increased production and export of Lachenalia bulbs may help South Africa to increase its share in the international bulb trade. To improve production and growing of bulbs, information is needed on the effect of climatic factors on growth and yield of bulbs, as South Africa has tremendous climatic diversity that



ranges from summer to winter rainfall regions, arid to humid zones, and temperate to tropical areas. Additionally there is much variation both in and between *Lachenalia* species that may also include optimal growing conditions. *Lachenalia* spp. follow the growth cycle of winter rainfall plants which entails rapid vegetative growth in autumn (April to May), followed by flowering in winter and spring (June to September). Flowering and fruiting is followed by a long dormant period during the hot dry summer months (November to March) (Duncan, 1988).

Temperature is the most important environmental factor in regulating the growth cycle of bulbs, whilst day length has little effect (Rees, 1992) in the Hyacinthaceae family to which *Lachenalia* belongs. For *Lachenalia*, the effects of temperature that have been studied, are long term *in vitro* storage of vegetative material (Louw, 1992), *in vivo* bulb storage for successful flower forcing (Louw, 1991) and *in vitro* bulblet formation (Slabbert and Niederwieser, 1999). No significant information on the effects of temperature on the growth and flowering of *Lachenalia* during the growing season has been reported previously (De Hertogh and Le Nard, 1993; Roodbol and Niederwieser, 1998).

The objectives in this chapter were to determine the effect of three temperature regimes on the growth and development of bulbs during the growing season. As this was the first study of its kind, temperature regimes were chosen to represent a cool, a moderate and a warm winter climate. This experiment was repeated for two consecutive seasons with very similar results. For practical reasons, only the second year's results are reported in this chapter.

3.3 Materials and Methods

The 1200 bulbs of cultivar Ronina, which weighed about 1g each (See phase 3 in Figure 1.1 for size and appearance), were obtained from the ARC-Roodeplaat Vegetable and Ornamental Plant Institute, after approximately four months of storage at 25°C.

The bulbs were planted singly into 9 cm plastic pots containing sterilized, composted bark. On the first of March 400 pots containing the bulbs were placed into each of three growth


cabinets (Model PGW-36, Conviron, Canada). The growth cabinets provided a 14 hr photoperiod with a light intensity of $\pm 200 \ \mu \text{mol.m}^2 \text{.s}^{-1}$ PAR at plant level. Lighting was provided by a combination of WHO fluorescent and incandescent bulbs. Each growth cabinet was adjusted to provide a different temperature regime as described in Table 3.1. The temperature regimes were chosen to represent a cool (LTR), a moderate (MTR) and warm (HTR) winter climate.

The plants were watered to field capacity three times a week using distilled water, except for the high temperature treatment in which plants were watered daily, because signs of water stress had been observed in a preliminary trial watered three times a week. From the fifteenth of August (22 weeks after planting) till the fifteenth of October (30 weeks after planting), watering frequencies in the cabinets were gradually reduced to simulate the onset of the dry summer season and to force the bulbs into dormancy.

The four hundred bulbs in each cabinet were randomly divided into ten replicates of 40 plants. On the fifteenth of every month during the growing season, one plant from each replicate (10 plants per cabinet) was selected at random and dissected into bulbs, roots, leaves and inflorescence (when visible), after which the fresh mass of each portion was determined. Previous trials had shown very high correlations between fresh and dry mass of bulbs, leaves and roots, which was also confirmed in Chapter 6. The percentage of plants with inflorescences at different stages of development (emergence, anthesis and senescence) was determined for the three temperature regimes.

Data were analysed using the PROC. G.L.M. (General Linear Models) procedure in the S.A.S. (Statistical Analysis System) program. Analysis of Variance was performed and Tukey's studentized range test (Steele and Torrie, 1980) was applied to compare treatment means.

3.4 Results and Discussion



3.4.1 Bulb growth

The fresh mass of the various parts of the plants grown under the three temperature regimes is shown in Figure 3.1. Bulb growth followed a typical sigmoidal curve up to flowering, irrespective of the treatments (Figure 3.1 a). Similar results were reported by Roodbol and Niederwieser (1998) on cultivar Romelia grown under moderate winter conditions. After full-bloom (June-July; ± 16 weeks after planting), further increase in bulb mass coincided with flower senescence. In all treatments, bulb mass continued to increase until late August to mid September, when the watering frequency was reduced from the 15th of August. This phenomenon is a result of translocation of assimilates from leaves that started senescing during August. In Chapter 5, the continuous decrease of sugars in leaves and increase of starch in bulbs during full-bloom is illustrated in Figure 5.1 and 5.2. Rees (1992) supports the concept that assimilates produced by the aerial parts of the plant during the active growing season are translocated to the storage organs until the aerial parts die down.

Bulbs from the LTR became dormant one month earlier (October) than those from the HTR and MTR as indicated by the absence of roots and leaves in the LTR plants in October (Figure 3.1 b and c). The low temperature regime initially reduced the developmental rate of the different plant parts, but subsequently resulted in a faster development (earlier plant maturity), which is an inducing effect of a low temperature treatment.

Bulb fresh mass decreased from October to November (30 weeks after planting) (Figure 3.1 a). This was probably due to moisture loss caused by the high temperature treatment $(35^{\circ}C)$ before the storage of the dormant bulbs (Table 3.1).

Significant differences in bulb size (Figure 3.1a) between the three temperature treatments were obtained at the end of the bulb preparation phase. Figure 3.1 a illustrates that the final bulb fresh mass of the LTR was greater than those of the HTR and MTR. It seems as if bulbs of the LTR (Figure 3.2) performed the best in terms of bulb fresh mass, but only until



September (week 26). After September there is no significant difference in fresh mass between the HTR, MTR and LTR bulbs.

3.4.2 Root growth

Root mass is shown in Figure 3.1 b. The fresh mass of the roots increased for the first four months in all treatments. The roots' maximum fresh mass was reached between July and August (18-22 weeks after planting) and coincided with the leaves reaching their maximum biomass (Figure 3.1 c) and the plants reaching full-bloom (Figure 3.1 d). After full bloom the fresh mass of the roots decreased rapidly as the plant became senescent. After full-bloom the maximum root fresh mass of HTR plants was almost always significantly greater than the other treatments and declined more slowly. This indicates that exposure to high temperatures for a long period promoted root growth. This observation confirms the results of similar studies done by Le Nard (1980) on tulips and Jennings and De Hertogh (1977) on tulips, daffodils and hyacinths. For the commercial grower, these results reflect that optimal root growth during the production phase does not necessarily promote the final bulb size.

3.4.3 Leaf growth

Leaf fresh mass increased until August in all treatments (Figure 3.1 c) after which it declined. It is also important to notice that the fresh mass of the LTR leaves was always significantly lower than those of the higher temperature regimes, although the quality of these bulbs was better at the end of the bulb preparation phase. In addition, there were obvious morphological differences between the leaves of different temperature treatments. The MTR leaves were robust, broad, lanceolate, upright and healthy. Leaves of the HTR were long, narrow and curved, whereas leaves of the LTR were broad. These results show that the MTR leaves grew more vigorously and appeared more attractive than those of the



LTR and HTR for much of the year. This phenomenon has an impact on the quality and appearance of the ornamental pot plants.

3.4.4 Whole plant growth

The LTR resulted in a significantly lower fresh mass of aerial leaf parts and also on roots, but it had a positive effect on bulb growth. The low fresh mass could primarily be due to diversion of nutrients from aerial leaf parts and roots to the bulbs for enlargement, thus restricting optimal leaf and root growth of LTR bulbs. Le Nard and Cohat (1968) also reported that, depending on the duration of a cold treatment, root growth and elongation of aerial organs can be retarded in *Tulipa*, while bulb growth increases.

3.4.5 Growth of inflorescences

During peak flowering (June to July; ± 16 weeks after planting), the fresh mass of the MTR and LTR inflorescences were significantly higher (Figure 3.1 d) than those of the HTR. The reason for the lower fresh mass of the HTR bulbs was that they produced a shorter peduncle and rachis and flower abortion occurred. Roh *et al.* (1995) recorded that when *Lachenalia* bulbs are forced at high temperatures before the inflorescence become visible, flower bud blasting (abortion) occurs and the scape fails to elongate. However, after the visible inflorescence stage, a high temperature, according to Roh *et al.* (1995), is supposed to accelerate flowering. As discussed in Chapter 2, bulb growth is modular, therefore the temperature did cause flower failure in the developing inflorescences. The high temperature regime was probably too extreme and therefore had a negative effect on inflorescence quality (De Hertogh and Le Nard, 1993).

During August, September and October (22 weeks after planting), additional inflorescences were observed in the HTR bulbs (Table 3.2 and Figure 3.3) and it seems as if the warm



temperature regime induced the initiation of additional inflorescences due to flower abortion that occurred after emergence in the growing season. Figure 3.3 illustrates the emergence of an additional inflorescence after the senescence of the primary one. Louw (1992) found a similar effect with *Lachenalia* cv. Romelia bulbs when stored at a high temperature for a long period.

MTR and LTR inflorescences emerged earlier than those of the HTR (Figure 3.1 d and Table 3.2). Similar results were reported by Le Nard (1972) and Beijer (1942) in tulips, where a high storage temperature (30° C) followed by a transfer to a lower temperature (20° C) resulted in earlier flower bud differentiation. Thus, when 25° C dry-stored bulbs from phase 2 (Figure 1.1) were planted and grown under an extended high temperature regime (HTR - 28° / 12° C day / night) in the bulb preparation phase (phase 3), a delay in inflorescence emergence followed. However, when these bulbs were subjected to lower temperatures (MTR - 22° / 10° C day / night and LTR - 15° / 5° C day / night) during the bulb preparation phase, inflorescence development was enhanced which resulted in earlier emergence. Roh and Meerow (1992) also stated that temperature plays an important role in inducing early flowering of *Eucrosia bicolor* bulbs. Gilford and Rees (1973) and Shoub and De Hertogh (1975) on the other hand, hypothesized that the lower flower shoot growth rate observed immediately after planting could be related to root growth and the possible fact that food reserves are diverted from the shoot and scales to the roots.

Although flower initiation and differentiation, according to Louw (1991), had taken place during storage before planting, the HTR, MTR and LTR during the bulb preparation phase affected the development rate as well as the appearance (fresh mass) of the inflorescences diversely.

3.5 Conclusion

For the potential farmer, bulbs of a commercial flowering size (±7g fresh mass) can



successfully be grown under moderate and low temperature regimes during the bulb preparation phase (phase 3 in Figure 1.1), which represent the cool and moderate winter climate in South Africa. Regions with a warm winter climate are probably unsuitable for *Lachenalia* bulb preparation as bulb yield was reduced under the HTR. It is also evident that temperatures to which the bulbs are subjected during their enlargement can affect their physiological state at harvest. It appears as if the cool to moderate winter climates are best suitable for *Lachenalia* production in South Africa.

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Table 3.1 Temperature regime treatments during the bulb preparation phase.

