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THE EFFECT OF TEMPERATURE ON INFLORESCENCE
INITIATION, DIFFERENTIATION AND DEVELOPMENT
OF LACHENALIA CV. 'ROMELIA'

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THE EFFECT OF TEMPERATURE ON
INFLORESCENCE INITIATION,
DIFFERENTIATION AND DEVELOPMENT
OF *LACHENALIA* CV. 'ROMELIA'

by

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FOR GOD, AND THROUGH GOD, AND TO GOD,
ARE ALL THINGS: TO HIM BE GLORY FOR EVER!



Lachenalia cultivar 'Romelia'

CONTENTS

INTRODUCTION	1
1. Description	1
2. Distribution	1
3. Environmental conditions	1
4. The economic potential of <i>Lachenalia</i>	2
5. The breeding program in South Africa	2
6. The aim of this study	3
7. References	3
CHAPTER 1 - LITERATURE REVIEW	4
1.1 Historical aspects	5
1.2 Stages of development during flower formation	5
1.3 Factors controlling flower initiation and development in bulbs	6
1.3.1 Bulb size	6
1.3.2 Stage of apex development	6
1.3.3. Light intensity and photoperiod	7
1.3.4. Temperature	7
1.3.4.1. Temperature requirements for floral initiation and subsequent commencement of differentiation	8
1.3.4.1.1. High temperature after lifting	8
1.3.4.1.2. Vernalization	8
1.3.4.2. Temperature requirements for flower differentiation elongation	9
1.3.4.2.1. Pre-cooling	9
1.3.4.2.2. Post storage	10
1.3.4.3. Growth at higher temperatures	11
1.4. Manipulation of the flowering date	11
1.4.1. Example I: Tulip forcing	11
1.4.2. Example II: Hyacinth forcing	12
1.4.3. Year-round culture	13
1.4.4. Conclusion	14
1.5. References	14

CHAPTER 2 - MORPHOLOGY OF FLOWER DEVELOPMENT	17
2.1. Introduction	17
2.2. Materials and Methods	17
2.3. Results and discussion	20
2.3.1. Life cycle and developmental morphology	20
2.3.2. Anatomical changes in the vegetative apex during the life cycle	20
2.4. Conclusion	26
2.5. References	27
CHAPTER 3 - THE EFFECT OF STORAGE TEMPERATURES ON FLOWERING DATE AND FLOWER QUALITY	28
3.1. Introduction	28
3.2. Materials and Methods	28
3.2.1. Flower development and flowering date	29
3.2.2. Flower quality	29
3.3. Results and Discussion	31
3.3.1. Flower development and flowering date	31
3.3.1.1. Temperature effect on flower initiation and development	31
3.3.1.2. The time-lag between planting and flowering	34
3.3.1.3. Flowering date	36
3.3.2. Flower quality	36
3.3.2.1. Floret number	38
3.3.2.2. Rachis length and compactness	40
3.3.2.3. Peduncle length	42
3.3.2.4. Peduncle cross section	44
3.3.2.5. Secondary inflorescences	44
3.3.2.6. Keeping ability	44
3.4. Conclusion	46
3.5. References	48
CHAPTER 4 - RETARDING THE FLOWERING DATE	49
4.1. Introduction	49
4.2. Materials and Methods	50
4.2.1. Experiment I	50
4.2.2. Experiment II	50

4.3. Results and Discussion	52
4.3.1. The effect of 10°C on flower initiation and flowering date	52
4.3.2. The influence of the environmental conditions on differentiation	55
4.3.3. Flower quality	55
4.4. Conclusion	58
4.5. References	59
GENERAL DISCUSSION AND CONCLUSION	60
OPSOMMING	66
SUMMARY	68
ACKNOWLEDGEMENTS	70

INTRODUCTION

The genus *Lachenalia* is endemic to Southern Africa and belongs to the family *Liliaceae* (or *Hyacinthaceae sensu stricto*). The genus presently comprises 90 species and according to Duncan (1988) twenty new species have yet to be formally described and published.

1. Description

Lachenalia is a small, bulbous geophyte. The genus exhibits remarkable variety in the number and appearance of its leaves. Some species produce only one leaf, while others may have up to eight leaves. The colour, spotting and banding patterns, texture and shape also vary and contribute to the attractiveness of the plant. Three different types of inflorescences are encountered: spikes, subspicates and racemes. A wide spectrum of flower colours exists in the genus from yellow to blue. Three flower shapes occur, namely, horizontal pipes, hanging bells and hyacinth shapes. Some species also exhibit a pleasant odour (Duncan, 1988).

2. Distribution

Lachenalia has a wide distribution. These plants are found in the Cape Province, Ciskei and further eastwards to Transkei. In the west the distribution is northwards to the southern parts of Namibia with a concentration of species in the winter rainfall area of the south western Cape (Duncan, 1988).

3. Environmental conditions

In order to ascertain the cultivation conditions of a newly bred plant, a knowledge of the environmental conditions of their natural habitat is important. The soil in the areas where *Lachenalias* grow varies, but generally is sandy and well drained.

Lachenalia depends on seasonal winter rain; they survive the hot, dry summer in the form of a resting bulb. In the winter, when there is enough moisture, active growth commences (Duncan, 1988).

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 (Hanke, 1983 pers. comm.).

Lachenalias have a low light requirement, and active growth can occur at relatively low light intensities (250-375 W/m²) and few sunshine hours per day (Hanke, 1983 pers. comm.).

4. The economic potential of *Lachenalia*

Lachenalia is suited to commercial potplant production for the following reasons (Hancke, 1991);

- Large variation in appearance exists within the genus.
- The genus has a long flowering period from May to September.
- The inflorescence is 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 bulblet formation from the 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.

Lachenalia has the potential to generate large amounts of foreign exchange.

5. The breeding program in South Africa

In 1966 a breeding program on the genus *Lachenalia* was initiated at the Vegetable and Ornamental Plant Research Institute in Pretoria. The aim was to develop an improved potplant by exploiting the above-mentioned potential. Since 1966, hundreds of crossings have been made from which 51 selections were selected. Thirty two of these were released as cultivars (Lubbinge, Ferreira & Van der Laarse, 1983a, 1983b, 1983c, 1983d; Hancke & Coertze, 1988; Malan, Ferreira & Van der Laarse, 1983 and Hancke, 1991 pers. comm.).

The cultivars are now in a multiplication phase and will shortly be available to the public.

6. The aim of this study

Although 32 *Lachenalia* cultivars are released, there is still a lack of information with regard to the cultivation of high quality pot plants.

The aim of this study was threefold: Firstly to make a morphological and anatomical study of the flowering process. Secondly to determine the optimum storage and growth conditions for flowering and thirdly to investigate manipulation of the flowering date.

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CHAPTER 1

LITERATURE REVIEW

A bulb is an underground storage organ which consists mainly of fleshy leaf bases and scales. These leaf bases, which are the storage organs, are attached to a very short stem. The growing point is found in the centre between the leaf bases (Reyneke, Coetzer & Grobbelaar, 1979). Like *Hyacinthus* (hyacinths), *Tulipa* (tulips), *Narcissus* (daffodils) and *Ornithogalum*, *Lachenalia* is also a bulbous plant (Rees, 1972; Jansen van Vuuren, 1990; Duncan, 1988).

The term corm and bulb are often confused. A corm differs from a bulb in that the short, thickened stem is the storage organ. Dead leaf bases enclose the stem. Axillary buds are found in the axils of these leaves. *Gladiolus* and *Watsonia* are examples of corms (Reyneke *et al.*, 1979). There exist major differences in the flower formation between these groups. Since *Lachenalia* is a bulbous plant, only the flower formation of this group of plants will be discussed in this literature study.

The method by which the potted plant or cut flower is produced from a storage organ, is called forcing. According to De Hertogh (1974) the principal prerequisite to forcing is environmental control and, more specifically, temperature control. In some instances, forcing is accomplished by utilizing naturally occurring climatic conditions in combination with artificially controlled ones. In other cases, growth is regulated entirely artificially. The exact technique to be used depends on the species and cultivar being forced, how and when the pot plant or cut flower is to be marketed, and the climatic conditions existing in the forcing locality.

1.1 Historical aspects

The forcing of hyacinth bulbs was already commonplace in the early 18th century (De Hertogh, 1974). Systematic research on the influence of temperature on bulb development, however, did not begin until the early 20th century. According to De Hertogh (1974) Nicolaas Dames demonstrated that Dutch-grown hyacinths could be forced before

Christmas by a combination of early harvesting and a sequence of post-harvest temperature treatments. Blaauw and co-workers studied the influence of temperature on the flower development of a wide range of bulbous plants (Hartsema, 1961). A book on the growth of bulbs by Rees (1972) reviews all the important research that was done in the first half of this century on the basic needs for flower development in bulbs. This book of Rees (1972) and the review article by Hartsema (1961) were the main sources of information for this literature study. The methodology of this study is a combination of that used by Hartsema (1961) and Jansen van Vuuren (1990).

1.2 Stages of development during flower formation

The flowering process can be divided into several successive stages. The number of stages which can be distinguished in different bulbous plants is not the same. Beyer (In Hartsema, 1961) therefore proposes the use of letter symbols, relating to the morphological stage attained. Hartsema (1961) distinguished between the following stages of flower development in hyacinths:

stage I		apex of growing point still low and flat
stage II		apex of growing point dome-shaped
stage III	(Pr)	primordia of two lowest flowers visible
stage IV	(Br)	lower flower initials all present, each with bract initial but no further differentiation
stage V	(P1)	3 outer sepals to be distinguished as separate primordia
stage VI	(P2)	3 inner sepals to be distinguished as separate primordia
stage VII	(A1)	3 primordia of the first whorl of stamens to be distinguished
stage VIII	(A2)	3 primordia of the second whorl of stamens to be distinguished
stage IX	(G)	3 carpel-primordia visible
stage X	(G)	margins of 3 carpels infold to form ovary, while anther lobes appear on stamens

Jansen van Vuuren (1990) distinguished nine developmental stages in the inflorescence formation of *Ornithogalum thyrsoides*. He used the differentiation of the subsequent flower primordium whorls to distinguish the stages. He also measured the length of the inflorescence as an indication of the development stages. The stage when the carpel

primordia were formed in the oldest flower was considered to be the last stage.

Observations concerning the transformation of the vegetative apex to a reproductive apex are not uniform. Hartsema (1961) described the vegetative apex as low and flat and the transformed apex as domeshaped for *Tulipa* and *Hyacinthus*. Similar observations were made by Shoub & Halevy (1971) for *Ornithogalum arabicum* and by Van Bragt, Luiten & Sprenkels (1986) for *Eucharis*. Uhring (1973) described the transformed apex of bulbous iris as being broadened and lengthened. The vegetative apex of *Narcissus* also broadened and thickened during transformation (Hartsema, 1961).

1.3 Factors controlling flower initiation and development in bulbs

The terms flower initiation and flower differentiation are not always well defined in the literature. The term flower initiation is often used to describe the commencement of Stage II or III (e.g. Shoub & Halevy, 1971 and Ohkawa, 1986). The terms flower differentiation or flower formation are used to describe the processes proceeding until all the flower organs of the inflorescence are completed. In this study, flower initiation refers to the physiological process that precedes Stage III. When the first signs of transformation to the floral phase are noticed, differentiation has commenced.

1.3.1 Bulb size

It is well-known that bulbs below a certain size do not flower (Rees, 1972). Each species and cultivar has a minimum bulb size at which flowering will occur. This is, however, not the only internal factor determining flowering. It often happens that a small bulb attached to a large bulb will flower. According to Rees (1972) this indicates the possible transfer of a flowering stimulus.

1.3.2 Stage of apex development

The stage of development of the apex is important in determining onset of flower differentiation. In some cases (e.g. tulip) all the leaf primordia are formed before flower formation, while in other cases (e.g. iris) the number of leaves formed prior to flower formation is variable. In hyacinth the change-over to the flowering state can be induced

at any time by high temperature treatment (Salisbury, 1963).

In an experiment with asiatic hybrid lilies Zang, Beattie & White (1990) found that the bulbs required a certain stage of maturity to initiate flower buds, regardless of the bulb sizes.