		High		Moderate		Low	
Duration		Tempe	erature	Temperature		Temperature	
Duration		Regime (HTR) °C		Regime (MTR) °C		Regime (LTR) °C	
	Months						
Weeks							
		Day	Night	Day	Night	Day	Night
		14 hr	10 hr	14 hr	10 hr	14 hr	10 hr
1-14	1 March - 15 June ¹	28	12	22	10	15	5
14-18	15 June -15 July ²	28	12	22	10	20	10
18-22	15 July - 15 August	28	12	27	15	25	15
22-30	15 August -15 October ³	33	17	32	20	30	20
30-34	15 October - 15 November ⁴	35	35	35	35	35	35

¹ Planting to foliage emergence (FE)

- ² FE to full-bloom (Anthesis) (FB)
- ³ FB to foliar and inflorescence senescence (FIS)
- ⁴ FIS to harvesting



Weeks after	Months	Developmental	% of Inflorescences reaching a parti-				
planting		Stage	cular stage at relevant temperatures		emperatures		
			HTR ^d	MTR °	LTR ^f		
		Emergence ^a	90	100	100		
10	May	Anthesis ^b	0	0	0		
		Senescence ^c	0	0	0		
		Emergence	100	10	60		
14	June	Anthesis	0	90	40		
		Senescence	0	0	0		
		Emergence	30	0	0		
18	July	Anthesis	60	20	40		
		Senescence	0	80	60		
		Emergence	50 *	0	0		
22	August	Anthesis	0	0	0		
		Senescence	70 ***	100	100		
		Emergence	0	0	0		
26	September	Anthesis	20 **	0	0		
		Senescence	100	100	100		
		Emergence	20*	0	0		
30	October	Anthesis	0	0	0		
		Senescence	100	100	100		

a Inflorescence visible above soil

- **b** Oldest flower of the inflorescence opened
- c 50% of the flowers of the inflorescence wilted
- d High temperature regime treatment
- e Moderate temperature regime treatment
- f Low temperature regime treatment

* Percentage of additional inflorescence emerged

** Percentage of additional inflorescence at anthesis

*** Inflorescence/ flower abortion occurred





Treatment means of each month, with letters in common are not significantly different at $P \le 0.05$

Figure 3.1 The fresh mass of different plant parts of bulbs grown under the high (HTR), moderate (MTR) and low (LTR) temperature regimes.

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Figure 3.2 Photographical illustration of the low (LTR) temperature regime treated bulbs at the end of the bulb preparation phase.



Figure 3.3 Photographical illustration of the high (HTR) temperature regime treated pot plant producing an additional inflorescence during September.



CHAPTER 4

TEMPERATURE EFFECT ON BULB DEVELOPMENT AT THE END OF THE BULB PREPARATION PHASE AND DURING STORAGE

4.1 Summary

Temperature plays an important role in the production of quality *Lachenalia* bulbs, which is required for successful international bulb trade. The effect of three growth temperature regimes (HTR, MTR and LTR) on the development of bulbs prior to harvest and during the dormancy period were studied. Bulbs ($5 \ge 9$ cm in circumference) were harvested on the 15^{th} of November where-after they were stored at 25° C. From mid- September (bulbs in a pre-dormancy stage) until before the next planting season, ten plants were sampled randomly from each treatment at two week intervals and morphological studies were conducted on these bulbs by means of serial hand sections and taking bulbs apart.

The high temperature regime treated bulbs developed more modules, but inflorescence abortion occurred. Bulbs subjected to a low temperature regime treatment developed slightly slower than those of the moderate and high temperature regime treatments. In all the treatments, daughter bulbs were observed in the axils of the swollen leaf bases from mid - November. In spite of the slower development of bulbs subjected to the lower temperature regime, the overall quality was better than bulbs grown in the moderate and high temperature regimes.

4.2 Introduction

Lachenalia cv. Ronina has a sympodial modular growth system, with each module consisting of two cataphylls (bulb scales / bracts), one to three leaves and a terminal inflorescence (Chapter 2). Bulb



structure is not static and even during dormancy, the bulb goes through a sequence of morphological changes during which new modules develop and parts of previous modules senesce.

The growth pattern of cultivar Ronina bulbs is pronouncedly affected by temperature during the bulb preparation phase, especially under a high temperature regime (Chapter 3). Leaves of the high temperature regime treated plants were long narrow and curved compared to the robust, broad, lanceolate, upright and healthy looking leaves of the of the moderate temperature regime plants and the broad, spreading leaves of the low temperature regime plants. Uneven flowering is the main problem faced by commercial *Lachenalia* flower growers. This may be due to damage caused to inflorescence apices at a particular developmental stage (See Chapter 3 for confirmation).

The temperature requirement for floral and bulb development in cultivar Ronina is still not understood and need to be established in order to produce good quality pot plants. No precise information on the possibility of, or the techniques for accelerating or delaying flowering on *Lachenalia* has been published (De Hertogh and Le Nard, 1993; Niederwieser *et al.* 1997). A basic knowledge on the ontogeny of the inflorescence and the periodical development of the bulb under different temperature regimes is necessary in order to understand and manipulate the bulb environment for increased flower production.

The objective in this chapter was to study the morphological changes of *Lachenalia* bulbs occurring in the bulb prior to harvest (after flowering) and during dormancy. This trial was repeated, but due to similar results and for easier explanation, only the second year's results are presented in this chapter.

4.3 Materials and Methods

Bulbs were collected from ARC - Roodeplaat Vegetable and Ornamental Plant Institute after they had been grown for one year (phase 3 in Figure 1.1) under the natural growing conditions of the



Pretoria region, and thereafter stored at 25°C for four months.

As described in Chapter 3, bulbs (± 1 g, 4 cm in circumference) were planted in 9 cm pots and grown in three temperature controlled cabinets and set at three different temperatures (HTR, MTR, LTR) with 14 hours illumination at $\pm 200 \ \mu \text{mol.m}^2$.s⁻¹ PAR. The different temperature regimes applied, is given in Table 4.1. Pot plants in both the moderate (MTR) and low (LTR) temperature regime treatments were watered three times a week, while those of the high temperature regime (HTR) were watered daily. From mid-August the watering frequency was decreased, until the 15th of October when no water was applied and temperatures of all three treatments were raised to a constant 35^oC, until harvest to force the plants into a dormant stage before harvesting and storage. Bulbs were harvested on the 15th of November, where-after they were stored at 25^oC until mid-December.

From mid-September to mid- December ten plants were sampled randomly from each treatment at two- weekly intervals until they were ready to be planted for the next growing season, when differentiation of the new inflorescence had been completed (Louw,1991). Morphological studies were conducted on these bulbs by means of serial hand sections, \pm 1mm thick, made at planes both perpendicular and parallel to the axis of the bulb. At the end of the storage period the inflorescence dissected from the temperature treated bulbs were prepared for visual observations under the scanning electron microscope according to the method of Louw (1991).

Additional information dealing with the statistics on the fresh mass of bulbs, leaves, roots and inflorescences, as well as the monthly percentage of plants with inflorescences under the three different temperature regimes, is presented in Chapter 3.

4.4 **Results and Discussion**

Figure 4.1 is a diagrammatic comparison between the modular growth pattern of the high (HTR), moderate (MTR) and low (LTR) temperature regime treated bulbs prior to and post harvest. The



first sections of the MTR and LTR bulbs, which were made in mid-September revealed that 100% of the bulbs at this stage consisted of two modules. The first module consisted of an outer membranous covering representing the second cataphyll (MxC2) in Figure 4.1 a, b and c, two outer swollen leaf bases that remained after the abscission of the terminal parts of the leaves (MxL1;MxL2) and remnants of the past seasons terminal inflorescence (MxInf). The first cataphyll (MxC1), which protected the leaf primordia early in the growing season, degenerated and eventually totally disappeared later in the growing season, but some remnants were still visible in a few bulbs on the outside of basal plate (Figure 4.1 a, b & c). The second module (Mx1) consisted of two cataphylls (Mx1C1;Mx1C2), two leaf primordia (Mx1L1;Mx1L2) and an inflorescence primordium (Mx1Inf). This second module was slightly more developed in 100% of the bulbs of the MTR treatment (Figure 4.1 b) compared to those in bulbs of the LTR treatment (Figure 4.1 c). On the other hand, the HTR bulbs had developed a third module with the second module (module x1) containing a differentiating inflorescence (Mx1Inf) that was already visible, two leaves (Mx1L1;Mx1L2) and two cataphylls (Mx1C1;Mx1C2) (Figure 4.1 a). Module x2 in the MTR and LTR treatment consisted only of a young undifferentiated bud (Figure 4.1 b, c). This suggests that bulbs grown at high temperature regimes will develop more growth modules, therefore more inflorescences will develop the following year. In Chapter 6 this speculation is discussed. Similar results were found on Lachenalia cv. Pearsonii by Roh et al. (1995), where floral development was accelerated when the growing temperature was increased from \pm 15° C to 23° / 27 °C after flowering before harvest and stored at 25°C.

By mid-October, the Mx1 module inflorescence (Mx1Inf) in 80% of the HTR bulbs had aborted, but around mid-October to mid-November flower differentiation was visible in the Mx2 module of those bulbs (Figure 4.1 d). Inflorescence abortion is a common physiological phenomenon within bulbs that are subjected to too high or too low temperature extremes (De Hertogh and Le Nard, 1993). It also seems as if a viable terminal inflorescence suppresses the initiation of new modules, whereas after the abortion of the terminal inflorescence, a new module (apical bud) was immediately initiated (Figure 4.1 d and g). Although both the MTR and LTR bulbs exhibited approximately the same stage of development by middle of September, with the Mx inflorescence already spent and a new bud visible but not fully developed, this new bud (module x1) was fully differentiated in both



treatments by mid-October, but bulbs of the MTR were slightly further developed than those of the LTR (Figure 4.1 e and f).

From mid-November to mid-December the differentiation of the Mx1 inflorescence was visible in the MTR bulbs (Figure 4.1 h), but in LTR bulbs this process only started in December (\pm six weeks later) (Figure 4.1 l). Fifty percent of the MTR bulbs also showed a new developing module (module x2 in Figure 4.1 k). During this period the 80% of HTR bulbs had already formed an additional module (Mx3), after the abortion of the Mx1 inflorescence and after complete differentiation of the Mx2 inflorescence (Figure 4.1 j). As described in Chapter 3 and illustrated in Figure 3.3, the high temperature regime treated bulbs formed additional inflorescences late during the growing season. These inflorescences probably emerge from underdeveloped modules, in the sense that the vegetative leaves do not develop, but produce an additional inflorescence in the axil of the inner leaf bases (Figure 4.1 j). These inflorescences therefore differ from inflorescences developing from daughter bulbs, a shown in Figure 7.2.

Closer to the end of the storage period (\pm 4weeks after harvesting; mid-December) the inflorescences in 100% of the bulbs of the MTR and HTR treatment were completely differentiated (Stage G, Louw (1991)), while those (Mx1Inf) of the LTR bulbs were not yet completed (Figure 4.2 a, b and c). Scanning electron microscopic observations of the inflorescence development of the LTR, MTR and HTR treated bulbs during mid-December (\pm 4 weeks after harvesting) are illustrated in Figure 4.2 a, b and c. Therefore, the low temperature regime retarded module development in the growing and dormant bulbs compared to the higher temperatures. With the oldest flower in the G-stage (Figure 4.2 b and c), the MTR and HTR bulbs were therefore ready to be planted for the next flowering season and consisted of two to three modules which will produce pot plants with more than one inflorescence during the coming season. However, low quality inflorescences and flower abortion may occur in the bulbs, as observed in Table 3.2 and Figure 3.3 in Chapter 3.

Approximately 50% of the HTR and MTR bulbs formed daughter bulbs in the axil of module x leaves (leaf bases). However, in the LTR these daughter bulbs were only observed at the beginning of



December (Figure 4.1 g, h and 1 and Figure 4.3). Figure 4.3 is a diagrammatic illustration of a transverse section of a LTR bulb during mid-December. In LTR bulbs (Figure 4.1 c, f, i and l), the development of Mx1 module was retarded which was due to the fact that the bulbs 'energy' was probably relocated for daughter bulb development instead of inflorescence development which will be explained in Chapter 6 where the mass of daughter bulbs is discussed.

4.5 Conclusion

It is clear that bulbs produced under different climatic conditions will not necessarily be in the same physiological state, even if they are harvested on the same date as pointed out in Chapter 3. Another important observation is that these bulbs are normally not physiologically at rest. It is particularly important to be aware of the effects of temperature on the physiological processes which can be put into practical use when it comes to controlling bulb growth. The growth rate of the modules, emergence of additional inflorescences from underdeveloped modules, daughter bulb development as well as flower abortion are therefore important factors that need to be considered. The mapping of bulb development in terms of modular growth could be a valuable tool for comparing bulb development under different conditions.

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Table 4.1 Temperature regime treatments during growth, harvest and dormancy.

DURATION	High Temperature Regime (HTR) °C		Mod Tempe Reg (M'	erate erature jime TR) C	Low Temperature Regime (LTR) °C	
	Day 14 hours	Night 10 hours	Day 14 hours	Night 10 hours	Day 14 hours	Night 10 hours
1 March - 15 June ¹	28	12	22	10	15	5
15 June -15 July 2	28	12	22	10	20	10
15 July - 15 August	28	12	27	15	25	15
15 August -15 October ³	33	17	32	20	30	20
15 October - 15 November 4	35	35	35	35	35	35
15 November- 15 December ⁵	25	25	25	25	25	25

- ¹ Planting to foliage emergence (FE)
- ² FE to full-bloom (Anthesis) (FB)
- ³ FB to foliar and inflorescence senescence (FIS)
- ⁴ FIS to harvesting
- ⁵ Bulb storage



Figure 4.1 Diagrammatic illustration of the modular growth pattern of the high (HTR), moderate (MTR) and low (LTR) temperature regime treated bulbs prior to and post harvest.



Figure 4.2 Scanning electron microscopic observations of the inflorescence development in temperature regime treated bulbs during mid-December (± 4 weeks after harvesting).





Figure 4.3 Diagrammatic illustration of a transverse section of a low temperature regime (LTR) bulb during mid-December.

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CHAPTER 5

PLANT CARBOHYDRATE PARTITIONING DURING THE BULB PREPARATION PHASE

5.1 Summary

Carbohydrate partitioning was investigated in the different plant organs of *Lachenalia* cv. Ronina during the bulb preparation phase (phase 3 in Figure 1.1) under a low temperature regime at 4-week intervals. The low temperature regime was chosen due to the fact that a high quality bulb (6-9 cm in circumference) was produced under this temperature regime. Figure 3.2, in Chapter 3, pictures an example of a low temperature regime treated bulb that was produced during the bulb preparation phase. Each plant was dissected, the dry mass of the bulb, roots, leaves and inflorescence was recorded and carbohydrate analysis was performed. The roots and especially the bulb were found to be the main sinks of the plant, whilst the leaves and the inflorescence were the main source for soluble sugars.

Changes in the starch concentration closely followed dry weight changes in the bulb during the growing season. When bulbs were initially exposed to a low temperature, starch was converted to soluble sugars, but thereafter sugars were low, indicating continued export and conversion to starch. Low sugar levels in the leaves and high levels in the inflorescence, with continuous starch increase in the bulb and roots, probably indicate that the inflorescence, but especially the leaves, produced ample photosynthates during the growing season.

5.2 Introduction

Carbohydrates are the most abundant components in plants, however their interest lie not in their



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abundance but in the functions they fulfill (Smith, 1999). They provide the plant with a source of energy for growth and development, the material to synthesize many structural components and they provide the means by which the plant can distribute energy and substrates between its different tissues (Smith, 1999).

Carbohydrate reserves in flower bulbs, including starch, soluble sugars (non-reducing sugars and reducing sugars) as well as glucomannan and fructan are essential during the initial growth, but little is known about the biochemistry and the metabolism of these carbohydrates (Miller, 1992). Starch is the major storage carbohydrate in plants (Duffus and Duffus, 1984) and may accumulate to about 70-80% of the dry weight of storage organs such as bulbs, it also accumulates in the chloroplast, though not to the same extent as in the bulb amyloplasts (Smith, 1999). Sugars on the other hand play a critical role as products of photosynthesis, whereas sucrose (non-reducing sugar) is the main storage sugar in many plants and is the principle form in which carbon is transported through the plant (Smith, 1999). Glucomannan plays an important role in *Lilium longiflorum* growth (Matsuo and Mizuno, 1974) and fructans are also commonly found in storage organs of Liliaceae, Amaryllidaceae and Iridaceae family (Archbold, 1940; Miller, 1992).

Literature dealing with carbohydrate metabolism in *Lachenalia* is limited . Ndou (2000) observed no starch granules in leaf tissues during anatomical studies on cultivar Romelia and Robyn leaves. Therefore the objectives of this study were to discern the location of carbohydrate concentrations in various organs during the growing season.

Carbohydrate partitioning was investigated in bulbs grown under a low temperature regime. This temperature regime was chosen due to the fact that the best quality, commercial size bulbs were harvested under these cool climatic conditions (see Chapter 3).

5.3 Materials and Methods



Four hundred bulbs of cultivar Ronina were obtained from ARC - Roodeplaat Vegetable and Ornamental Plant Institute. These bulbs, which were stored for four months at 25 °C, weighed about 1g each.

As described in the Materials and Methods of Chapter 3, on the first of March, the LTR bulbs were individually planted in 9cm plastic pots containing sterilized, composted bark and placed in a temperature controlled cabinet at 15° / 5° C day / night with 14hours illumination at \pm 200 μ mol.m².s ⁻¹ PAR. Afterwards, the pots were watered to field capacity three times a week. Fourteen weeks after planting (mid-June), the day - night temperatures increased with 5 °C every four weeks. Eight weeks later (mid-August) the watering frequency was gradually decreased until no water was applied in mid-October (30 weeks after planting) and the temperature was set to 35 °C. This temperature was used to force the bulbs into a dormant stage before storage, whereas four weeks later the bulbs were harvested.

At every 4-week interval, 10 plants were randomly selected and dissected into bulbs, roots, leaves and inflorescences when visible and freeze dried and milled to a fine powder. Five repetitions of each sample were analysed. The carbohydrate determinations were done on a Sanplus Segmented Flow Analysis System by the Department of Horticultural Sciences, University of Stellenbosch (Anon.,1999). Half a gram of sample, to which 0.5g PVP (polivinylpyrrolidone, insoluble) was added, was extracted with 25ml 80% ethanol by shaking for 14hr in a 100ml Erlenmeyer flask. The contents were transferred proportionately to 50ml centrifuge tubes and centrifuged at ± 3500 rpm for 10 minutes. The supernatant was decanted into 250ml beakers and the pellet homogenized with distilled water and centrifuged. The supernatants were combined and the alcohol evaporated on the steam bath. This aqueous fraction contained the alcohol / water -soluble sugars and the pellet contained the starch fraction.

The aqueous fraction was transferred to 100ml volumetric flasks and 10 ml glycerol - C (1000-ml 50% water/glycerol + 200g activated charcoal) added. Samples were made up to volume with



distilled water and filtered using no. 3 filter paper. Sucrose (non-reducing sugar) was hydrolysed with ß-fructosidase and then all reducing sugars were determined after a copper reduction reaction was illustrated on a Sanplus Segmented Flow Analysis System according to the method used by the Department of Horticultural Sciences, University of Stellenbosch (Anon., 1999).

The starch fraction was transferred to 100ml volumetric flasks with acetate buffer, pH 4.8 (0.2 M acetic acid + 0.2 M sodium acetate), placed in a boiling water bath for 2 h, cooled to below 60°C, and then 100 μ l AGS (Amyloglucosidase, 200mg in 10 ml acetate buffer) was added. After incubation for 18 h at 55°C, flasks were made up to volume with distilled water and then filtered through no. 3 filter paper. Starch was determined colorimetrically as glucose by a Sanplus Segmented Flow Analysis System according to the method used by the Department of Horticultural Sciences, University of Stellenbosch (Anon.,1999).

Data were analysed using the CORR (Pearson Correlation) and GLM (General Linear Models) Procedures in the SAS (Statistical Analysis Systems) program.

5.4 **Results and Discussion**

The total starch content in *Lachenalia* cultivar Ronina plant parts is illustrated in Figure 5.1. In Figure 5.2 a and b the carbohydrate partitioning in the inflorescence and leaves is represented. Carbohydrate partitioning in bulbs and roots is illustrated in Figure 5.3 a and b.

5.4.1 Starch

Neither the inflorescence nor the leaves are important storage organs for starch, as indicated by the low starch concentrations in these organs (Figure 5.1), but the roots and especially the bulbs are the principle plant organs where it is stored (Figure 5.1). Figure 5.3 a indicates that a maximum amount



of 160 mg starch /g dry weight is stored in a bulb directly after anthesis (\pm 20 weeks after planting), which is very low compared to the \pm 500 mg starch /g dry mass in *Lilium longiflorum* (Miller, 1990; Matsuo and Mizuno, 1974), \pm 600mg/g dry weight in *Narcissus* (Ruamrungsri *et al.* 1999) and \pm 500mg/g dry weight in *Hippeastrum hybridum* (Stancato *et al.*, 1995) bulbs. In this case glucomannan may play an important role in *Lachenalia* bulbs. Glucomannan may account for 5-20% of the bulb dry weight as been observed in many *Lilium* spp. (Meier and Reid, 1982; Herold and Lewis, 1977; Matsuo and Mizuno, 1974; Tomado *et al.*, 1978). Speculations have been made that starch is the precursor for glucomannan synthesis, but there has been no research conducted on specific metabolic pathways leading to glucomannan synthesis or degradation in *Lilium* (De Hertogh and Le Nard, 1993).

The starch concentration in the bulb highly correlated (R=0.91; $P \le 0.001$) with the total dry mass of a bulb. Changes in the starch concentration therefore closely followed the dry mass changes in the bulb (Figure 5.3 a). Six weeks after the bulbs were planted, the starch concentration decreased (Figure 5.3 a), probably because of the preformed leaves and roots which were utilizing the starch until they could produce photosynthates (Figure 5.2 b). During this period the starch was converted for mother bulb respiration and was also allocated to the roots for development (Figure 5.3 a and b). Thereafter, the starch concentration in the mother bulb started to increase and reached its maximum (Figure 5.3 a) after anthesis and then slowly decreased during the senescence of the above growth and this decrease persisted during dormancy.

During the first six weeks after planting, when the temperature dropped from a storage temperature of 25°C to a 15° / 5°C day / night growing temperature, there was a drastic drop in starch concentration of the bulb (Figure 5.3 a). A negative correlation was also found between the bulb starch concentration and the reducing sugar (R=-0.71; P \leq 0.05) and non- reducing sugar (R=-0.63; P \leq 0.05) concentrations. One of the main reasons could be the conversion of starch to sugars in response to low temperature acclimatization. Similar results have been found on *Tulipa* by Davies and Kempton (1975) and on *Nerine bowdenii* by Theron and Jacobs (1996). According to Haaland and Wickstrøm, (1975) the starch conversion in tulip occurs in response to an increased activity of \approx - amylase and \approx - glucanphosphorylase. Furthermore, Weiser (1970) mentioned that sugar levels



in *Tulipa* are probably necessary to protect the bulb against low temperature damage. In the case of cultivar Ronina the converted soluble sugars in the bulb after the initial temperature drop was probably used for scape elongation within the bulb and for root development. This statement is supported by Louw (1991) whereas a drop in storage temperature before planting improved scape elongation and faster growth in cultivar Romelia.

5.4.2 Soluble sugars

Reducing and non-reducing sugars (sucrose) are the main transportable carbohydrates in bulbous plants (De Hertogh and Le Nard, 1993; Miller, 1992; Smith, 1999; Theron and Jacobs, 1996). This seems to be true for cultivar Ronina, which is clearly illustrated in Figure 5.2 and 5.3. Ten weeks after planting (mid-May), the soluble sugar levels of the emerging inflorescence increased (Figure 5.2 a), while those of the bulbs (Figure 5.3 a), roots (Figure 5.3 b) and leaves (Figure 5.2 b) decreased. This indicates continuous export of sugars as the growing season progresses. After the rapid decrease of sugars in the bulbs (Figure 5.3 a), it remained at low levels. About eight weeks later (after full-bloom) the imported sugar in the inflorescence also rapidly decreased, indicating the conversion to starch (Figure 5.2a).