1.3.3 Light intensity and photoperiod

Bulbs can be divided into two groups on the basis of their light requirements. In the first group light does not play an important role in flower development, but effects overall quality. Examples of this group are tulips, hyacinths and daffodils (De Hertogh, 1974).

Light plays a significant role in floral development of the second group which includes Dutch Iris (Mae & Vonk, 1974) and Easter lilies (Wilkins & Waters, 1971). Both light intensity and photoperiod influence flower development of these plants.

When these results are compared with those of Hartsema (1961), it is apparent that light effects on flower development are mainly observed in those bulbs where flower differentiation commences after planting. Photosynthetic leaves are present at this stage to intercept light effects.

1.3.4 Temperature

Temperature is the most important factor affecting initiation and subsequent flower development (De Pagter, 1976). Much work has been done on this subject, and the review article of Hartsema (1961) is regarded as the most significant as will be discussed underneath.

The apical meristem is regarded as the site of perception of the temperature stimulus. In order for the temperature to be perceived, the cells at the apical meristem must be metabolically active (Salisbury, 1963).

1.3.4.1 Temperature requirements, for floral initiation and the subsequent commencement of differentiation

Most rapid floral initiation and commencement of differentiation for *Tulipa* and *Narcissus* occurs at 17 to 20 °C, for *Hyacinthus* at 25 °C, for *Lilium* at 20 to 23 °C, for *Iris* at 13 °C and for *Ornithogalum arabicum* at 25 °C (Hartsema, 1961, Shoub & Halevy, 1971). *Eucharis amazonica* requires a 27°C treatment for 4 weeks, followed by 21°C for flower initiation (Van Bragt, Luiten & Sprekels, 1986) With the exception of *Iris*, and *Ornithogalum thyrsoides* all have high optima. The results of Jansen van Vuuren (1990) for *Ornithogalum thyrsoides* showed that the optimum for flower initiation and commencement of differentiation is 5 °C. Although optimum temperatures are often well-defined, the range over which flower differentiation will eventually commence is very wide.

1.3.4.1.1 High temperatures after lifting

The use of high storage temperatures (30 to 35°C) immediately after lifting has been shown to advance flower initiation in tulips, daffodils and hyacinths. In tulip bulbs, a high temperature treatment of 30°C for 1 to 5 weeks shortened the period necessary for flower bud differentiation until Stage G, increased flower bud height at stage G, and had a favourable effect on subsequent rooting (Le Nard, 1980). The flowering date of *Narcissus* can be advanced by several high temperature treatments e.g. burning over the field, clear polyethylene coverage or warm storage (Tompsett, 1980).

An interaction exists between the lifting date and effectivity of high storage temperatures. Early lifted bulbs benefit from a high temperature treatment, while high temperatures do not have an effect on late lifted bulbs (Rees & Goodway, 1970 and Rees, 1972).

1.3.4.1.2 Vernalization

Some plants (e.g. *Lilium*) require a certain minimum temperature for flower initiation (vernalization) (Salisbury & Ross, 1978). This low temperature requirement needs to be satisfied before flower differentiation can commence. Both the low temperature and the duration have to be taken into consideration. Many species which respond to vernalization also exhibit photoperiodism (Leopold & Kriedeman, 1975). The interaction of these two

environmental cues are either supplementary or complementary. According to Roh (1985) exposure of shoots to "long days" can substitute for bulb vernalization of *Lilium longiflorum*.

1.3.4.2 Temperature requirement for flower differentiation and elongation

Hartsema (1961) reported that the optimum temperature for rapid flower development for most bulbs showed a general downward shift (6-13°C) after flower initiation. Shoub and Halevy (1971) also noticed this tendency in *Ornithogalum arabicum*. Jansen van Vuuren (1990) however, did not observe such a phenomenon in *Ornithogalum thyrsoides*. According to Hartsema (1961) Blaauw ascribes this shifting of the optimum to the co-operation of two processes: in the beginning of flower formation cell division prevails with a rather high optimal temperature, while after some time extension growth predominates and this process seems to be favoured by much lower temperatures.

In some species like *Narcissus* and *Tulipa* there is a low temperature requirement after the completion of flower differentiation, which must be satisfied before normal extension growth can occur. Bulbs grown in the field in temperate climates normally have their low temperature requirements satisfied by the low temperatures of winter (Charles-Edwards & Rees, 1975). According to Rees (1969) a large bulb industry is based mainly on the replacement of the natural cold of winter by artificial cold.

The low temperature period is divided into two: the pre-plant period, also called pre-cooling, and the post-planting period, also known as the rooting period.

1.3.4.2.1 Pre-cooling

The timing of this operation has been dictated by outdoor temperatures; if the pre-cooling is started too early, the bulbs will be ready to be taken outside when the outdoor temperatures are not optimal. The stage of development of the flower at the time of shifting from the high to the low temperature is critical. Floral initiation and organogenesis must be completed (Stage 'G') prior to movement of tulip bulbs to low temperatures (De Hertogh, 1974). At this stage, the primordia of six tepals, six androecium and a trilobed gynoecium are visible.

For tulips and daffodils a temperature of 9 °C and lower is necessary to satisfy their low temperature requirements. Hyacinths have a higher optimum of 13 °C. The temperature and duration of the low temperature requirements vary largely between cultivars (Rees & Turquand, 1969).

A "five-degree forcing" technique, also called "direct forcing" was developed for tulip bulbs to provide all their cold requirements before planting. Although the whole low temperature treatment can be given to the dry bulb at 9 °C, flower quality is poor and 5 °C was found to be more suitable. The prepared bulbs are then planted in a warm rooting medium so that growth starts immediately (Rees,1972).

1.3.4.2.2 Post storage

Early forced bulbs usually receive part of their cold requirement as dry bulbs before planting. Late forced bulbs however, are usually stored at 17 or 20 °C and their low temperature treatment is started at planting. "Five-degree" tulips, on the other hand receive all their low temperature requirement as dry bulbs which are then planted into conditions warm enough to allow rapid growth to anthesis (Rees,1972).

Controlled temperature rooms, also called rooting rooms, (bulbs are planted and rooted during this phase) are used to give the bulbs their necessary cold requirement before they are transferred to the glasshouse. As with the pre-plant treatment, the temperature and duration of the post-storage low temperature treatment are important and vary between cultivars (Rees,1972). According to Rees (1972) Turquand found that low rooting temperatures of tulip bulbs increase stem length and reduce flower size. High rooting temperatures on the other hand resulted in short stems and large flowers. Both too high and too low temperatures retard anthesis. Rees & Briggs (1975) found that for tulips the time that the crop is kept in the glasshouse is shortened and flower quality is improved when the low temperature treatment is not constant but is raised from 4°C to 13°C in three week intervals.

The readiness of the bulbs to be transferred to the glasshouse is a difficult decision to make, since there is no readily observable stage. The normal criteria for "readiness to house" is when the flower buds have grown above the neck of the bulb. Experiments by

Turquand (Rees,1972) showed, however, that at higher temperatures, misleadingly good growth of shoots occurs but this is not a satisfactory indication of readiness to transfer to the glasshouse. In recent years research on flowering assays for cold treated bulbs has started (Boonekamp, Beijersbergen & Franssen, 1990).

Moe and Hagness (1975) found that a high temperature treatment (15 or 21°C for 3-6 days) during or after pre-cooling of tulip bulbs, promoted shoot growth and reduced the forcing time, while prolonged high-temperature treatments retarded shoot growth, and produced poor flower quality.

1.3.4.3 Growth at high temperatures.

When the low temperature treatment is completed in both daffodils and tulips, they can be transferred to a higher temperature to bring the plants to anthesis as rapidly as possible. The rate of subsequent growth is rapid, when a temperature of 18-20 °C is maintained. According to Rees (1972) anthesis is delayed for a week for every 2,5 °C below 18-20 °C.

1.4. Manipulation of the flowering date

For marketing purposes it is important to be able to manipulate the flowering date. The ability to control the specific stages of growth and development by temperature in combination with other factors permits the manipulation of flowering date (De Hertogh,1974). This researcher set two basic goals in forcing. The bulbs are either accelerated to flower at the earliest possible date or retarded to flower at the latest possible date. The limits of these manipulations are under genetic control.

1.4.1 Example I: Tulip forcing

For tulip bulbs grown in the Netherlands (De Hertogh,1980):

Early flowering (December):

- harvested: mid-June to late-June
- pre-treatment: 1 week at 34 °C

- flower initiation and organogenesis: 17 to 20 °C until stage 'G'
- pre-cooling: 6 weeks at 6 to 9 °C
- planting: rooting at 9 °C, then at 5 °C until 15 weeks of cold treatment have passed
- greenhouse: 18 °C

Mid season flowering (February):

- harvested: late June to early July
- flower initiation and organogenesis: 17 to 20 °C until Stage 'G'
- pre-cooling: cut flowers are precooled for 2 weeks starting early September, pot-plants are not pre-cooled
- planting: rooting conditions are the same as for early flowering
- greenhouse: 17°C

Late flowering (April):

- harvested: July
- flower initiation and organogenesis: 23 °C until September, at 20 °C until October, and then at 17 °C
- planting: rooting conditions are the same as for early forcing, cut flowers are planted late October, early November and pot plants in early November
- greenhouse: 17 °C

1.4.2 Example II: Hyacinths forcing (De Hertogh,1980)

Early flowering (December and January):

- harvested: mid-June
- pre-treatment: 2 weeks at 30 °C and 3 weeks at 25 °C
- interim treatment: 23 °C until uppermost floret reaches stage A1
- after-treatment (no pre-cooling treatment): 17 °C until planted in September
- planting: rooting at 9 °C for 10 to 12 weeks
- greenhouse: 23 °C

Late flowering (February and March):

- harvested: late June, early July
- pre-treatment: 25 °C until planted

- planting: late September to early November at 9 °C until rooted, then at 5 °C. When the shoots are 5cm, the temperature must be lowered to 0 to 2 °C until the remainder of the cold requirement is satisfied.
- greenhouse: 15 to 17 °C

1.4.3 Year-round culture

Year-round production can be achieved by retarding the flowering date. Temperature is used to retard the flowering process at different stages. Hartsema (1961) prevented flower differentiation by storing tulip bulbs at -1 °C. After storage at low temperatures (-1 °C for 6 to 8 months), tulips were found to continue the formation of leaves and floral parts, as soon as the bulbs had been transferred to suitable temperatures (20-25 °C). When low temperatures are used to delay flowering, it is important that this must be done before flowers start differentiating, otherwise they will be damaged (Hartsema,1961).

Le Nard (1975) delayed the flowering of tulips by storing the bulbs at 2 °C immediately after lifting. For flower differentiation the bulbs were transferred to 20 °C. From his experiments it was clear that the physiological state of the bulb at the start of storage, influenced the behaviour of bulbs after storage at 2 °C.

To prevent inflorescence initiation in hyacinths, low temperatures (1 to 5 °C) can be used as well as high temperatures (31 °C). Hartsema (1961) recommended that the flowering date of hyacinths be delayed at the extension stage. Bulbs are therefore allowed to initiate and start to differentiate flowers at the optimal 28 °C, but thereafter are shifted to a high temperature of 31 °C to inhibit extension growth. This same approach was also used to retard the flowering date of *Narcissus* (Yahel, 1986).

In recent years a new technique "ice-tulips" has been developed for the year-round production of tulips. The general method for preparing and forcing "ice-tulips" is as follows. Bulbs are lifted and stored at 20 °C for 2,5 months . Thereafter the temperature is set at 17 °C for six weeks until the bulbs are planted and thereafter cooled at 5 °C for four weeks. The bulbs are then frozen in at -2 °C. Thawing out is done in the greenhouse where forcing takes place, at 12-15 °C (De Jong, De Greef & Dop,1990).

1.4.4 CONCLUSION

A bulb is an underground storage organ which consists mainly of fleshy leaf bases and scales. The growing is found in the centre between the leaf bases. After the growing point has become reproductive, it proceeds through a number of successive stages into an inflorescence. Factors controlling flower initiation and development in bulbs are: bulb size, stage of apex development, light intensity, photoperiod and temperature.