During inflorescence emergence and flowering (10-18 weeks after planting) its soluble sugar concentrations increased (Figure 5.2 a). At the same time the starch concentration in the bulb increased (Figure 5.3 a) and this continued until leaf senescence in August (22 weeks after planting). This increase was subsequently accompanied by an increase of the starch concentration in roots during full-bloom(± 18 weeks after planting) (Figure 5.3 b). This indicates that the leaf-producing photosynthates at no stage become limited for inflorescence growth, thus ensuring high starch concentrations in bulbs as well as roots. Smith (1999) made a similar statement by reporting that when sucrose is synthesized in a mature leaf, it is immediately exported via the phloem to other parts of the plant, therefore, it is not held for long in the leaf. Starch in the chloroplast in leaves also turns over very rapidly. It accumulates during the light period, usually following a delay after



photosynthesis has begun, and is broken down in the following dark period (Smith, 1999). Miller and Langhans (1989) also found little starch in *Lilium longiflorum* leaves during the growing season. The high concentration of soluble sugars in the roots before inflorescence emergence (Figure 5.3 b) also emphasizes the fact that the leaves are the main manufacturer of carbohydrates.

In the bulb, starch accumulation began 12 weeks before accumulation in the roots, reaching maximum levels four weeks prior to that in the roots (Figure 5.3 a and b). It is therefore important to notice that the soluble sugars that were translocated to the roots, were probably not exported back to the bulb, but was converted to starch instead and remained there until disintegration of the roots. This is confirmed by the negative correlation between the starch concentration in the roots and the reducing sugar (R=-0.83; P \leq 0.05) as well as the non-reducing sugar (R=-0.79; P \leq 0.05) concentrations, as illustrated in Figure 5.3 b. This indicates that some unknown factor caused the roots to keep their sugars and probably prevented the converted starch to break down into sugars. According to Smith (1999) starch accumulation in the amyloplasts of non-photosynthetic tissues (in these circumstances the roots and bulbs) occurs over long periods, sometimes over several months of the growing season. Turnover of this starch is very slow. Once it has been converted, it normally remains unchanged until the next growing season, when it is rapidly mobilized to support new growth. Therefore, starch degrading enzymes are not active, because they are either not present, in an inactive form or are inhibited. Regarding the soluble sugars, Smith (1999) mentions that the transportation through the phloem can also be inhibited by external factors such as too low temperatures or anoxia (oxygen deficiency). The latter could therefore be a possible explanation for no translocation of the soluble sugars from the roots.

5.5 Conclusion

The bulb is the main storage organ for starch, but the roots also reserve starch at the end of the growing season. The leaves are the main effective manufacturer of carbohydrates for the plant followed by the small contribution by the inflorescence. Therefore, the removal of the scape during



cut-flower production may not significantly effect the production and quality of the inflorescences in the next growing season.

It is important to note that plants, which grow under such a low temperature regime, might still be able to photosynthesize optimally, although their leaf fresh mass is lower than those of plants that grow under higher temperature regimes (see Chapter 3 for explanation). As a result, quality bulbs were harvested.

Carbon partitioning is controlled by a number of factors which include the supply of photosynthates, the number and size of competing sinks, their location on the plant and the potential for temporary storage in leaves and along the path of transport. Understanding the control of organ initiation and development as well as the awareness of the acquired balance between source and sink tissues are essential elements for manipulating carbon partitioning in plants.

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Figure 5.1 Percentage of total starch content in different plant parts of *Lachenalia* cv. Ronina, subjected to a low temperature regime.



Weeks - ■- Dry mass →→ Starch →→ Reducing sugars →→ Non-reducing sugar



Figure 5.2 Carbohydrate partitioning in the inflorescences (a) and leaves (b) of Lachenalia plants, subjected to a low temperature regime.

a)







Roots



Figure 5.3 Carbohydrate partitioning in the bulb (a) and roots (b), of *Lachenalia* plants subjected to a low temperature regime.


CHAPTER 6

TEMPERATURE EFFECT ON PLANT AND FLOWER QUALITY DURING THE POT PLANT PHASE

6.1 Summary

Temperature treated bulbs obtained from the bulb preparation phase experiment were planted for the pot plant phase to investigate the flowering date, quality and shelf life of these pot plants. Plants were grown in a growth cabinet at a $15^{\circ} / 10^{\circ}$ C day / night temperature regime. When the oldest flower of the inflorescences opened, the pot plants were transferred to a growth cabinet that provided a constant temperature of 22°C with lower lighting conditions to simulate office conditions. The flowering date, keeping ability as well as the morphology of the inflorescences were evaluated. After the senescence of the inflorescences, the plants were harvested and dissected into different plant parts for evaluation.

The flowering date of bulbs, produced after exposure to three temperature regimes, was eight weeks earlier than bulbs that normally grow in outdoor conditions in the Pretoria region (summer rainfall area). Furthermore, the low temperature regime (LTR) treated bulbs produced inflorescences with the longest keeping ability and simultaneous flowering was noticed. The lower the temperature regime during the bulb preparation phase the greater the peduncle length, rachis length, floret number as well as the peduncle diameter of the primary, secondary and tertiary inflorescences. The moderate (MTR) and low (LTR) temperature regime treated bulbs produced more inflorescences than the high (HTR) temperature regime treated bulbs.

The LTR treated bulbs produced broader leaves than the MTR and HTR treated bulbs. The LTR treated bulbs produced leaves with more spots on, but it is rather insignificant when it comes to improving the quality of the pot plant. Furthermore, the temperature treatments during the bulb



preparation phase influenced the final size and quality of the bulbs of the pot plants as portrayed by the performance of the pot plants. At the end of the pot plant phase, the LTR treated mother bulbs produced almost the same amount of daughter bulbs than those of the HTR and MTR, however, the LTR treated bulbs formed larger ones. Finally, the LTR and MTR treated bulbs developed more roots than the HTR treated bulbs at the end of the pot plant phase.

6.2 Introduction

Defining an attractive pot plant is not always easy, since it is a criterion that is difficult to measure or quantify and varies with each country (De Hertogh and Le Nard, 1993).

Since cultivar Ronina was developed as a pot plant, certain morphological standards such as the overall appearance, proportionality of the leaves and flowers etc. need to be met. According to De Hertogh (1990), bulbs that are used for forced potted plants need some general desired characteristics, namely:

- The product must have a plant life in excess of 10 days at 20°C
- There should be a minimal post-greenhouse growth of the flowering potted plant
- Double usage of the plants is desired, e.g., in the home, then in the garden
- Must force readily at 13-16°C greenhouse temperature
- Must not be susceptible to flower abortion or abscission
- Cultivars should be available for year-round forcing
- Cultivars should not require growth retardants

It was established by Professor Blaauw and his co-workers (Hartsema, 1961) that temperature is the major external factor controlling growth, development and flowering in bulbs. In Chapter 3 and 4, differences in plant growth and bulb development between the high, moderate and low temperature



regime treated bulbs were discussed. In addition, Louw (1991) recorded that a specific storage temperature will affect the time of flower initiation and differentiation as well as inflorescence quality of cultivar Romelia during the pot plant phase.

Therefore, the objectives in this chapter were to determine if the effect of different temperature regimes during the bulb preparation phase would influence the plant and flower quality during the pot plant phase (phase 4 in Figure 1.1). As mentioned before in Chapter 3, this experiment was repeated for two consecutive seasons with very similar results and for uncomplicated reporting, only the second year's results will be documented.

6.3 Materials and Methods

One hundred bulbs from the HTR, MTR and LTR treatment, which were harvested after the bulb preparation phase (see Chapter 3), were used in this experiment to evaluate the affect of the different temperatures during the bulb preparation phase on the growth during the following year (pot plant phase). These bulbs were lifted on the 15th of November (at the end of the bulb preparation phase) and then stored dry at 25°C.

In order to determine the planting date, the apical bud was excised from the bulbs. The stage of flower development of these bulbs was then determined by dissecting the buds using a dissection microscope. Chapter 4 describes the developmental stage in which the treated bulbs were before harvest and during the storage period at 25°C. At five-day intervals the bulbs were observed and when the oldest flower of the inflorescence of more than 50% of the 10 bulbs sampled was at the G-phase (the three carpel primordia are formed in the oldest floret), the bulbs were then further stored dry for \pm 14 days at 13°C before planting (Louw, 1991). During this period, sprouting of the bulbs were observed, since this is used as a parameter when bulbs no longer can be stored without damaging the quality of the inflorescence. This forcing treatment was recommended by Louw (1991) for further flower differentiation and elongation of the inflorescence inside the bulb as well improving



the quality of the inflorescence.

During the microscopic observations, it was concluded that the different temperature regimes affected the time of flower differentiation inside the bulbs (see Chapter 4), therefore, the bulbs of each treatment were planted on different dates when they were ready, namely on the 23rd of December for both the MTR and HTR and on the 15th of January for the LTR.

One hundred bulbs of each of the HTR, MTR and LTR, weighing about 5 to 10g $(5-\ge9$ cm in circumference) each, were planted singly into 9 cm plastic pots containing sterilized, composted bark and arranged, according to Steele and Torrie (1980), in a randomized block design in one growth cabinet. A 12hr photoperiod with a light intensity of $\pm 200 \ \mu$ mol.m².s ⁻¹ PAR at plant level was supplied with a 15/10°C day/night temperature. Lighting was provided by a combination of WHO fluorescent and incandescent globes. When the oldest flower of the inflorescence opened, the pot plant was transferred to a growth cabinet that provided a constant temperature of 22°C and a 12hr photoperiod with only flourescent tubes ($\pm 35 \ \mu$ mol.m².s ⁻¹ PAR) to simulate office conditions.

6.3.1 Flower quality

The following observations were used to evaluate flower quality. Some of these parameters were also used by Louw (1991).

- Date when the oldest flower of the inflorescence opened (Flowering date)
- Date when 100% of the flower of the inflorescence opened (Full-bloom)
- Date when 50% of the flower of the inflorescence wilted
- Number of inflorescences
- Number of flower per inflorescence
- Length of rachis



- Length of peduncle
- Diameter of the peduncle base

From the above mentioned observations the following calculations were made:

- Compactness of the inflorescence (Floret number divided by the rachis length (cm))
- The flowering date time-lag (Simultaneous-flowering)
- Date when 100% of the florets of the inflorescence opened substracted by the date when the first floret opened (Keeping ability)
- Date when 50% of the florets of the inflorescence wilted substracted by the date when 100% of the inflorescences opened (Keeping ability)

6.3.2 Plant quality

After 100% of the flowers on the inflorescences had wilted, the plants were harvested and dissected into different plant parts. The following observations were used to evaluate plant quality.

Leaves:

- % Spots on leaves
- Leaf number
- Total leaf area (cm²)
- Fresh mass (g)
- Dry mass (g)

Bulbs:

Mother bulb

• Fresh mass (g)



- Dry mass (g)
- Size in circumference (cm)
- Moisture content = Fresh mass Dry mass

Daughter bulbs

- Number
- Total fresh mass (g)
- Total dry mass (g)

Roots:

- Fresh mass (g)
- Dry mass (g)

Data were analysed using the CORR (Pearson Correlation) and GLM (General linear Model) procedure in the SAS (Statistical Analysis Systems) program. Analysis of Variance was also performed. Tukey's studentized range test (Steele and Torrie, 1980) was applied to compare treatment means.

6.4 **Results and Discussion**

6.4.1 Planting and flowering date

As illustrated in Figure 1.1 the current bulb preparation phase practice for *Lachenalia* in South Africa according to Louw (1991), is as follows:

After leaf senescence from October to November, the bulbs are lifted, stored at $\pm 25^{\circ}$ C and before they are planted out at end-February to mid-March, they are stored at 13°C for two weeks to



66

improve inflorescence quality. The flowering period for cultivar Ronina starts in middle of May, which was confirmed in Chapter 3 during the bulb preparation phase. However, in Chapter 2 and 4 it was observed that inflorescence differentiation not only took place during the dormancy (storage) period, as observed by Louw (1991) in cultivar Romelia, but also occurred during the growing season. Consequently, these bulbs were ready to be planted out about eight weeks earlier (from end-December to mid -January) than bulbs that are planted in outdoor conditions in March (Louw, 1991). Thus, the flowering date was shifted to eight weeks earlier, which is illustrated in Figure 6.1.

Above mentioned finding is very important for the grower's marketing strategies, because bulbs can be forced to flower during the Easter holiday season (April). A possible explanation for the earlier flowering date was that the temperatures in the cabinets were controlled and did not fluctuate during the growing season. In addition, a 14hr photoperiod was applied instead of a 12hr one. In general, bulb plants are not profoundly responsive to photoperiodic effects and in *Lachenalia*, a critical day length has not yet been defined. For example, flower initiation is apparently unaffected by photoperiod in *Ornithogalum* (also a member of the Hyacinthaceae family), as well as in spring flowering bulbs like narcissus and hyacinth (Rees, 1992). However, according to Hanks and Rees (1979), long days increased shoot growth of *Tulipa* to about 50% greater final stem length at anthesis, but there was no effect on flowering date. The mentioned results therefore illustrate that these photoperiodic effects, although small, could be exploited commercially for improved flower quality, or in the case of the *Lachenalia*, an early flowering date.

Although the planting date of the HTR and MTR bulbs was earlier than those of the LTR, the flowering date of the LTR treated bulbs was not notably later, as seen in Figure 6.1 a and b. Figure 6.1 a graphically illustrates that the oldest flower on the primary inflorescence of the LTR pot plants, as well as those of the MTR, opened about seven weeks after planting. As a result, the suppressed development of the LTR treated bulbs (see Chapter 4), was alleviated during the following year. A reasonable explanation was that flower initiation and differentiation was suppressed by the low growing temperature (see Chapter 4), however, with the increase in temperature before (35°C) and during storage (25°C) the process was alleviated and further development could take place. After



flower differentiation occurred, the storage temperature was lowered to a temperature of 13° C late during storage (two weeks before planting) and afterwards bulbs were planted under a low temperature of $15^{\circ} / 10^{\circ}$ C day / night which accelerated scape elongation. Therefore, flower differentiation and scape elongation are two different processes and needs different optimal temperatures. Similar thermoperiodic responses in *Tulipa* has been recorded by De Hertogh and Le Nard (1993), where flower differentiation takes place under a warm temperature climate (summer) and induction of scape elongation under cooler conditions (fall-winter).

On the other hand, the flowering date of those of the HTR pot plants were two weeks later. All these results are explained in Chapter 4, whereas the HTR during the bulb preparation phase had an negative effect on flower development.

More simultaneous-flowering occurred in bulbs which were grown under a LTR during the bulb preparation phase than those that were grown under the MTR and HTR (Figure 6.1 a), as anthesis occurred in 100% of the LTR plants within three weeks compared to six weeks for MTR plants and 13 weeks for HTR plants. The reason for the uneven flowering of the HTR inflorescences is illustrated in Figure 6.1b. The time-lag from planting to flowering (flowering date) of the primary, secondary and tertiary inflorescences of the HTR treated bulbs was much longer than those of the MTR and LTR. This again implies that the high temperature regime (HTR) during the bulb preparation phase retarded the growth of the inflorescences during the following year (see Chapter 3 and 4 for explanation).

6.4.2 Flower quality

The best quality inflorescences were found in plants grown from the LTR treated bulbs (Figure 6.3 and 6.4). However, MTR treated bulbs also produced good quality inflorescences. In Figure 6.2 a, b and c, it was also obvious that the lower the temperature treatment during the bulb preparation phase, the higher were the peduncle length, rachis length, floret number as well as the peduncle cross



section (firmness) of the primary, secondary and tertiary inflorescences of these bulbs during the pot plant phase. This was confirmed by the strong correlation, which was calculated between peduncle length, rachis length, flower number and peduncle cross section (Table 6.1). The peduncle length, rachis length, flower number and peduncle diameter decreased with the subsequent emergence of the primary, secondary and tertiary inflorescences.

Flower number per inflorescence is one of the main factors by which quality is judged and according to Louw (1991), a high flower number is a very favourable characteristic. As mentioned before in Chapter 3, the temperature regime at which bulbs are grown during the bulb preparation phase, has a significant effect on flower emergence and number. The low temperature regime during the bulb preparation phase delayed flowering (see Chapter 3) and also retarded modular growth sequence of bulbs (see Chapter 4), but it seems as if enough carbohydrates were stored (see Chapter 5) and this was probably a reason why the flower number increased.

During the bulb preparation phase in Chapter 3, the high temperature regime produced inflorescences with a lower fresh mass and flower abortion occurred (see Chapter 4) and this substantiates why the flower number on the inflorescences of the treated bulbs were lower during the pot plant phase.

The peduncle and rachis length is an important aspect in pot plants and according to De Hertogh (1980), it must also be in proportion to the rest of plant and pot. Since cultivar Ronina is produced as a pot plant, a short peduncle and rachis is required. In Figure 6.2 a, b and c, however, the LTR bulbs rendered long flower stems, however they did remain upright because of the increase in peduncle diameter and firmness and therefore did not fall over. Figure 6.4 shows an example of an inflorescence which can be regarded as a high quality pot plant and was produced by a bulb subjected to LTR treatment during phase 3 (Figure 1.1 in Chapter 1).

A commercially acceptable pot plant must have a compact inflorescence. The compactness of the inflorescence is determined by the rachis length and flower number. The MTR, but especially the LTR treated bulbs, produced the most compact inflorescences, whilst the HTR treated bulbs



produced less compact and blasted inflorescences (Figure 6.5). Figure 6.6 shows an example of a blasted inflorescence. According to Louw (1991) a slow differentiation rate resulted in more compact inflorescences in cultivar Romelia. Similar results were obtained in cultivar Romina, where bulbs subjected to the low temperature regime showed retarded bulb development (see Chapter 4). To support these results, the HTR treated bulbs were less compact (Figure 6.5). Figure 6.7 shows a poor quality inflorescence of the HTR treated bulb during the pot plant phase.

6.4.3 Number of inflorescences

The bulbs of the MTR and LTR treatments, each produced an average of three inflorescences during the pot plant phase (Figure 6.8). The appearance of multiple inflorescences is very appealing for the consumer. As a result, these temperature regimes are recommended during the bulb preparation phase for multiple inflorescences. However, in the case of the HTR treated bulbs, an average of one to two inflorescences were produced. The reason for the low inflorescence count on the HTR bulbs can be blamed to flower abortion (see Chapter 4). Figure 4.1, in Chapter 4, gives a schematic illustration on how the developmental rate of new growth modules was enhanced by this temperature regime, but unfortunately flower abortion occurred simultaneously in these growth modules. It is therefore significant to note that a too high temperature exposure during the bulb preparation phase will reduce the number of inflorescences of the treated bulbs during the pot plant phase, instead of promoting it.

6.4.4 Keeping ability of the inflorescences

Figure 6.9 illustrates the effect of the HTR, MTR and LTR during the bulb preparation phase on the shelf life of the pot plant (a) and on the keeping ability of the primary, secondary and tertiary inflorescence (b).



The keeping ability of the inflorescence is an important quality for a pot plant. According to De Hertogh (1990), a pot plant must have a keeping ability of more than 10 days when it is placed at 20°C. In all three treatments the sum of the keeping ability of all three inflorescences (shelf life) of the potted plants averaged 24 days (Figure 6.9 a). However, one has to consider the flowering date. As mentioned before, the flowering date for the primary, secondary and tertiary inflorescences produced by the LTR treated bulbs occurred within a shorter period than those of the MTR and HTR. This means that the keeping ability was longer as illustrated in Figure 6.9 b. The time from flower to full-bloom in all three treatments was basically the same, but significant differences from full- bloom to wilt was observed between the different treatments, with the LTR treated bulb's primary, secondary and tertiary inflorescences showing the best longevity. In addition, Louw (1991) and Jansen van Vuuren (1990) concluded that the storage conditions before planting do not determine the keeping ability of the inflorescence of cultivar Romelia and *Ornithogalum* respectively. However, results of this investigation show that the low temperature regime during the bulb preparation phase will improve the keeping ability of the inflorescences during the pot plant phase.

6.4.5 Leaf quality

It is illustrated in Figure 6.10 that although the HTR, MTR and LTR treated bulbs produced an average of six leaves (two leaves / module) per plant at the end of the pot plant phase, the total leaf area as well as the total dry mass of the LTR was higher compared to those of the MTR and HTR. As a result, the LTR treated bulbs produced plants with broader leaves than those of the MTR and HTR treatments. Table 6.2 imparts the relationships between the different measurements conducted on the leaves at the end of the pot plant phase. Leaf number did not correlate with the total leaf area nor the dry mass (Table 6.2) which confirms the mentioned results. Figure 6.11 shows the differences in leaf width between the leaves of the MTR (left)and LTR (right) bulbs during the pot plant phase.

As mentioned before, defining an attractive plant is not always easy. In this case, the higher temperature treatments during the bulb preparation phase resulted in a smaller total leaf area of these



plants during the pot plant phase. As a result, the decision remains with the grower to grow a pot plant with either narrow or broad leaves which is one of the features that will affect the quality of the pot plant. Marketing research will therefore play a very important role in consumer preferences towards leaf morphology.

6.4.6 Spotting on leaves

Spotting on *Lachenalia* leaves is a conspicuous feature of many species. The colour and density of spots varies with aspect and locality (Duncan, 1988). Spotting in cultivar Ronina usually occurs on the adaxial leaf surface, but sporadic spots may also occur on the abaxial surface. Well defined spots are regarded as an attractive feature of *Lachenalia* pot plants.

During the bulb preparation phase it was observed that more spots were visible on the leaves of plants that grew under lower temperature regimes, but at the end this growing phase, when the temperature of all three treatments increased, the spots faded. During the pot plant phase the percentage of these spots was calculated and as a result the LTR treated bulbs of the previous year produced leaves with more spots (Figure 6.12) than those of the MTR and HTR. Figure 6.12 presents the effect of the temperature regimes during the bulb preparation phase on the percentage of spots on leaves of the treated plants during the pot plant phase. It seems as if not only the genetic composition of the plant, but also the low growing temperature regime are accountable for the percentage of spots on the leaves. One must contemplate that the percentage of spots on the LTR treated bulbs leaves was only about 24% (Figure 6.12). This is still very sparse and does not significantly improve the quality of the pot plant.

6.4.7 Bulbs

At the end of the bulb preparation phase, mother bulbs were harvested, stored dry and afterwards



planted for the pot plant phase (see Materials and Methods). In Figure 6.13 it is illustrated that although the fresh mass of the HTR and MTR treated mother bulbs was lower than those of the LTR, after the bulb preparation phase (phase 3 in Figure 1.1) and the storage phase at planting, these bulbs never made up their loss after developing into mature plants during the pot plant phase (phase 4 in Figure 1.1). As a result, the affect the temperature regimes during the previous year (phase 3 in Figure 1.1) had on the fresh mass of the mother bulb, will have an effect on the final fresh mass of the mother bulb the following year and partially as a consequent also the morphology of the pot plant. It is also important to notice that the mother bulbs at the end of the pot plant phase (phase 4 in Figure 1.1) are mainly smaller due to daughter bulbs that are formed to the expense of the mother bulb.