The most important factor in the flowering process is temperature. Temperature affects flower initiation, differentiation and quality. A sequence of temperatures is needed to achieve the desired quality at the desired time. The optimum temperature for flower initiation and commencement of differentiation is high for most bulbs. For elongation of the inflorescence a downward shift in optimum temperature occurs. After the low temperature requirement, higher temperatures are needed to bring the plant to anthesis.

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CHAPTER 2

MORPHOLOGY OF FLOWER DEVELOPMENT

2.1 INTRODUCTION

Lachenalia cv. 'Romelia' is one of the 32 *Lachenalia* cultivars that were recently released (Hancke & Coertze, 1988). The inflorescence of 'Romelia' bears up to 30 bright yellow bell-shaped flowers. It develops two relatively large leaves in autumn and is one of the first *Lachenalia* cultivars to start flowering in winter. The inflorescence of 'Romelia' remains attractive for 6 to 8 weeks.

The temperature requirements for floral initiation and development of *Lachenalia* are still unknown and need to be established in order to produce good quality potplants. A basic knowledge of the ontogeny of the inflorescence and the normal periodical development of the plant is necessary in order to understand and manipulate the influence of the environment on flower production (Holtzhausen 1991 pers. comm.). The objective of this study was to elucidate the developmental morphology and histological changes during floral development of *Lachenalia* cv. 'Romelia'.

2.2 MATERIALS AND METHODS

Flowering size bulbs (15 - 20 mm cross-section) of *Lachenalia* cv. 'Romelia' were used in this study. The life cycle and development of *Lachenalia* were determined by dissection and macroscopic observation of the bulbs. Three bulbs were used respectively for dissection and micromorphological studies. Samples were taken every second week. Inflorescences were fixed in formalin acetic acid for scanning electron microscopy and wax embedding. Standard procedures were used for the preparation of specimens for observation with the scanning electron microscope (Hayat, 1978). The basic wax microtechnique of Brooks, Bradley and Anderson (1950) was used with some modifications (Jansen van Vuuren, 1990).

Dehydration and infiltration of specimens for wax embedding were done in an automatic tissue processor. The following sequence of solutions was used with two hour intervals: Water, 50% ethyl alcohol, 75% ethyl alcohol, 100% ethyl alcohol, 75 ethyl alcohol: 25 xylol, 50 ethyl alcohol: 50 xylol, 75 xylol: 25 ethyl alcohol, 100% xylol, 50 xylol: 50 liquid paraffin, 25 liquid paraffin: 75 paraffin wax (Histosec) at 61 °C and paraffin wax at 61 °C. The specimens were then embedded in paraffin wax with the use of a tissue embedding system.

A rotary microtome was used for sectioning and longitudinal sections of 6 µm were made. The wax ribbons were cut into suitable lengths and placed onto a microscope slide that was covered with a very thin layer of Haupt's albumine and sufficient 4% formalin. The slides were then placed onto a hotplate at 45 °C. After the sections had stretched to their full capacity, but before all the formalin had evaporated, they were tentatively studied underneath a light microscope. Only those sections that might be useful, were retained, the rest were discarded. When the formalin had evaporated to such an extent that the sections no longer moved when the microscope slide was tilted, they were removed from the hot plate and left to dry at room temperature.

The following staining process was used: xylol (3x5 min), 1 xylol: 1 ethyl alcohol (5 min), ethyl alcohol (5 min), 95% ethyl alcohol (5 min), 70% ethyl alcohol (5 min), Safranin (6 hours), distilled water (5x1 sec), 95% ethyl alcohol and 0,5% picric acid (5x1 sec), 95% ethyl alcohol and 5 drops ammonia (5x1 sec), ethyl alcohol (5x1 sec), 1 g fast green/100 ml clove oil (12 sec), 50 clove oil: 25 ethyl alcohol: 25 xylol (rinse), 50 clove oil: 25 ethyl alcohol: 25 xylol (20 sec), xylol and 5 drops ethyl alcohol (rinse), xylol (2x5 min).

The safranin solution was made as follows: Twenty-five grams of safranin were dissolved in 715 ml 95% ethyl alcohol, mixed with 360 ml of water and filtered.

Mounting was done with canada balsam.

A Nikon Microphot-fx microscope was used for studying and photographing of the wax sections.

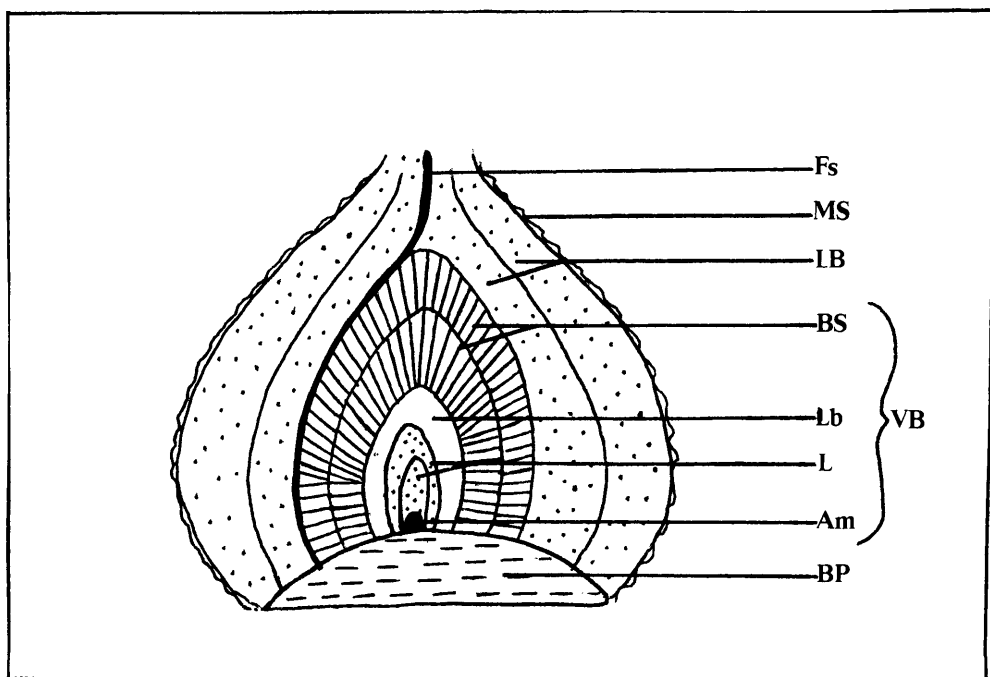


Figure 2.1 : Diagram of a longitudinal section of a bulb of *Lachenalia* cv. 'Romelia' at harvesting time.
 Ms - membranous scales; LB - leaf bases; BS - bulb scales; Lb - leaf bract; L - young leaves; AM - apical meristem; BP - basal plate;
 VB - vegetative bud; Fs - flowering shoot.

2.3 RESULTS AND DISCUSSION

2.3.1. Life cycle and developmental morphology

After flowering, at the end of September, the inflorescences die followed by the leaves. Bulbs are harvested in November during the dormant period. At this stage, the bulb (Fig. 2.1) consists of an outer covering of membranous tunics (Ms), two outer leaf bases (LB), and a vegetative bud (VB). At this stage the vegetative bud consists of two bulb scales (BS) and 2 young leaves enclosed by a bract. The tunics are remnants of the original leaf bases and bulb scales. In the axil of the second leaf base close to the vegetative bud, the remains of the flowering shoot (Fs) of the past season's growth can still be seen.

The formation of the vegetative bud (B1) starts in middle January, in the axil of the youngest leaf of the old bud, as soon as the apical meristem of the old bud transforms into inflorescence. The two leaves and bract of the old vegetative bud elongate, together with the newly formed inflorescence and enclose it until emergence of the leaves above the soil.

In April, the leaves emerge through the soil. The elongation of the bract stops after emergence from the bulb. The true leaves continue to elongate until May when the inflorescence appears. At this stage their bases begin to swell to form the new inner bulb scales. At the same time the leaf bases which were swollen two years earlier start to shrink. Towards harvesting time these leaf bases are shrunken entirely and become membranous tunics.

The inflorescence enclosed by the leaves emerges from the bulb during April, 10 weeks after floral differentiation has commenced. After a further 12 weeks the oldest floret of the inflorescence has opened. The inflorescence lasts for an average of 6 weeks after which it dies down together with the leaves to enter the dormant period.

2.3.2 Anatomical changes in the vegetative apex during the life cycle

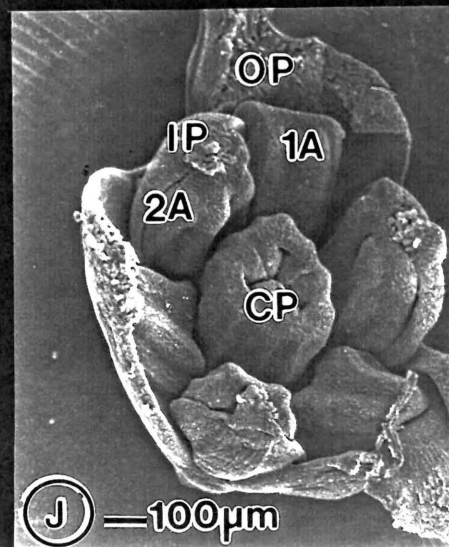
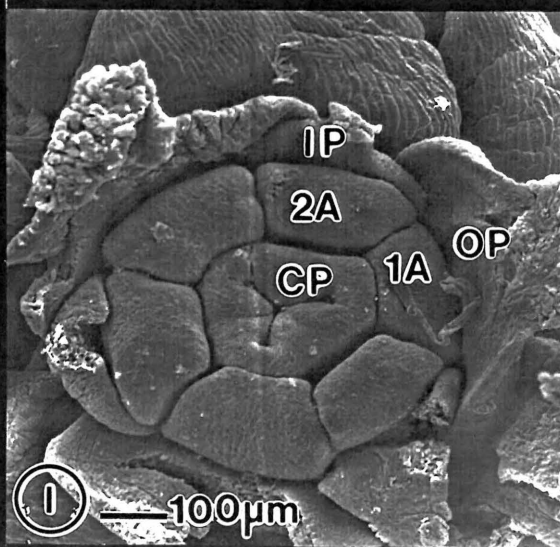
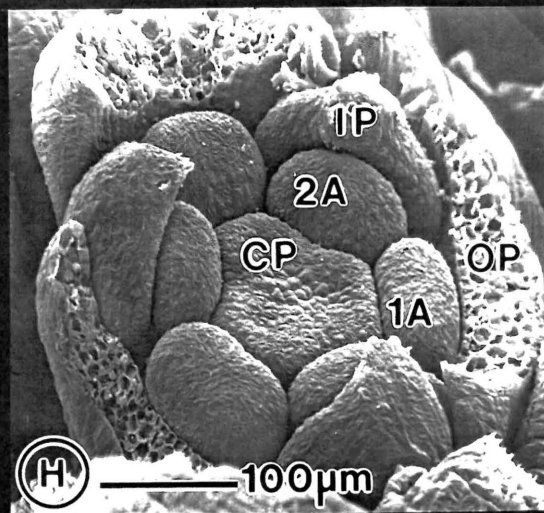
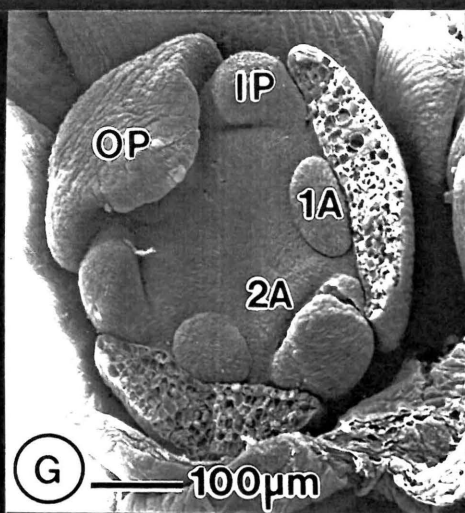
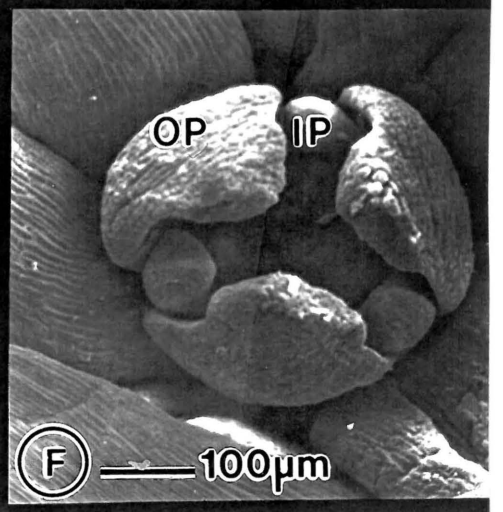
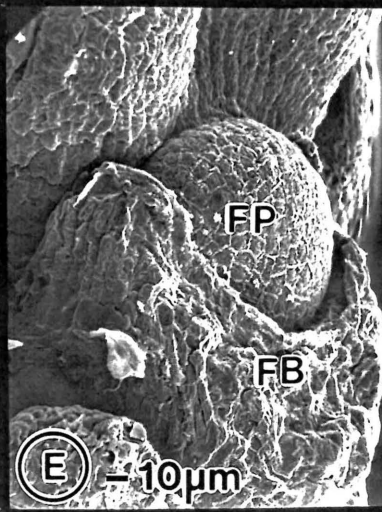
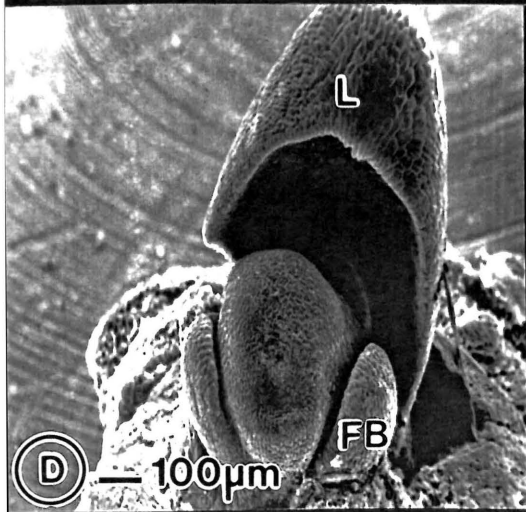
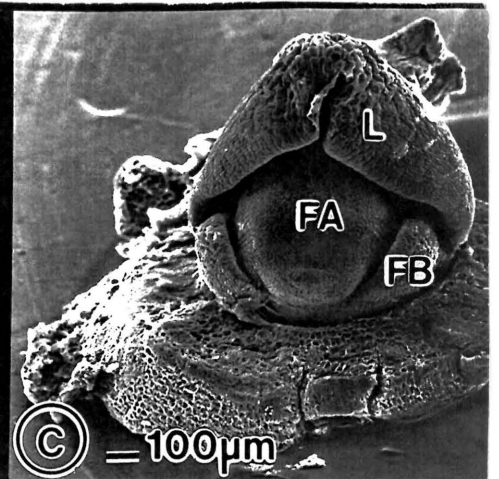
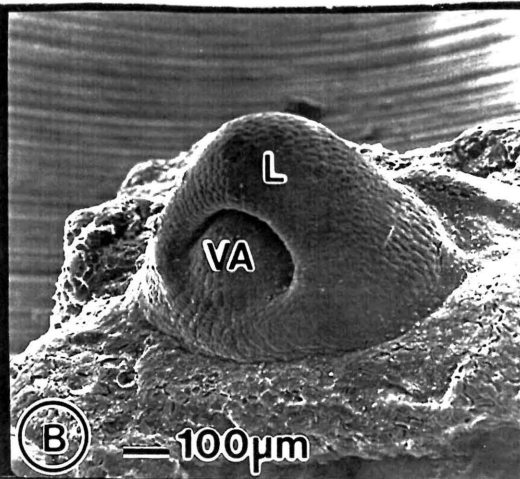
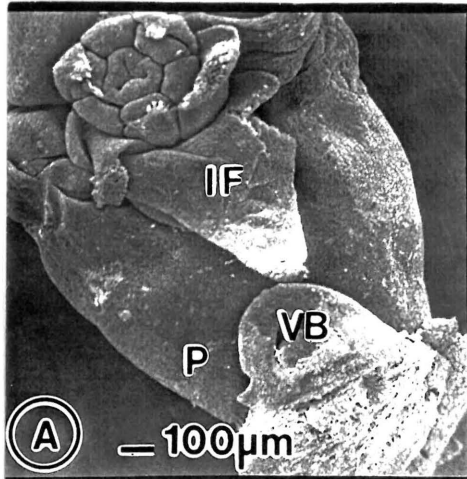
The terminology used to describe the early developmental stages of the apex is according to that used by (Shoub & Halevy, 1971; Shillo & Halevy, 1976); while terms used for later stages of flower development are according to Beyer (Hartsema, 1961). The vegetative

phase starts with the initiation of the new vegetative bud, as soon as the old bud becomes reproductive. While floral differentiation is proceeding in the old bud, active cell division takes place in the new bud. By the time that the newly formed inflorescence is ready for emergence from the bulb, the formation of the vegetative bud is complete. It consists of the dome-shaped apical meristem, two leaves and a bract (Figure 2.2A and Figure 2.3A + B). Throughout the actively growing and flowering period of the bulb, no further development occurs in the vegetative bud. The vegetative shoot apex has a two-layered tunica enclosing a central zone of larger cells (Figure 2.3C). The two leaves enclosing the apical meristem consist of meristematic cells, while the bract consists of parenchyma cells (Figure 2.3C).

The transition of the vegetative apex into a flowering bud is apparent when active cell division is evident over the entire surface of the apex and when the apex starts to elongate (Shoub & Haley, 1972). Although Jansen van Vuuren (1990) stated that the flattening of the apex is the first sign of flower initiation in *O. thyrsoides*, there is no proof to support his results. This transitional phase is sudden and is rapidly completed for *Lachenalia* cv. 'Romelia' at 20 °C and was therefore missed. Shoub and de Hertogh (1975) reported the same tendency in *Tulip gesneriana*. In order to observe the transitional stage of *T. gesneriana*, samples needed to be taken every 2 to 3 days.

The prefloral phase follows the transitional phase. This prefloral phase was noted 10 weeks after storage at 20°C has started. The most pronounced changes in the development of the apex during this phase are its rapid increase in height and the formation of a bulge where the first flower bracts will later be formed (Figure 2.2 C, D and Figure 2.3 D, E). This prefloral phase was the first visible sign of the reproductive phase, since the transitional phase was not observed.

The floral phase commenced after 12 weeks storage, when flower primordia were initiated in the axils of the lower flower bracts (Figure 2.2 E and Figure 2.3 F,G). The organogenesis of the flower parts occurred centripetally. The three inner perianth primordia are formed between the three outer perianth primordia after 13 weeks storage (Figure 2.2F). The three primordia of the first whorl of anthers are formed next to the outer perianth primordia. The first signs of the second anther whorl are visible in Figure 2.2 G and Figure 2.3 H on the inside of the inner perianth primordia. After 14 weeks

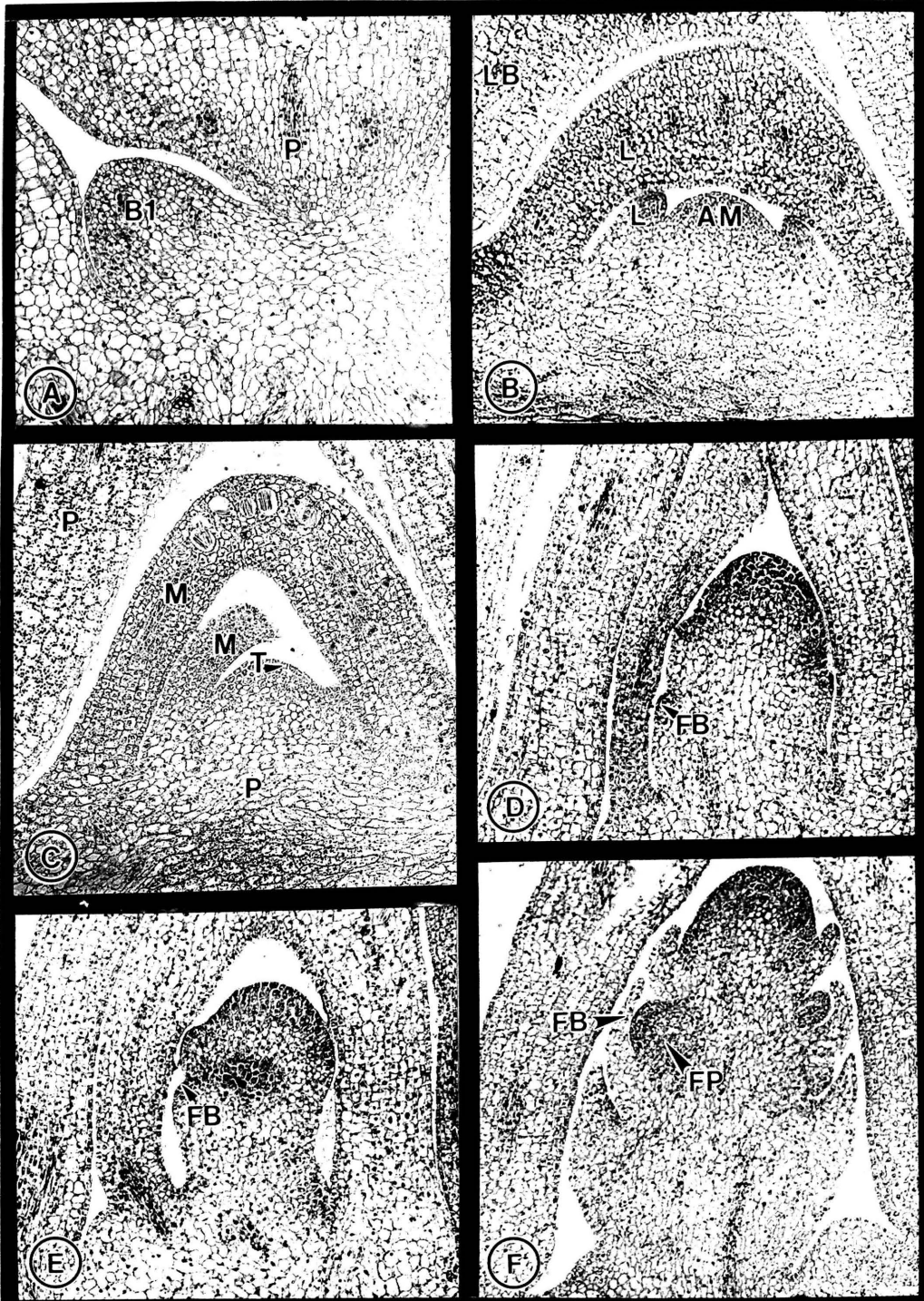


storage the three carpel primordia can be seen (Stage 'G') (Figure 2.2 H and Figure 2.3 H). Later these primordia are separated (Figure 2.2 I and Figure 2.3 I). In Figure 2.2 J and Figure 2.3 I, J the four loculi of the stamens are distinguishable. The lower flowers have reached this stage of development 6 weeks after differentiation of the inflorescence commenced.

The development of the florets is acropetal. Flowers at different stages of development are found on the axis at any one time - fully developed florets at the base and primordia towards the tip.

Figure 2.2 : Micromorphological observations of the inflorescence development of *Lachenalia* cv. 'Romelia'.