No significant differences were found between the number of daughter bulbs formed by the HTR, MTR and LTR treated mother bulbs (Figure 6.14). However, daughter bulbs produced by the LTR treated mother bulbs were larger (Figure 6.14). This is verified by the strong correlation between the number of daughter bulbs and the dry mass (Table 6.3) in the lower temperature regimes.

In all three treatments there were a strong correlations between mother bulb fresh mass, dry mass and size (Table 6.2). Measuring bulb size in circumference, which is a cheap and easy measurement, can therefore be recommended as a method for assorting bulbs for marketing purposes.

In addition, the moisture content of the mother bulbs was determined at the end of the pot plant phase (Figure 6.15). In Figure 6.15 the high moisture content of the LTR treated mother bulbs in comparison with the MTR and HTR treated bulbs is shown. It appears as if a bulb, which grows under a too high temperature regime, is fleshier, probably with thicker tunics to protect it from drying out under those conditions.

6.4.8 Roots



The LTR treated as well as the MTR treated bulbs had a tendency to produce more roots than the HTR treated bulbs at the end of the pot plant phase (Figure 6.16). According to Schuurman (1971) the amount of roots formed per bulb are related to its size. Thus, the larger the basal plate, the more root primordia are formed. In Figure 6.13 it is illustrated that the higher the temperature regime treatment during the bulb preparation phase, the smaller is the bulb size at the end of the pot plant phase the following year. This emphasizes that temperature directly affects bulb size and as a result indirectly affects root formation.

6.5 Conclusion

The bulb preparation phase plays an important role in the final pot plant production phase. It is therefore essential that the grower consider the bulb's origin of the previous year before it is sold as a marketable size bulb for the pot plant production phase. In this chapter it was also concluded that the flowering date can be shifted and in this case two months earlier than under normal climatic conditions. The lower the growing temperature during the bulb preparation phase, the more simultaneous flowering took place during the pot plant phase. Therefore, by subjecting the bulbs to a low temperature before planting, might improve simultaneous flowering. The LTR treated bulbs rendered the highest quality inflorescences with a considerable keeping ability. The LTR treated bulbs also produced broad leaves with more spots on than other temperature regime treated bulbs at the end of the pot plant phase which may improve the attractiveness of the foliage.



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Inflorescence type	Inflorescence measurement	Inflorescence measurement	R-value
Primary	Rachis length	Peduncle length	0.899 **
		Floret number	0.956 **
	Peduncle length	Peduncle cross section	0.889 **
Secondary	Rachis length	Peduncle length	0.936 **
		Floret number	0.958 **
	Peduncle length	Peduncle cross section	0.936 **
Tertiary	Rachis length	Peduncle length	0.948 **
		Floret number	0.985 **
	Peduncle length	Peduncle cross section	0.948 **

Table 6.1 Relationships between different measurements conducted on the inflorescence.

** Significant correlation at 1% level ($P \le 0.01$)





Treatment means with letters in common are not significantly different at P≤0.05

Figure 6.1 Effect of high (HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase on the time-lag when the flowering date of the primary inflorescence took place in all (100 %) of the bulbs that were potted (a) and on the flowering date of the primary, secondary and tertiary inflorescence (b).

a)

b)



Primary inflorescence



Secondary inflorescence

35 30 25 20 15 b b 10 b 5 0 HTR MTR LTR HTR MTR LTR Floret number HTR MTR LTR HTR MTR LTR HTR MTR LTR Peduncle cross **Rachis** length Total length Peduncie length (cm) section (cm) (cm) (cm) Tertiary inflorescence 35 30

25 c 20 15 b 10 5 а 0 HTR MTR LTR Total length Peduncle length (cm) Rachis length Floret number Peduncle cross section (cm) (cm) (cm)

Treatment means with letters in common are not significantly different at P < 0.05

Figure 6.2 Effect of the high (HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase on the total length, peduncle length, rachis length, floret number and the peduncle cross section of the primary (a), secondary (b) and tertiary inflorescence (c) during the pot plant phase.

a)

b)

c)





LTR MTR

Figure 6.3 Photographical illustration of plants in the pot plant phase, grown from low (LTR) moderate (MTR) and high (HTR) temperature regime treated bulbs.



Figure 6.4 Photographical illustration of a low (LTR) temperature regime treated bulb grown into a high quality pot plant, early in the pot plant phase.





Treatment means with letters in common are not significantly different at $P \le 0.05$

Figure 6.5 Effect of the high (HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase on the compactness of the primary, secondary and tertiary inflorescence during the pot plant phase.





Figure 6.6 Photographical illustration of flower blast on an inflorescence produced by a high (HTR) temperature regime treated bulb during the pot plant phase.



Figure 6.7 Photographical illustration of a high (HTR) temperature regime treated bulb bearing a poor quality inflorescence during the pot plant phase.





Treatment means with letters in common are not significantly different at $P \le 0.05$

Figure 6.8 Effect of high (HTR), moderate (MTR) and low (LTR) temperature regime treatments on the bulbs during the bulb preparation phase on the number of inflorescences produced during the pot plant phase.



a)



b)



Treatment means with letters in common are not significantly different at $P \le 0.05$

Figure 6.9 Effect of the high(HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase on the shelf life of the pot plant (a) and on the keeping ability of the primary, secondary and tertiary inflorescence (b).



 Table 6.2 Relationships between different measurements conducted on the leaves, mother bulb,
daughter bulbs and roots during the pot plant phase.

Plant part	Plant measurement	Plant measurement	R-value
Leaves	Leaf number	Total leaf area	0.347 ^{NS}
		Dry mass	0.332 ^{NS}
	Total leaf area	Fresh mass	0.989 **
		Dry mass	0.989 **
	Dry mass	Fresh mass	0.982 **
Bulbs	Fresh mass	Mother bulb size	0.966 **
		Mother bulb dry mass	0.981 **
	*****	Daughter bulb fresh mass	0.771 **
		Daughter bulb dry mass	0.753 **
	Mother bulb size	Mother bulb dry mass	0.952 **
		Daughter bulb fresh mass	0.758 **
		Daughter bulb dry mass	0.745 **
	Mother bulb dry mass	Daughter bulb dry mass	0.773 **
	Daughter bulb dry mass	Daughter bulb fresh mass	0.994 **
Roots	Dry mass	Fresh mass	0.902 **

[№] Non Significant ^{**} Significant correlation at 1% level (P≤0.01)



Table 6.3 Relationships between different measurements conducted on daughter bulbs, which were formed by the high (HTR), moderate(MTR) and low (LTR) temperature regime treated mother bulbs at the end of the pot plant phase.

Temperature treatment	Plant measurement	Plant measurement	R-value
HTR	Daughter bulb number	Fresh mass	0.719 *
		Dry mass	0.623 ^{NS}
MTR	Daughter bulb number	Fresh mass	0.698 *
		Dry mass	0.723 *
LTR	Daughter bulb number	Fresh mass	0.747 *
		Dry mass	0.718 *

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^{NS} Non Significant

* Significant correlation at 5% level (P≤0.05)





Treatment means with letters in common are not significantly different at $P \le 0.05$

Figure 6.10 Effect of the high (HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase on the leaf number, total leaf area (m^2) and dry mass (g) of the treated plants during the pot plant phase.



Figure 6.11 Differences in leaf width between the leaves of plants during the pot plant phase, grown from a MTR (left) and a LTR (right) treated bulb.





Treatment means with letters in common are not significantly different at $P \le 0.05$

Figure 6.12 Effect of the high (HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase on the percentage of spots on the leaves of the treated plants during the pot plant phase.





Treatment means with letters in common are not significantly different at $P \le 0.05$ Figure 6.13 Fresh mass (g) and size (cm) differences between bulbs at planting(after they have been treated with the high (HTR), moderate (MTR) and low (LTR) temperature regime during the bulb preparation phase) and bulbs at harvest (on termination of the pot plant phase).



Daughter bulbs

Treatment means with letters in common are not significantly different at $P \le 0.05$ Figure 6.14 Number and mass of daughter bulbs at the end of the pot plant phase, formed by the high (HTR), moderate (MTR) and low (LTR) temperature regime treated mother bulb of the bulb preparation phase.





Treatment means with letters in common are not significantly different at $P \le 0.05$ Figure 6.15 Moisture content of high (HTR), moderate (MTR) and low (LTR) temperature regime treated mother bulbs at the end of the pot plant phase.



Treatment means with letters in common are not significantly different at $P \le 0.05$ Figure 6.16 Root dry mass (g) of the high (HTR), moderate (MTR) and low (LTR) temperature regime treated mother bulbs at the end of the pot plant phase.



CHAPTER 7

MODELLING BASED ON RESULTS OBTAINED

7.1 Summary

The quality and shelf life of a pot plant are major concerns for the grower. Therefore, the grower needs an instrument to predict the morphology of the pot plant. In this study the fresh mass and size of harvested bulbs at the end of the bulb preparation phase were measured before planting and plotted against measurements (variables), which were conducted on leaves and the inflorescences during the pot plant phase, to determine if the one variable can predict another by using the regression analysis procedure. In addition, the leaf number and total leaf area of the high (HTR), moderate (MTR) and low (LTR) temperature regime treated bulbs during the pot plant phase were plotted against the number of inflorescences to determine if they are related.

Neither the fresh mass nor the size of treated bulbs from the bulb preparation phase can be used to predict the eventual pot plant quality during the pot plant phase. The leaf number and total leaf area of the HTR and MTR treated bulbs are also not related to the number of inflorescences at the end of the pot plant phase. A possible explanation was that the HTR and MTR bulbs produced more than one module (two cataphylls, two leaves and an inflorescence), but abnormalities eg. flower abortion could have occurred or even additional inflorescences could have formed within these modules during the bulb preparation phase. In addition, these bulbs produced daughter bulbs that were probably not large enough to produce an inflorescence.

The only significant result obtained was the relation that was found between the leaf number of the LTR treated bulbs and the number of inflorescences at the end of the pot plant phase, at a stage too late for predicting pot plant quality. A possible explanation for the good relationship was that these bulbs grow strictly modular with no abnormalities during the bulb preparation phase and additional



inflorescences seldom develop. In addition, these bulbs produce daughter bulbs which are normally large enough to flower.

7.2 Introduction

Major concerns of the pot plant grower is the quality and shelf life of the end-product. The grower therefore needs an instrument to predict the quality of the pot plant before it is potted. In the previous chapters it was concluded that the three temperature regimes influenced the bulb end-product during the bulb preparation phase and consequently the quality of the pot plant. In this chapter therefore, the fresh mass and size of bulbs, that were harvested at the end of the bulb preparation phase, were measured just before planting and plotted against measurements which were conducted on the leaves and inflorescences during the pot plant phase to determine how they are related or if the one variable can predict another by means of using the regression analysis procedures.

According to Chatterjee and Price (1977), regression analysis is one of the most widely used statistical tools, because it provides a simple method for establishing functional relationships among variables. In addition, correlation (applied in previous chapters) and regression are two aspects of the same phenomenon; correlation only indicates that a relationship exists, while regression describes the trend of the relationship (Steele and Torrie, 1980).

7.3 Materials and Methods

Data were analysed using the REG (Regression) procedure in the SAS (Statistical Analysis Systems) program and an analysis of variance was performed.

Snedecor and Cochran (1967) and Steele and Torrie (1980) are two of many text books which



describes and explains regression in detail, but what is important for this study, is that when simple linear relationships are drawn, only two variables are involved. The one variable is the independent one (X) which may cause the response of the dependent one (Y).