- A : The new vegetative bud close to the developing inflorescence (IF), (P) = peduncle; (BS) = young newly-formed bulb scale; (VB) = vegetative bud.
- B : Stage I (Vegetative): The vegetative bud at the start of the storage period (VA) = Vegetative apex.
- C,D : Stage III (Prefloral): Primordia of two lowest flower bracts (FB) are visible. (FA) = Inflorescence apex.
- E : Stage IV (Floral): Flower primordia (FP) is present in the axil of a flower bract (FB)
- F : Stage VI (P): Inner perianth primordia (IP) are formed between the outer perianth primordia (OP).
- G : Stage VIII (A): The first anther whorl (1A) is already present and the first signs of the second anther whorl (2A) can be seen.
- H : Stage IX (G): The three carpel primordia (CP) are formed.
- I : Stage X (G): Carpel walls separate the three ovaries.
- J : The oldest floret of the inflorescence at planting time. The four loculi of the stamens are distinguishable.



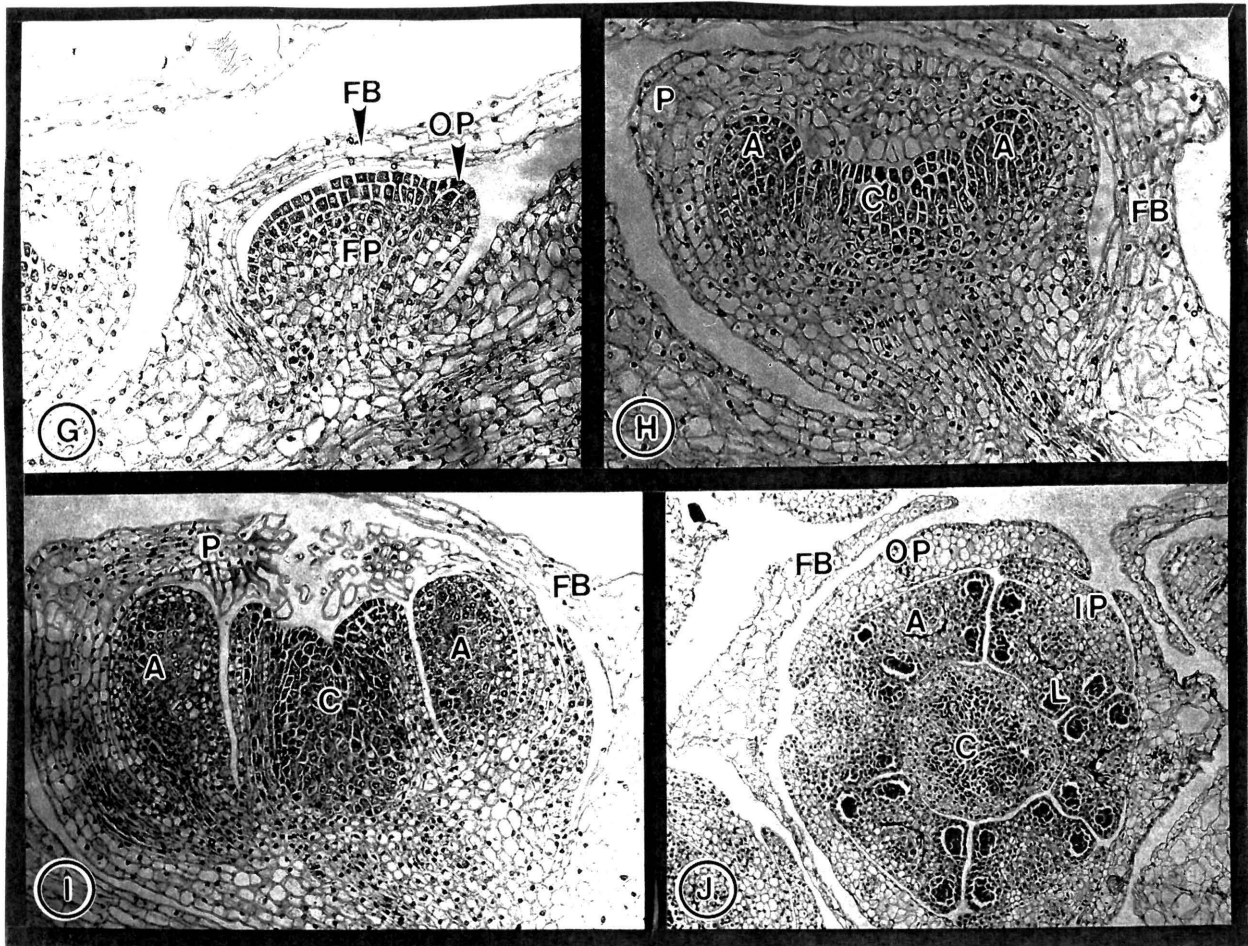


Figure 2.3: Anatomical observations of the inflorescence development of *Lachenalia* cv. 'Romelia'.

Plates A - I are longitudinal sections and Plate J is a cross-section.

- A :** The new vegetative bud (VB) close to the developing inflorescence. (P) = peduncle (enlargement x 100).
- B :** Stage I (Vegetative): The vegetative bud consists of an apical meristem (AM), 2 young leaves (L) and a leaf bract (LB) (enlargement x 100).
- C :** Stage I: A two-layered tunica (T) encloses the central zone of the apex. The two young leaves consist of meristematic cells (M). The leaf bract and central zone consists of parenchyma cells (P) (enlargement x 100).
- D, E :** Stage III (Prefloral): The flower apex elongated rapidly. (FB) = flower bract (enlargement x 100).
- F :** Stage IV (Floral): Flower primordia (FP) are visible in the axils of the flower bracts (FB) (enlargement x 100).
- G :** Stage V (P1): Outer perianth (OP) primordia is formed (enlargement x 200).
- H :** Stage IX (G): Anther (A) and carpel (C) primordia are formed. (P) = perianth (enlargement x 200).
- I, J :** Stage X (G): The four loculi (L) of each anther are visible. (IP) = inner perianth. The three carpels (C) unfold to form ovary (enlargement x 200).

2.4 CONCLUSION

The morphological development of *Lachenalia* corresponds to that of *O. arabicum* (Shoub & Halevy, 1971). The only difference is that in *Lachenalia* cv. 'Romelia' both true leaves of the next growing season are already formed before harvesting of the bulbs. In *O.arabicum* the vegetative bud produces additional leaves before it transforms into a flower bud.

Lachenalia can be classed together with *Tulipa*, *Hyacinthus* and *Iris reticulata* (Hartsema,1961), *Ornithogalum arabicum* (Shoub & Halevy, 1971) and *O.thyrsoides* (Janse van Vuuren,1990) with regard to the time of flower initiation. All these plants initiated flowers following the previous growing period and before replanting in autumn. The developmental stages of the *Lachenalia* apex in the process of flower formation, correspond to that of a typical bulb as described by Hartsema (1961), *O.arabicum* (Shoub & Halevy, 1971) and *O. thyrsoides* (Jansen van Vuuren,1990).

Knowledge of the sequence of events occurring at the shoot apex may give a better understanding of the effects which environmental factors may have on *Lachenalia* bulbs at different stages of development.

Since the transition to the reproductive phase was rapidly completed and missed therefore, no conclusions can be made on the histological and morphological changes that occurred during this stage of apex development.

The two developmental stages with practical value as far as a knowledge of the appearance and time of commencement are concerned, are the prefloral stage and stage 'G'. The prefloral stage is the first floral stage that can clearly be distinguished using a dissection microscope. When this stage is observed it indicates that flower initiation is completed and differentiation has commenced. A knowledge of stage 'G' has value, in that those bulbs which have two temperature optimums: one for initiation and organogenesis of the inflorescence, and another for elongation of the inflorescence, are transferred to lower temperatures for elongation at stage 'G'.

In this study inflorescence differentiation commenced 10 weeks after storage at 20°C

started. Six weeks later the oldest florets were at stage 'G'. According to De Hertogh (1974) the exact moment at which these stages commenced in tulips varies however from year to year, and it is therefore necessary to take yearly periodic samples. De Hertogh and Aung (1968) have developed a simple technique for identification of floral development in tulips. This technique can also be applied for *Lachenalia*.

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CHAPTER 3

THE EFFECT OF STORAGE TEMPERATURES ON THE FLOWERING TIME AND FLOWER QUALITY

3.1 INTRODUCTION

A knowledge of the cultural requirements for flower initiation, differentiation and development is essential in order to produce good quality flowers. The possibility of production out of season and in environmental conditions that are different from those in their native environment also needs investigation (De Hertogh, 1974).

The method by which flowers are produced from a storage organ is called forcing (De Hertogh, 1974). The principle requirement in forcing is environmental control and more specific temperature control. Temperature is the most important factor affecting initiation and subsequent flower development in bulbs (Rees, 1972).

In this study the effect of storage temperature on flower initiation, differentiation, flower quality and eventual flowering date of *Lachenalia* cv. 'Romelia' was studied.

3.2 MATERIALS AND METHODS

Flowering size bulbs (15-20 mm cross section) of the cultivar 'Romelia' were used. As soon as the leaves had died (early November), the bulbs were lifted and treated with Benomyl (50% benzimidazole). Samples of thirty bulbs were selected at random and put into perforated plastic containers and stored in incubators at different temperatures, namely: 5 °C, 10 °C, 15 °C, 20 °C, 25 °C, 30 °C and 35 °C. The temperature in the incubators was monitored by minimum-maximum thermometers. The temperatures in the incubators were very constant, with only a 0,4 °C variation. Every fortnight for 18 weeks a container with 30 bulbs was sampled at each temperature. Ten of these bulbs were used to determine the stage of floral development and 20 were planted in a glasshouse for quality evaluation.

No quality evaluation was done on bulbs that were stored at 5 and 35°C.

3.2.1. Flower development and flowering date

The terms flower initiation and differentiation are often confused. In this study initiation refers to the process that precedes inflorescence differentiation. During this phase the apical meristem receives the stimulus to change into a floral apex. Differentiation commenced as soon as the first signs of transition to the floral apex was evident.

In order to determine the stage of floral development the buds were excised from the bulbs. The stage of development of these buds was determined by dissecting them underneath a dissection microscope. During the microscopic observation an event was noted when at least 50% of the bulbs sampled were at that stage. Only two events were noted: the beginning of flower differentiation (when the primordia of the two lowest florets had differentiated) and sprouting of the bulbs. Bulb sprouting was used as a parameter since at this stage the bulbs have to be planted and can no longer be stored without damaging the quality of the inflorescence. By the time that leaves emerged from the bulb the inflorescence that they enclosed was also a few millimeters from emergence. The time-lag between commencement of differentiation and sprouting was used as an indication of the differentiation rate at the different temperatures.

3.2.2 Flower quality

The following observations were used to evaluate flower quality of the bulbs planted in the glasshouse. These parameters were also used for *O. thyrsoides* (Jansen van Vuuren, 1990).

- Date when the oldest floret of the inflorescence opened (flowering date).
- Date when 50% of the florets of the inflorescence wilted.
- Number of florets per inflorescence.
- Length of the rachis.
- Length of the peduncle.
- Cross section of the peduncle base.
- Number of secondary inflorescences.

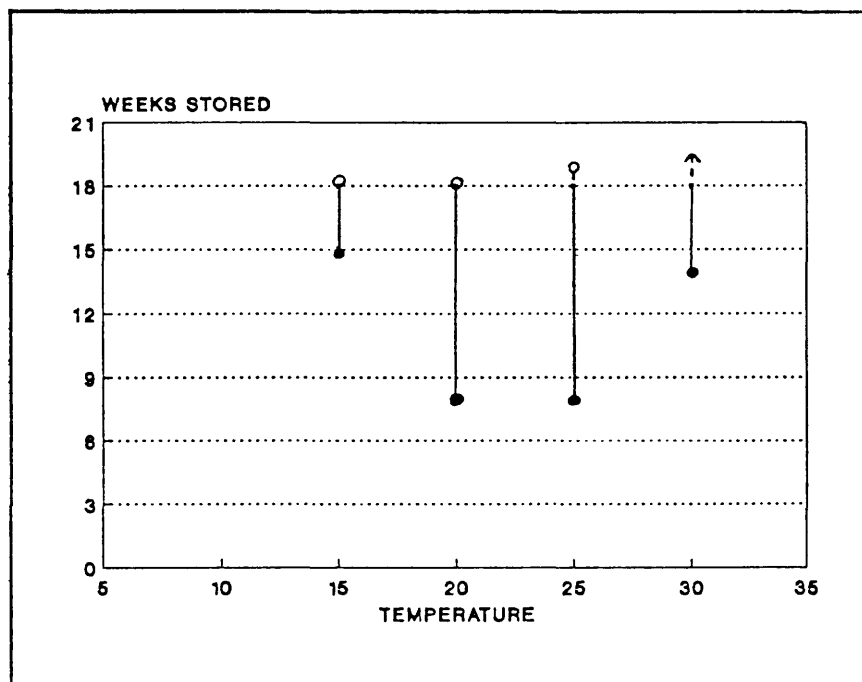


Figure 3.1: The effect of bulb storage on flower formation of *Lachenalia* cv. 'Romelia'

- (•) When flower initiation was completed and differentiation had commenced in 50% of the bulbs
- (◦) When 50% of the bulbs sprouted

From these observations the following were calculated:

- Compactness of the inflorescence (floret number divided by the rachis length (cm)).
- The number of days that the inflorescence is acceptable. (Date when 50% of the florets of the inflorescence wilted subtracted by the date the first floret opened).

Only the primary inflorescence was used for these data. The temperature and humidity of the glasshouse were monitored continuously by a thermohygrograph.

A 5 by 9 factorial experimental design was used. Significant differences between the treatments were detected by the LSD-test in the computer programme Statgraphics.

3.3 RESULTS AND DISCUSSION

3.3.1 Flower development and flowering date

3.3.1.1 Temperature effect on flower initiation and development

In Figure 3.1 the effect of storage temperatures on the flowering process is illustrated. Flower initiation was completely inhibited at 5, 10 and 35 °C. Flower formation occurred over a range of temperatures from 15 to 30 °C (Figure 3.1). The flower initiation process was completed after 8 weeks storage at 20 and 25 °C. A storage temperature of 15 and 30 °C retarded initiation. At 15 °C initiation was completed during the 15th week of storage and at 30 °C during the 14th week. A high percentage of the bulbs at 35 °C were dried and rotten, probably due to the so-called "mummy" disease (*Fusarium* sp.) (Naude, 1991 pers. comm.). It appeared that this temperature promoted the disease and 35 °C could therefore not be recommended. The high optimum temperature of 20 - 25 °C for flower initiation and commencement of differentiation is common for most bulbs (Rees, 1972).

According to Jansen van Vuuren (1990), flower differentiation commenced first at 5 °C for *Ornithogalum thyrsoides*. This low temperature is, however, inconsistent with that of all other bulbs. When this trail was repeated by him, the results of the 5°C storage treatment showed an inhibition of flower initiation. This inhibition at low temperatures was not only

in accordance with *Lachenalia* but also with *Tulipa* and *Hyacinthus* (Hartsema, 1961), and *Ornithogalum arabicum* (Shoub & Halevy, 1971). It is therefore more likely that the incubator in the first trial, than the one in the second trial was out of order, as was postulated by him. The temperature requirements of bulbs can be directly related to their natural habitat. *O. thyrsoides* is classed together with *Tulipa*, *Hyacinthus*, *Iris*, *O. arabicum* and *Lachenalia* with regard to the time of flower initiation (Chapter 1). All these bulbs initiate and start flower differentiation during the hot summer months. An optimum temperature of 5 °C is thus contradictory to what one would expect.

After flower initiation, differentiation of the flower parts and elongation of the inflorescence commenced. The stage when the inflorescence emerged from the bulb was used as a parameter to determine the stage of development and consequently the differentiation rate. At 20 °C the time-lag between the commencement of inflorescence differentiation and sprouting was 10 weeks. At 25 °C the differentiation rate was slightly slower, about 12 weeks. The 30 °C treatment markedly retarded differentiation, since 4 weeks after differentiation had started 60% of the bulbs dissected were still at the prefloral stage. The 15 °C treatment accelerated differentiation, only 3 weeks after differentiation had started 50% of the bulbs had sprouted (Figure 3.1).

Two definite optimums exist for the flowering process. The optimum temperature for flower initiation was found to be between 20 and 25 °C and the optimum temperature for differentiation was 15 °C. The existence of two optimums was also noted for *Tulipa gesneriana*, *Hyacinthus orientalis* (Hartsema, 1961), and *Ornithogalum arabicum* (Shoub and Halevy, 1971). These optimums, however, consider only the rate of the flowering process and not necessarily the quality of flowers obtained.

It must be stated that the differentiation rate of the inflorescence included both the organogenesis rate of the flower parts and the initial elongation rate of the inflorescence. Since the differentiation rate of the inflorescence was measured as a length function, the elongation rate must have made a larger contribution. The lower temperature optimum for differentiation of the inflorescence therefore refers more to the elongation rate of the inflorescence than to the organogenesis rate. Hartsema (1961) ascribes the shifting of the optimum to the co-operation of two processes: at the beginning of flower formation cell division prevails at a rather high optimal temperature, while after some time extension

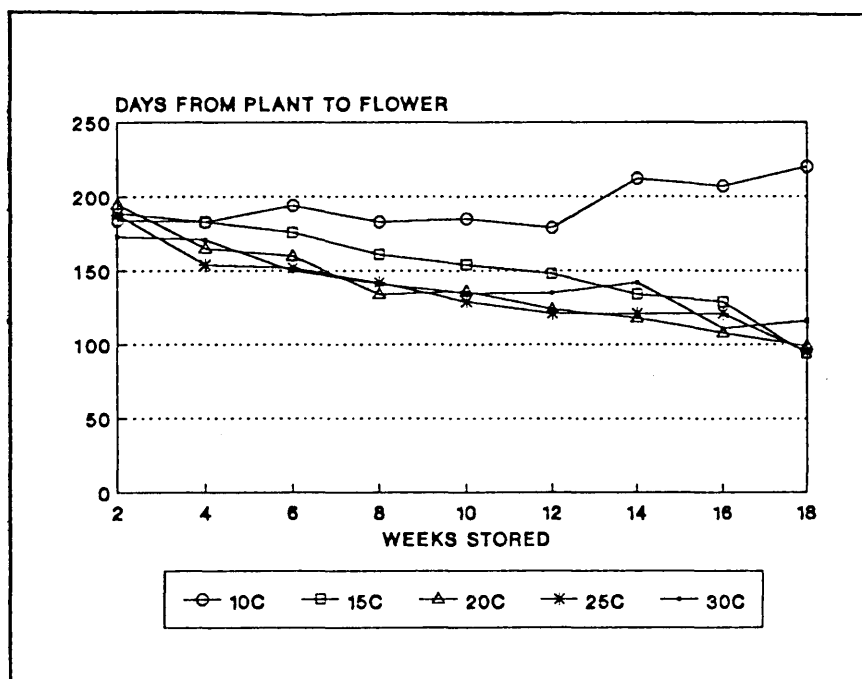


Figure 3.2: The effect of bulb storage at different temperatures and durations on the time-lag between planting of the bulbs and flowering of *Lachenalia cv. 'Romelia'* at Roodeplaat.

growth predominates and this process seems to be favoured by much lower temperatures.

Jansen van Vuuren (1990) calculated the differentiation rate of inflorescences at different storage temperatures by using the whole storage period. In this study only the period from commencement of differentiation was used. Jansen van Vuuren (1990) consequently concluded that a fast differentiation rate was obtained at those temperatures where differentiation commenced first. His results, however, showed a constant differentiation rate at all the storage temperatures where differentiation occurred.

3.3.1.2 The time-lag between planting and flowering

Before flower differentiation commenced, a natural 8 week period passed. Although no histological changes were observed during this period (Chapter 2), some physiological processes that are a prerequisite for flower differentiation must have taken place (flower initiation). Rees (1972) refers to a stage of apex development that has to be reached, before what he called flower initiation can occur. According to the definition of initiation used in this study the process he refers to is initiation. According to Rees (1972) this 'initiation time-lag' was also observed in *Tulipa* and *Narcissus*, but not in *Hyacinthus*. In hyacinths the vegetative apex immediately transforms into a floral apex when the bulbs are transferred to high temperatures.

In Figure 3.2 the time-lag between planting and flowering date for the different storage treatments is illustrated. As the storage period increased, a decrease in the time-lag between planting and flowering was observed. This indicated that the pre-flowering process (initiation) had already started during storage. This corresponds with the microscopic observations (Chapter 2). The 10 °C treatment, however, resulted in a relatively constant time-lag between planting and flowering for the first 12 weeks of storage. This implies that not only differentiation (as indicated by the microscopic observations) but also initiation was inhibited at this temperature. The initiation process resumed as soon as the bulbs were removed from the inhibition temperature. Between the 12th and 14th storage week, however, this time-lag increased significantly by 30 days, whereafter it stayed relatively constant.

It is evident from Figure 3.2 that 15 °C also inhibited flower initiation. This inhibition was,

however, not complete, since the time-lag decreased with an increased storage period. After 14 weeks at 15 °C, when differentiation started, the time-lag did not differ from the other temperatures.

3.3.1.3 Flowering date

Normal cultural procedure for *Lachenalia* in South Africa is as follows: After leaf senescence in November, the bulbs are lifted, stored at 20 °C and planted at end-February to mid-March. The flowering period for cultivar 'Romelia' starts at the end of May.

Figure 3.3 illustrates the effect of different storage temperatures and durations on the flowering date. It is evident that none of the temperatures tested could advance the flowering date. It was only by planting in advance that a few weeks could be gained. By planting early in December (after 2 to 6 weeks storage), the flowering date was shifted to middle May. By late planting (after 18 weeks storage) the flowering date was shifted to end June for bulbs stored at 15, 20, 25 and 30° C.

The most pronounced retardation of the flowering date was, however, obtained after storage at 10°C. Bulbs that were stored at 10°C for 18 weeks flowered at the end of September. Since storage at 10 °C inhibited flower initiation (Fig. 3.1), it is possible to shift the flowering date to a later date.

3.3.2. Flower quality

Since *Lachenalia* is developed as a pot plant, there are certain standards that have to be met, such as a minimum floret number, peduncle length, etc. These standards must be determined for each cultivar.

One of the objectives of this study was to determine the effect of storage temperature on flower quality. It is expected that the storage conditions will have an influence on quality, since initiation and differentiation occurred during this stage.

Flower quality depended not only on the storage temperature, but also on the duration at that temperature. These two factors had a direct and indirect influence on flower quality.

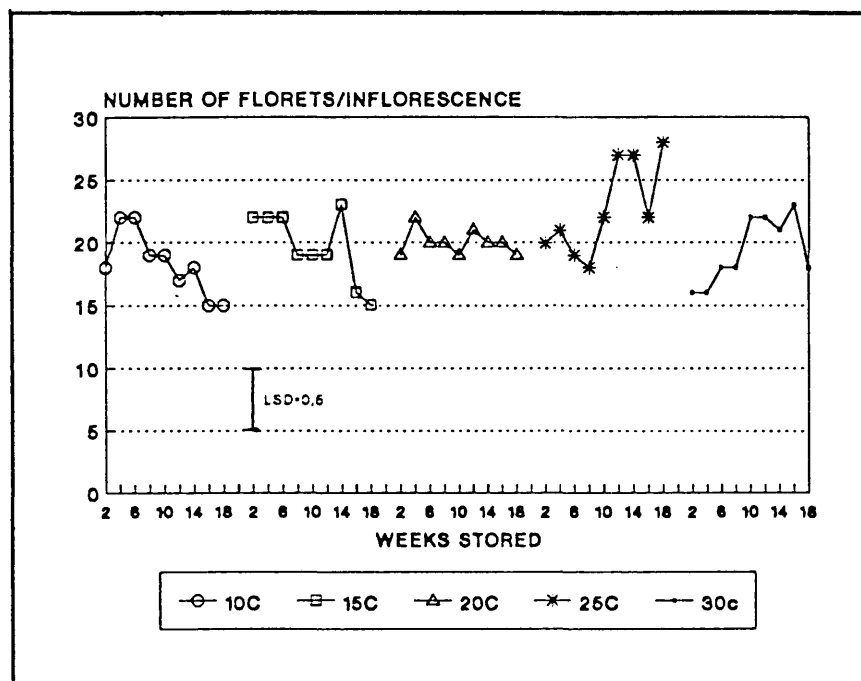


Figure 3.4: The effect of bulb storage at different temperatures and durations on the number of florets/inflorescence of *Lachenalia* cv. 'Romelia' at Roodeplaat

They had a direct effect when initiation or differentiation occurred during storage, and an indirect effect when these two events took place after storage, for example at 10 °C where flower initiation is inhibited during storage and commenced after planting. The storage period had a dual function; it determined the duration of bulb exposure to the storage temperature and determined the planting date.