In this study there were more than one independent variable (X) which affected the response (dependant variable Y) and may therefore have caused a number of regression problems. Multiple regression is then applicable to obtain the combined effect of all these variables (Snedecor and Cochran, 1967). However, a prediction equation containing a variable that has little or no effect and another which may be highly correlated thus having the same prediction effect is unwieldy. Fitting a multiple regression model (equation) can become very complex, therefore by using the stepwise regression procedure a predictor variable (X) can be forced in and out of the model. In this procedure the poorest independent variables were taken out of the model.

Firstly, the bulb fresh mass and bulb size were the independent variables that were selected to predict various variables (Table 7.1) and secondly the leaf number and total leaf area were selected to determine if these measurements (variables) were related to the number of inflorescences. By using the stepwise regression procedure, it led to only two variables and therefore the statistical model for this 'simple linear regression' is as follows (Steele and Torrie, 1980; Snedecor and Cochran, 1967):

Y = bx + a

where	Y	=	the estimated dependent variable
	а	=	the estimate of the intercept of the line on the Y-axis
	b	=	the estimate of the slope of the line
and	Х	=	the independent variable



7.4 **Results and Discussion**

7.4.1 Bulb fresh mass and size versus quality and keeping ability of pot plant

The relationship between the fresh mass or size of the temperature treated bulbs and the shelf life, number of inflorescences as well as the length and compactness of the inflorescences of the treated bulbs during the pot plant phase accounted for less than 50% of the variation, thus more than 50% variation remain unexplained (Table 7.1). In addition, Table 7.1 depicts that the relationship between the bulb fresh mass or size and the number of leaves accounted for less than 60% and consequently more than 40% variation remain unexplained. According to Snedecor and Cochran (1967) such relationships between variables are considered as poor. As a result the fresh mass or size of a bulb cannot be used to predict the quality and keeping ability of the pot plant. It is therefore significant to note that although the HTR treated bulbs produced smaller bulbs with a lower fresh mass than those of the LTR and MTR (see Chapter3), these measurements do not necessarily lead to a poor quality pot plant, therefore the structure of the bulb (see Chapter 4) has a more profound effect on the morphology of the pot plant.

7.4.2 Leaf number and total leaf area versus number of inflorescences

The number of leaves counted on the LTR treated bulbs related 75% to the number of inflorescences (Table 7.2). This is considered satisfactory for biological variables (Snedecor and Cochran, 1967). The modular growth pattern of the LTR bulbs is described in Chapter 4 and it was concluded that mainly one inflorescence will emerge after two leaves have been produced by the bulb, no flower abortion occurred and additional inflorescences seldomly developed in the axil of the inner leaf bases of these bulbs. Figure 7.1 illustrates that for every two leaves counted on the plant, one inflorescence was present. The LTR bulbs also produced larger daughter bulbs compared to the other temperature treatments (Chapter 6, Figure 6.14), which means that these bulbs were probably large enough to produce two leaves and thereafter an inflorescence emerged (Figure 7.2).



The leaf number counted on the HTR treated bulbs did not relate to the number of inflorescences and the total leaf area was related rather poorly (27%) to the number of inflorescences (Table 7.2). The other 73% variation was probably due to flower blast (abortion), because the HTR treated bulbs, which produced about six leaves per pot (Figure 6.8, Chapter 6), rendered only an average of 1.5 inflorescences (Figure 6.6, Chapter 6). Even additional inflorescences, which occur under this temperature regime (Chapter 3 and 4), could not make up the loss for inflorescences due to abortion.

Furthermore, the leaf number counted on the MTR treated bulbs also did not relate to the number of inflorescences in the same way as the total leaf area related to only 59% to the number of inflorescences emerging from these bulbs (Table 7.2). As mentioned before, this is a poor relationship (Snedecor and Cochran, 1967), and the remaining 41% was probably due to the fact that although a bulb developed by means of a modular growth pattern (see Chapter 4), it could have formed additional inflorescences in the axil of inner leaf bases. Referring to Chapter 3, this phenomenon is common under warm temperatures. Another possible explanation for the poor relationship was that the daughter bulbs ,which are produced in the axil of the swollen leaf bases, unless they are of a minimum size, their inflorescences will abort or not develop.

7.5 Conclusion

The different temperature regimes during the bulb preparation phase manipulated the bulbs to develop into a specific quality pot plant irrespective of the bulb fresh mass or size. As a result it is not recommended for the grower to use the fresh mass or size of the bulb before planting to predict the quality of and the keeping ability of the pot plant during the pot plant phase. Even the leaf number and total leaf area measurements are poor tools to use to correlate the number of inflorescences of the HTR and MTR treated bulbs. In this study, the leaf number counted on the LTR treated bulbs was the only measurement that was related to the number of inflorescences. This in turn, was related to the number of growth modules as well as the daughter bulb size in the axils of the leaf bases, which could not be determined without destroying the bulb.



7.6 References

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Table 7.1 Regression analysis of the relationships between the fresh mass / size of high (HTR), moderate (MTR) and low (LTR) temperature regime treated bulbs before planting and measurements conducted on leaves and inflorescences of these bulbs during the pot plant phase.

Treat- ment	X-variable	Y-variable	Intercept (a)	Slope of line (b)	R- value
HTR	Bulb fresh mass / size	Shelf life of pot plant	-	-	-
MTR	Bulb fresh mass / size	Shelf life of pot plant	-	-	-
LTR	Bulb fresh mass	Shelf life of pot plant	28.085	-0.408	0.08
HTR	Bulb fresh mass	Number of inflorescences	0.593	0.207	0.09
MTR	Bulb fresh mass	Number of inflorescences	-1.038	0.659	0.45
LTR	Bulb fresh mass	Number of inflorescences	0.583	0.264	0.12
HTR	Bulb size	Flower number on primary inflorescence	-1.995	1.584	0.074
MTR	Bulb fresh mass	Flower number on primary inflorescence	-	-	-
LTR	Bulb fresh mass	Flower number on primary inflorescence	-	-	-
HTR	Bulb fresh mass	Total length of primary inflorescence	96.095	13.704	0.09
HTR	Bulb fresh mass	Total length of secondary inflorescence	-4.924	16.838	0.08
HTR	Bulb fresh mass	Total length of tertiary inflorescence	-22.309	9.143	0.06
MTR	Bulb fresh mass	Total length of primary inflorescence	133.392	16.135	0.22
MTR	Bulb fresh mass	Total length of secondary inflorescence	-23.357	30.304	0.24
MTR	Bulb fresh mass	Total length of tertiary inflorescence	-126.644	40.645	0.40
LTR	Bulb fresh mass / size	Total length of primary inflorescence	-	-	-
LTR	Bulb size	Total length of secondary inflorescence	150.761	15.043	0.04



LTR	Bulb fresh mass	Total length of tertiary inflorescence	_	-	-
HTR	Bulb fresh mass / size	Compactness of primary inflorescence	-	-	-
HTR	Bulb size	Compactness of secondary inflorescence	0.232	-0.014	0.09
HTR	Bulb fresh mass /size	Compactness of tertiary inflorescence	-	-	-
MTR	Bulb fresh mass	Compactness of primary inflorescence	0.248	-0.014	0.27
MTR	Bulb fresh mass / size	Compactness of secondary inflorescence	-	-	-
MTR	Bulb fresh mass / size	Compactness of tertiary inflorescence	-	-	-
LTR	Bulb size	Compactness of primary inflorescence	0.088	0.007	0.03
LTR	Bulb fresh mass / size	Compactness of secondary inflorescence	-	-	-
LTR	Bulb fresh mass / size	Compactness of tertiary inflorescence	-	-	-
HTR	Bulb fresh mass	Number of leaves	1.230	0.975	0.15
MTR	Bulb fresh mass	Number of leaves	-1.585	1.366	0.34
LTR	Bulb fresh mass	Number of leaves	2.194	0.472	0.11
HTR	Bulb fresh mass	Total leaf area	33.575	18.592	0.22
MTR	Bulb fresh mass	Total leaf area	-22.761	41.274	0.57
LTR	Bulb size	Total leaf area	-38.842	34.483	0.08



Table 7.2 Regression analysis of the relationships between the number of leaves /total leaf area and the number inflorescences of the high(HTR), moderate (MTR) and low (LTR) treated bulbs during the pot plant phase.

Treat- ment	X-variable	Y-variable	Intercept (a)	Slope of line (b)	R- value
HTR	Total leaf area	Number of inflorescences	0.051	0.009	0.27
MTR	Total leaf area	Number of inflorescences	-0.179	0.014	0.59
LTR	Number of leaves	Number of inflorescences	-0.077	0.470	0.75



Figure 7.1 Illustration of the relationship between the number of leaves counted on the low (LTR)temperature regime treated bulbs and the number of inflorescences during the pot plant phase.



Figure 7.2 Photographical illustration of the correlation between the number of leaves counted on the low (LTR) temperature regime treated bulbs and the number of inflorescences during the pot plant phase.



CHAPTER 8

GENERAL DISCUSSION

The importance of pot plants, including bulbous plants for the local as well as international floral industry is increasing rapidly. A number of South African bulbous plants have been ennobled in other countries, though, little effort has been made by South Africans to develop new pot plant products from natural occurring species. The Vegetable and Ornamental Plant Institute launched the *Lachenalia* research program, during which more than 30 cultivars were released (Coertze, *et al.*, 1992). Cultivar Ronina, one of the varieties developed in the program, offered great potential for use as a pot plant due to its robust growth, colour and flower shape and therefore was selected for commercialization (Coertze *et al.*, 1992).

Bulbs in general usually need to reach a certain size before they can be used for flower or pot plant production (De Hertogh and Le Nard, 1993; Niederwieser *et al.*, 1997). According to Louw (1991) and Roodbol and Niederwieser (1998) a minimum bulb size of 5-6 cm in circumference is recommend for a *Lachenalia* bulb. Louw (1991) and Roh *et al.* (1995) stressed the importance of the storage phase for flower initiation and differentiation prior to planting for the pot plant phase and Roh *et al.* (1995) also suggested that a high temperature before harvest will promote floral development of bulbs after harvest. However, the lack of reliable information regarding the preparation of bulbs to reach this stage was the reason for this project. Due to the complexity of the different growth phases alterating with storage periods, rendered it necessary to base the discussions on a time scale program, as shown in Figure 1.1 (Chapter 1).

Louw (1991) based her descriptions of flower initiation and differentiation on cultivar Romelia during the storage period, whilst Roodbol and Niederwieser (1998), using the same cultivar, also incorporated the growing phase for their descriptions. Working with cultivar Ronina, it was found that a re-interpretation of bulb growth and flower differentiation was necessary. Besides this



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concern, it was contemplated by Roodbol and Niederwieser (1998) that similar studies should be repeated on other cultivars as there are vast differences in the behaviour of different cultivars. This led therefore to a thorough investigation of bulb structure and development as discussed in Chapter 2. One of the most prominent results of this investigation was the first ever interpretation of the bulb architecture of cultivar Ronina bulbs and the description based on the modular, sympodial growth pattern. Evidence was supplied that inflorescence differentiation occurred during the growing season, and not during dormancy (storage period) as observed in cultivar Romelia (Louw, 1991).

After this investigation, a further trial started where bulbs (phase 3, Figure 1.1) were grown under three temperature regimes to evaluate their performance. Surprising results were observed under these three temperature regimes during the bulb preparation phase, where higher temperature regime treatments resulted in increased developmental growth rate of the modules within the bulbs, but unfortunately inflorescence abortion occurred under the highest temperature regime. Flower blast or abortion, according to De Hertogh and Le Nard (1993), is when a bulb fails to produce a marketable flower. This physiological disorder is common in numerous bulb species, especially in *Tulipa* where flowers abort when plants are grown or stored under too high or low temperature extremes (De Hertogh and Le Nard, 1993).

Additional inflorescences, originating from underdeveloped growth modules, were detected in the axils of the inner leaf bases of the high temperature regime treated bulbs, late during the bulb preparation phase (Figure3.3, Chapter 3). Roodbol and Niederwieser (1998) found in cultivar Romelia that a secondary inflorescence was formed within the new apical bud, four weeks after planting. In cultivar Ronina similar results were found, where the second growth module developed approximately 10 weeks after planting (Figure 2.3, Chapter 2), however, the inflorescence of a growth module will not emerge unless a previous module's inflorescence has appeared or aborted, which was described in Chapter 2, 3 and 4. Roodbol and Niederwieser (1998) did not describe or explain the exact site of inflorescence initiation within the bulb and whether they flowered during the same growing season. In this thesis it was described and explained why and how additional inflorescences will always emerge without the enclosed leaves, as illustrated in Figure 3.3. Further



research on this topic thus need to be done.

Under all three temperature regime treatments daughter bulbs were observed in the axils of mainly the outer leaf bases during storage, after the bulb preparation phase. Similar results were found by Roodbol and Niederwieser (1998) in cultivar Romelia, where daughter bulbs were found in the axil of the swollen leaf bases of the bulbs during dormancy. No 'supernumery' bulblets, however, were observed in cultivar Romina bulbs during the growing phase, as observed in cultivar Romelia. A possible reason was that these bulblets did not develop under these controlled growing conditions or large differences exist in behaviour of the different cultivars. In spite of the slower development of the low temperature regime treated bulbs, the overall quality of these bulbs was better than those of the moderate and high temperature regime. The flower bulbs subjected to the low temperature regime apparently photosynthesized optimally during the bulb preparation phase, which was confirmed in Chapter 5.

With above mentioned results obtained, it was concluded that the best temperature regime for bulb production was the low temperature regime, which represented the cool winter climate in South Africa. However, it was observed that the moderate temperature regime, which simulate the mild winter climate in South Africa, also produced marketable size bulbs during the bulb preparation phase.

Surprising results were again obtained, showing that the temperature regimes during the bulb preparation phase, which influenced the quality and size of the bulbs, also influenced the quality of pot plants grown from these bulbs the following season. Several favourable results obtained during the pot plant phase were simultaneous flowering which more often occurred in bulbs that were subjected to the low temperature regime. Low temperature bulbs also rendered better quality inflorescences with a considerably better keeping quality than those of the moderate and high temperature regime. Furthermore, broader and more spotted leaves were produced by these bulbs.

In Chapter 7, it is illustrated how these low temperature regime treated bulbs produced two leaves



concurrently with one inflorescence during the pot plant phase. A modular, sympodial growth pattern, which was chronological through the bulb preparation and dormancy period, was observed in the low temperature regime treated bulbs (Chapter 4). It is therefore important to notice that no flower abortion was observed neither were additional inflorescences detected from the developing modules during bulb preparation phase, storage period and consequently during the pot plant phase. In addition, these bulbs produced daughter bulbs in lower numbers than those of the other temperature treatments, which was observed during the pot plant phase. However, these low temperature regime daughter bulbs grew to a size large enough to initiate inflorescences. In this study the bulbs were not dissected into different parts during the pot plant phase, therefore no information was obtained about further development and inflorescence differentiation of these daughter bulbs during this growing phase or the effect the temperature of the previous growing season (phase 3) had on these growth responses. It appears, according to the modular growth pattern and the daughter bulb size, that the low temperature regime control the plant growth in a manner which makes it more predictable and therefore more manageable to grow.

The above mentioned results in this thesis can be extrapolated to field conditions:

The cool winter climate would be optimal for the bulb preparation phase to produce a quality bulb and consequently a quality pot plant the following year.

Bulbs which are grown in a moderate $(22^{\circ} / 10^{\circ}C \text{ day} / \text{night})$ winter climate could be a slightly smaller size than those of the cool winter climate and more than one growth module could develop inside these bulbs at a faster rate which also could result in a slightly earlier planting date than those of the cool region. Usually the morphology of *Lachenalia* pot plants are unpredictable, because first of all, one to three growth modules may develop inside the bulb during the one season. This will lead to differences in leaf and inflorescence number between the different pot plants. Secondly, a high number of daughter bulbs differing in size and the ability to flower during the pot plant phase may develop. Thirdly, flower abortion may occur. Uniformity in morphology and simultaneous flowering



are therefore lost in this phase.

A warm (28° / 12°C day / night) winter climate or even a summer climate is not suitable for the bulb preparation phase, primarily because flower abortion may occur and poor quality bulbs will be obtained during this phase. During the following season (pot plant phase) flower abortion might still take place and poor quality inflorescences will definitely develop, even if the growing temperature is lower during this phase.

Another result with practical implications in this thesis was that in all three temperature regime treatments, the flowering date of the bulbs was shifted to approximately two months earlier, compared to those that normally grow under outdoor conditions. This indicates that there is an opportunity for the grower to manipulate the flowering date to co-inside with certain holiday events, for example Easter, since the experimental plants did flower during April. It is also important to consider that results obtained by these temperature regimes, which were controlled and did not fluctuate in growth chambers, while greatly enhanced our bank of knowledge, did not encompass the true growth pattern that exists in a natural growing habitat. Production areas for outdoor bulb production in South Africa therefore need to be identified by investigating the climatic conditions and especially the day /night temperatures in a proposed region. As mentioned before in Chapter 1, the bulb preparation phase is the last crucial growing phase during which the final bulb size and eventual pot plant quality are determined. It is therefore imperative that growers determine the best region for optimal growth during this phase.

Certain factors still need to be considered when bulbs are produced under outdoor conditions. For example, plants are more exposed to pests and diseases and to seasonal fluctuations (temperature, rainfall, light intensity etc.) during the growing phase, which might affect the quality of the bulb as well as the pot plant. Forcing bulbs for earlier or later flowering is also not possible under these conditions. The capital layout of the nursery and operation expenses in growing this product and the income when selling it overseas or locally should therefore be weighed against each other to decide if these bulbs will be grown in a climatic controlled greenhouse or underneath a shade net.



Another factor that should be taken into account is that the climatic conditions for the bulb preparation phase and the pot plant phase differed in this study. Roodbol and Hancke (1997) came to a similar conclusion that bulb multiplication and growing bulbs to a forcing size need different growing conditions. This may limit the grower to one production phase for his nursery and therefore it is important that growers collaborate to make *Lachenalia* production feasible in South Africa.

One valuable realization from this thesis was to learn that bulb size, although regarded as the major commercial method to evaluate future pot plant quality (De Hertogh and Le Nard, 1993; Rees, 1992), is not a reliable technique for *Lachenalia*. In Chapter 7 it was found that the bulb fresh mass / size at the end of the bulb preparation phase is not a suitable measurement tool to predict the quality of the pot plant. Therefore, primarily the bulb structure (growth modules) can give an idea how it will grow. Environmental conditions (temperature) and subsequently the amount of reserves thus also determines the bulb's ability to form flowers.

Generally, growing temperatures are more difficult to control than storage temperatures, since the former takes place more or less under outdoor or greenhouse conditions. As observed in this thesis, changing the seasonal thermoperiodism can lead to an important modification of growth and development. In *Lachenalia*, the different stages of bulb development showed various temperature requirements. For example, flower differentiation (new growth modules) was enhanced when it was subjected to moderate and high temperatures, whereas scape elongation required a lower temperature requirement (See Chapter 6, p63). Under specific growing temperatures, daily thermoperiodic changes may influence flowering. For example, the flowering of *Urginea maritima*, a garden bulb endemic to South Africa, can be promoted by producing these bulbs under a temperature differential between day and night which is larger than normal (McCrohan, 1990), however, this was not investigated in *Lachenalia*. Therefore, seasonal thermoperiodic effects on the growth and development of *Lachenalia* bulbs need more attention in future research.

The effect of differential day / night temperatures (DIF) on inflorescence scape length is another aspect that should be investigated in *Lachenalia*. De Hertogh and Le Nard (1993) mentioned that



the 'DIF' concept for height control in Easter lilies is when a high night temperature is used in combination with a low day temperature to reduce plant height. *Lachenalia* cv. Ronina inflorescences were slightly taller under the low temperature regime and therefore, this type of greenhouse forcing can be used to control height if scape length becomes a disadvantage to the grower.

A further study that should be considered is to manipulate the annual growing cycle of a *Lachenalia* bulb to an evergreen plant, which will produce flowers continuously. The reason for this potential, is that the high temperature regime bulbs during the bulb preparation phase repeatedly developed new growth modules and delayed senescence was observed when the temperature was increased before storage. It may therefore be possible, because *Ornithogalum thyrsoides* (also from the Hyacinthaceae family), a synanthous-deciduous plant in its native habitat in South Africa, kept on flowering as an evergreen plant when it was grown in the tropics (Halevy, 1990).

Bulb growth and development are generally less affected by light, especially for flower bulbs such as *Hyacinthus* and *Narcissus* (De Hertogh, 1974), since they can complete their growth cycle in darkness and when grown under light conditions, the quality of these plants were improved. However, in *Alstroemeria*, *Gladiolus*, *Iris* and *Lilium*, light greatly affects flowering (De Hertogh and Le Nard, 1993). For example, according to Rees (1992) *Alstroemeria* plants flower earlier if subjected to long days, whilst in *Gladiolus* long days increase flowering percentage, floret number per spike and spike length, but delays flower development and anthesis. In *Lachenalia*, a critical day length has not yet been determined. A 14hr photoperiod was provided in the growth cabinets which may have caused the earlier flowering date in all three temperature regime treated bulbs. It is therefore important to further investigate the effect different day lengths might have on the flowering date or inflorescence quality of *Lachenalia*. Interaction between light and temperature also needs to be addressed since it has been reported that the higher the growth temperature, the higher the light intensity required to avoid flower abortion (De Hertogh and Le Nard, 1993).

Another factor that should be considered for future research is the possible effect of root activity on



flower induction. In the case of *Lachenalia*, it appears that the high temperature regime favoured root formation in bulbs, but flower formation the following year was poor. In Tulipa it has been observed by Le Nard (1986) that the presence of actively growing roots unfavourably affects flower initiation in daughter bulbs. Therefore, more intensive research should be conducted on the effect root growth may have on flower induction in the mother bulb and also in daughter bulbs.

For the first time, carbohydrate partitioning in *Lachenalia* bulbs was described, in which valuable results were obtained. One significant observation was that bulbs, but also the roots, were the main sinks for carbohydrates, whereas the inflorescence and leaves are the main source for soluble sugars. Secondly, it was found that the starch content in the bulbs were not so high compared other bulbs and that different forms of carbohydrates (glucomannan) may play a role. Carbohydrate research was directed towards understanding the mobilization of carbohydrates from source to sink(s), however, research should be focussed on the competition between the emerging inflorescence and daughter bulbs for carbohydrates from the mother bulb during the bulb preparation phase. In addition, by studying the movement of carbohydrates as well as hormones between the cataphylls (bulb scales), euphylls (leaves) and developing inflorescence inside the developing modules might lead to a better understanding why mother bulbs initiate additional growth modules instead of daughter bulbs.

It can be concluded that the *Lachenalia* bulb is an extremely complex organ. Although one may evaluate a quality bulb on the outside, it does not necessarily mean that it will produce a quality pot plant. All relationships between physiological state of the bulbs and processes such as floral bud and root organogenesis, bulbing and flowering and their source/sink relationships as well as root activity and floral initiation must be considered and integrated to obtain a complete understanding of bulb growth and development.

The main contribution of this thesis is the plant architectural - based interpretation of bulb growth and the reaction of temperature manipulated bulbs. This together with a thorough knowledge of the carbohydrate household in the plant, might lead to a better understanding of bulb behaviour and



better planning for future research.

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