The prevailing temperature in the glasshouse where the bulbs were planted was not controlled but monitored. When bulbs were planted in middle March after 18 weeks storage, the glasshouse temperatures were 30 °C (day) and 15 °C (night). In May the temperatures fell to between 23 °C (day) and 8 °C (night). The lowest night temperature (4 °C) was recorded in July. In September the temperatures rose again to 30 °C (day) and 10 °C (night).

3.3.2.1 Floret number

Floret number per inflorescence is one of the main factors by which flower quality is judged (Shoub & Halevy, 1971). High floret numbers is a very favourable characteristic. Storage temperature had a significant effect on floret number. The duration of the storage treatment had a less significant influence on floret numbers than the temperature. There was, however, an interaction between temperature and duration. These interactions are illustrated in Figure 3.4.

A gradual lowering in floret numbers was observed at 10°C with increased storage duration. Although at first sight these observations were attributed to 10°C, the following facts had to be taken into consideration: flower initiation was completely inhibited at 10°C and commenced thus after planting in the glasshouse; at least 8 weeks of initiation was necessary before differentiation commenced. Differentiation of inflorescences from these bulbs commenced and proceeded thus gradually later, with increased storage duration, while the prevailing temperatures in the glasshouse were gradually lowered by winter temperatures. These observations resulted thus indirectly from 10°C but directly from the low prevailing temperatures in the glasshouse during differentiation. Jansen van Vuuren (1990) failed to take these facts into account when the effect of the inhibiting temperature on flower quality was discussed.

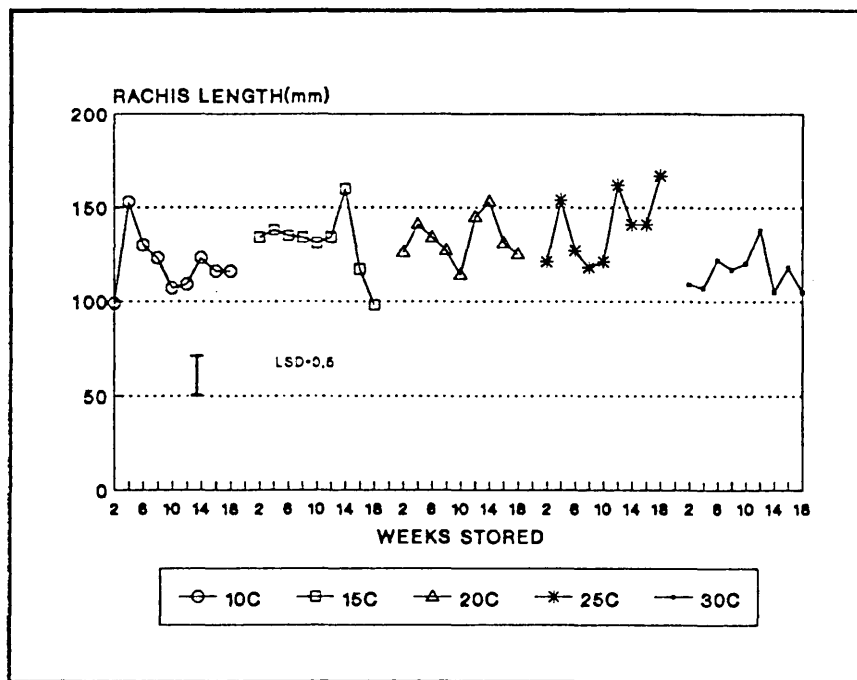


Figure 3.5: The effect of bulb storage at different temperatures and durations on the rachis length of the inflorescence of *Lachenalia* cv. 'Romelia' at Roodeplaat

A sudden significant drop in floret number was obtained after 14 weeks at 15 °C (Figure 3.4). This coincided with the start of inflorescence differentiation (Figure 3.1). The low floret number might thus have been the result of the rapid completion of the differentiation phase at this temperature (Figure 3.1). According to Shoub and Halevy (1971) rapid elongation of the inflorescence can stop the differentiation of many upper flowers. The 30 °C treatment, on the other hand, retarded differentiation which also led to a low floret number.

The 20 °C treatment was the only treatment that gave a relatively constant floret number throughout a storage period of 18 weeks (Figure 3.4). The moderate differentiation rate at this temperature might be regarded as the reason for this phenomenon.

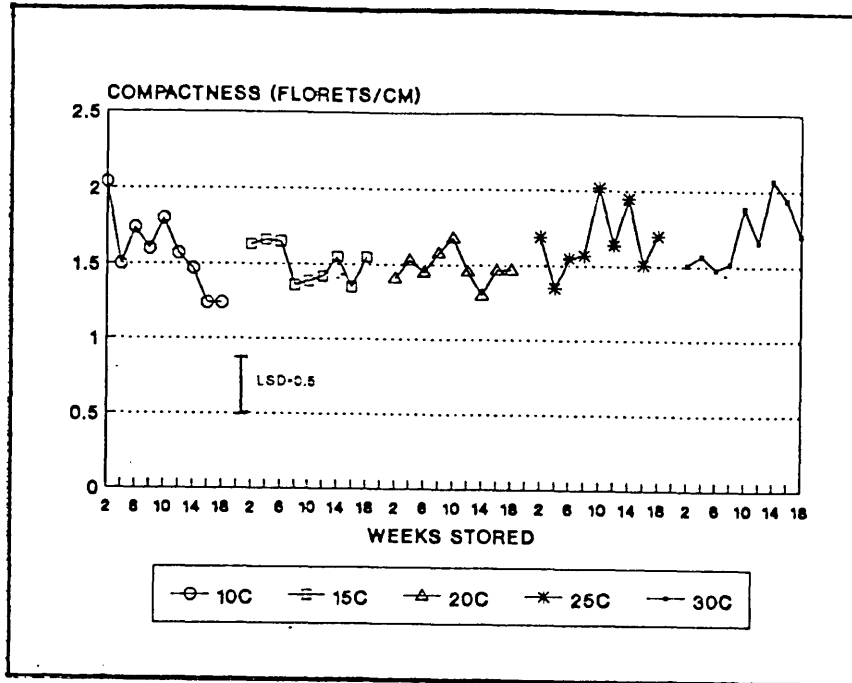
At the 25°C treatment an increase in floret number was observed after differentiation had started during the 8th week of storage. A mean number of 27 florets per inflorescence was observed after 12 weeks storage. Although there was a sudden drop after 16 weeks of storage, a high floret number of 28 was again obtained after 18 weeks of storage.

It appears from the above results that it is not the temperature during flower initiation, but the temperature during flower differentiation that determined flower number. The temperature during initiation determined only the time of differentiation commencement. The differentiation rate of the 25°C treatment appeared to be the optimum for floret number.

3.3.2.2 Rachis length and compactness

The rachis length, together with the floret number, determined the compactness of the inflorescence. A commercially acceptable pot plant must have a compact inflorescence. This implicated a short rachis with a high floret number. The rachis length must, however, be in proportion to the rest of the plant.

Except at the 25 °C treatment, a strong correlation was observed between floret number and rachis length (Figures 3.4 & 3.5). This correlation was also noted for *O. thyrsoides* (Jansen van Vuuren, 1990).



A gradual decrease in compactness was observed at 10°C with increased storage duration (Figure 3.6). Compactness of inflorescences from the 15 and 20°C treatments were relatively more constant throughout the 18 week storage period. Those bulbs that were exposed to 25 and 30 °C for longer than 10 weeks had the most compact inflorescences (Figure 3.6). As was previously discussed under floret number this tendency to compactness is most probably due to the differentiation rate at the subsequent temperatures. The slow differentiation rate at 25 and 30°C thus resulted in more compact inflorescences.

3.3.2.3 Peduncle length

The peduncle length is an important aspect of pot plants. Like rachis length, the length of the peduncle must also be in proportion to the rest of the plant and the pot (De Hertogh, 1980). Since *Lachenalia* is produced as a potplant, a short peduncle of approximately 150mm is desired.

The storage temperature and duration had a significant effect on the peduncle length. The storage duration, however, had a statistically greater effect than the temperature on peduncle length. As mentioned earlier, the storage duration had a dual function, it determined the period that bulbs were exposed to the storage temperature and determined the planting date.

The interaction between storage temperature and duration is shown in Figure 3.7. It is interesting to note that there is a correlation in the fluctuation of the peduncle length at 20, 25 and 30°C. Since the flowering date of these treatments also coincided, they must have received the same environmental impulses during peduncle elongation. The environmental factors after planting therefore seemed to affect the peduncle length significantly. These environmental factors include light and temperature.

Pilot trials indicated that light intensity played a major role in peduncle length, as *Lachenalia* grown under high light intensity produced short stems. It can therefore be postulated that it is possibly light intensity and temperature which correspond to planting date that caused this effect.

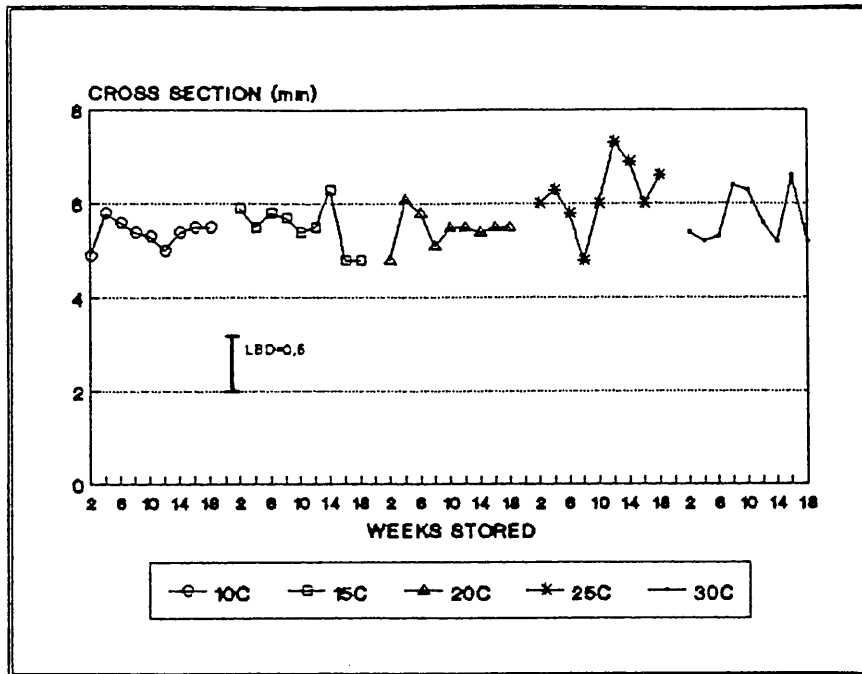


Figure 3.8: The effect of bulb storage at different temperatures and durations on the firmness of the peduncle of inflorescence of *Lachenalia* cv. 'Romelia' at Roodeplaat

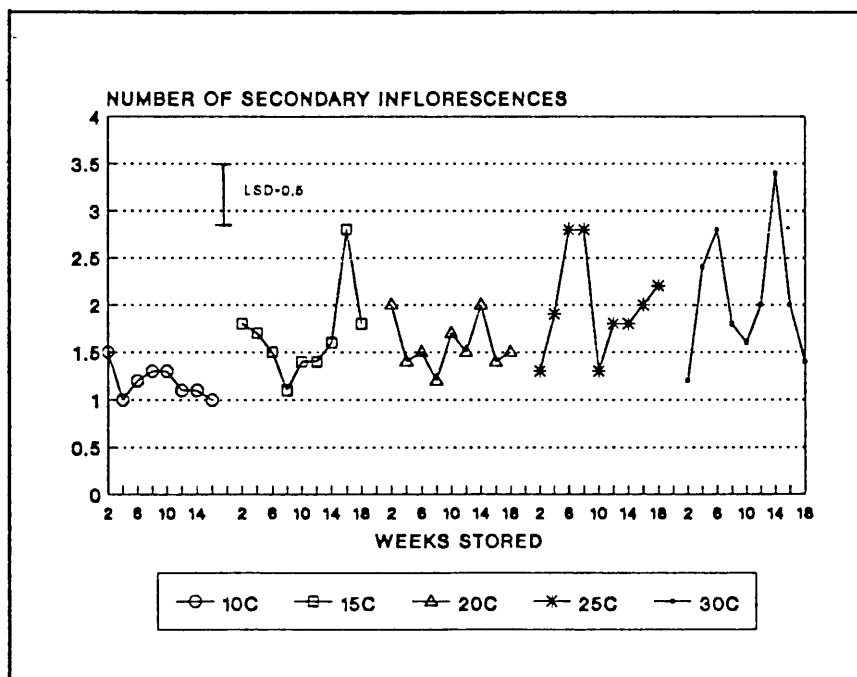


Figure 3.9: The effect of bulb storage at different temperatures and durations on the number of secondary inflorescences of *Lachenalia* cv. 'Romelia' at Roodeplaat

3.3.2.4 Peduncle cross section

Firmness of the peduncle is an important characteristic determining pot plant quality. The peduncle cross section was used as an indication of the firmness of the inflorescence. Temperature had a significant effect on peduncle cross section. The duration of the storage period did not have a significant effect, but there was an interaction between the temperature and the duration of storage (Figure 3.8). The 10 and 20°C storage temperatures resulted in fairly constant cross sections throughout the storage period of 18 weeks. As was the case with floret number a parallel was observed between differentiation rates at the various temperatures, and peduncle cross-section. After 14 weeks at 15 °C, when flower differentiation had started, a sharp decline in peduncle cross-section occurred. The results of the 25°C treatment are also in accordance with the floret number results; after 8 weeks, when differentiation commenced, a rise in cross section was observed.

3.3.2.5 Secondary inflorescence

The appearance of multiple inflorescences is a much sought after characteristic in pot plants. A positive correlation was observed between between temperature and number of secondary inflorescences. Duration of storage, however, also had a significant effect and there was an interaction (Figure 3.9). Large fluctuations were obtained between the different storage intervals at a specific temperature and no conclusions could therefore be made.

3.3.2.6 Keeping ability of the inflorescence

The keeping ability of the inflorescence is an important quality for pot plants. The inflorescence of Romelia is usually acceptable for a period of 40 days. The 10°C storage temperature resulted in inflorescences with significantly shorter keeping abilities than the other temperatures. One has to consider, however, the flowering date: bulbs stored at 10°C flowered later in the year when the temperatures were increasing. Bulbs stored at 10°C for longer than 12 weeks flowered in September (Figure 3.3) when much higher temperatures prevailed. In Figure 3.10 it can be seen that the 10°C at 14, 16 and 18 weeks storage, treatments resulted in inflorescences with a significantly shorter keeping ability.

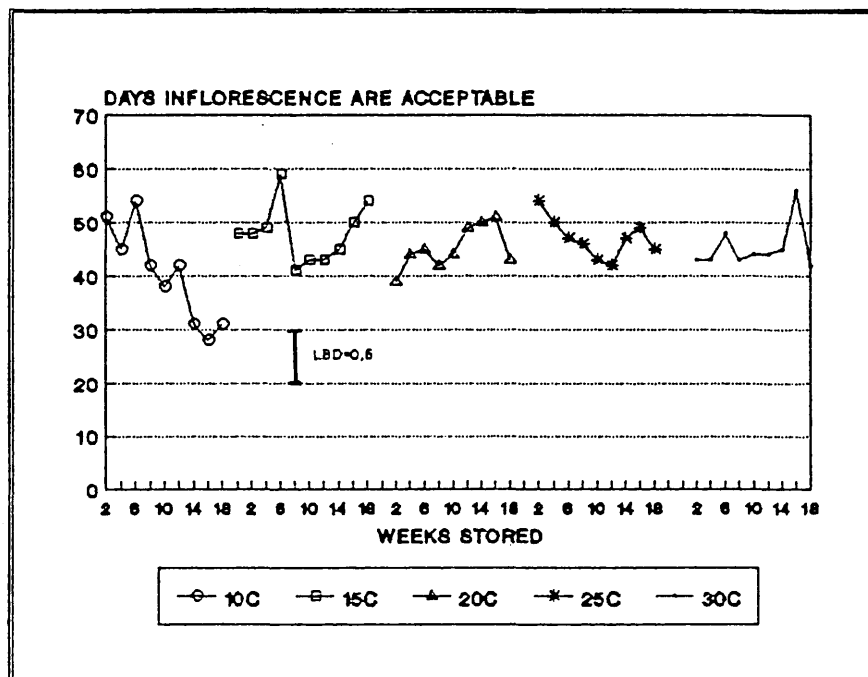


Figure 3.10: The effect of bulb storage at different temperatures and durations on the number of days the inflorescence are acceptable of *Lachenalia* cv. 'Romelia' at Roodeplaat

Consequently it can be deduced that the environmental conditions during flowering and not the storage conditions before planting determine the keeping ability of the inflorescence. These results correspond with those of *Ornithogalum* (Jansen van Vuuren, 1990).

3.4 CONCLUSION

The temperature and duration of the storage period did have an influence on flower initiation and development. Flower initiation is completed first at 20 and 25 °C. Ten degrees Celsius inhibited flower initiation completely. The rate of inflorescence elongation occurred most rapidly at 15 °C and most slowly at 30 °C.

With these facts in mind, it may be possible to shift the flowering date of *Lachenalia* cv. 'Romelia' to a later stage. This might be done in two ways : either by inhibiting flower initiation at 10 °C, or by extending the flower differentiation phase at 30 °C. Since high temperatures seemed to favour the 'mummy' disease, the first alternative might be a better choice.

The flowering date may be promoted by using a combination of 25 °C (for the fastest initiation) and 15 °C (for the fastest elongation). From these results it was, however, evident that the premature elongation of the inflorescence resulted in poor flower quality. If the shifting from 25 °C to 15 °C is done at the right stage, when differentiation of the floral parts is completed and elongation predominates this problem might, however, be solved. According to De Hertogh (1974) good quality inflorescences can be obtained when they are allowed to reach the proper stage of floral development before being transferred to a lower temperature. This stage is cultivar dependent, but most tulip cultivars can be transferred upon reaching stage 'G'.

Apart from the storage temperatures effect on the flowering date, temperature also influenced flower quality. The number of florets per inflorescence, rachis length, compactness of the inflorescence, the occurrence of secondary inflorescences, the peduncle length and peduncle cross section were influenced by the storage conditions. Keeping quality of the inflorescence was determined by the environmental conditions in the glasshouse, the storage conditions having no influence. It is by influencing the

differentiation rate of the inflorescence, that the storage temperature affects inflorescence quality. High flower quality was achieved by extending the differentiation phase. The 25 °C storage temperature yielded the best flower quality. The most compact inflorescences with the highest floret number and the firmest peduncle, were obtained after storage for 12 weeks or longer at this temperature. The occurrence of multiple inflorescences was also high after 25 °C storage. Although the peduncle length was influenced by storage temperature, the environmental conditions after planting seemed to play an important role.

Ten degrees Celsius could be used to shift the flowering date, since no flower formation occurred during storage at this temperature. The influence of 10 °C on flower quality is thus important. Flower initiation and differentiation of bulbs that were stored at 10 °C occurred after the bulbs were planted. The glasshouse conditions during flower formation thus determined the flower quality of these bulbs. If bulbs that were stored at 10 °C were allowed to initiate flowers at the optimum temperature of 25 °C, good quality flowers may be produced. Retardation of the flowering date by storage at 10 °C is reported in Chapter 4.

At this stage the following temperature treatments can thus be recommended for optimal inflorescence quality: Lift and fumigate bulbs with Benomyl (2g.l^{-1} for 30 min) as soon as their leaves have died down. Place the bulbs at 25 °C for 18 weeks. Plant them in a warm environment (30 °C, day and 15 °C, night). After 4 weeks, a cool environment (25 °C, day and 8 °C, night) until flowering is completed, is recommended. At Roodeplaat the best peduncle length was obtained when the bulbs were grown in a glasshouse beneath 40% shade cloth.

3.5 REFERENCES

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CHAPTER 4

RETARDING THE FLOWERING DATE BY TEMPERATURE TREATMENTS

4.1 INTRODUCTION

The flowering period of *Lachenalia* is from mid-winter to early summer (May to November). 'Romelia' is an early flowering cultivar that flowers from mid-June to early September. As with most other potplants, there is considerable interest in being able to advance or retard their growth and flowering in order to spread production, avoid depressing the market and, in particular, to take advantage of high prices during Christmas, New Year and Easter (Tompsett, 1980).

In Chapter 3 the storage temperature requirements for flower formation of *Lachenalia* cv. 'Romelia' were determined. The following results were obtained from this study: floral initiation was optimal at 20 and 25 °C while 10 °C completely inhibited floral initiation. After initiation, differentiation of the floral parts and elongation of the inflorescence were accelerated at 15 °C and delayed at 30 °C.

With these results in mind, the flowering date of *Lachenalia* cv. 'Romelia' might be retarded by two means : either by delaying flower differentiation at 30 °C after initiation has taken place at 25 °C, or by total inhibition of floral initiation at 10 °C.

Shoub and Halevy (1971) used the first technique to shift the flowering date of *Ornithogalum arabicum* to a later date. By storing the bulbs at a high temperature of 30 °C the further development of the inflorescence, which was already initiated, was inhibited. Differentiation proceeded at a slow rate at this temperature and thus provided an opportunity to delay the flowering date. Le Nard (1975) retarded floral initiation of tulips by storing the bulbs at 2 °C.

In this study the second technique was used for the retardation of the flowering date of *Lachenalia* cv. 'Romelia'.

4.2 MATERIALS AND METHODS

4.2.1 Experiment I

Flowering size bulbs (15 to 20 mm cross section) were used. After the leaves had died, the bulbs were lifted, treated with benomyl and stored. The control treatment consisted of 36 bulbs stored at 22 °C for 18 weeks before being planted in the glasshouse. Five hundred bulbs were stored at 10 °C. After storage at 10 °C for 20, 24, 28, 33, 38 and 42 weeks respectively, a sample of eighty bulbs was taken from these bulbs and four bulbs from each sample were dissected and studied under a dissection microscope to determine whether floral differentiation had commenced. The remaining 76 bulbs were placed in an incubator at 22 °C with the expectation that initiation and differentiation would occur within a few weeks at this optimum temperature.

Every second week five of these bulbs at 22 °C were sampled and examined for floral initiation. After 21 weeks at this optimum floral initiation temperature, floral differentiation was eventually noticed in the bulbs that were stored at 10 °C for 20 weeks. Since the 10 °C treatment resulted in such a long inhibiting after-effect on bulbs that were inhibited at 10 °C for 20 weeks, the expectation was that those bulbs that were exposed to 10 °C for longer than 20 weeks, would experience an even longer after-effect. A decision was consequently made to plant all the bulbs of the experiment in the glasshouse. At that stage the bulbs stored at 10 °C for 20, 24, 28, 33, 38 and 42 weeks were already exposed to 22 °C for 21, 18, 14, 9,4 and 0 weeks respectively (Table 4.1). In the glasshouse these bulbs were exposed to day and night temperature fluctuations and watering. A thermohygrograph monitored the temperature and relative humidity in the glasshouse. Every second week four of these bulbs were studied for flower differentiation. The date of commencement of differentiation was noted.

The flowering date and flower quality were recorded as described in Chapter 3. Differences between the treatments were detected with the Tukey test on the computer programme Statgraphics.

4.2.2 Experiment II

The results concerning the after effect of bulbs stored at 10 °C in Experiment I, could not be interpreted due to the fact that the bulbs were exposed for different durations at 22 °C

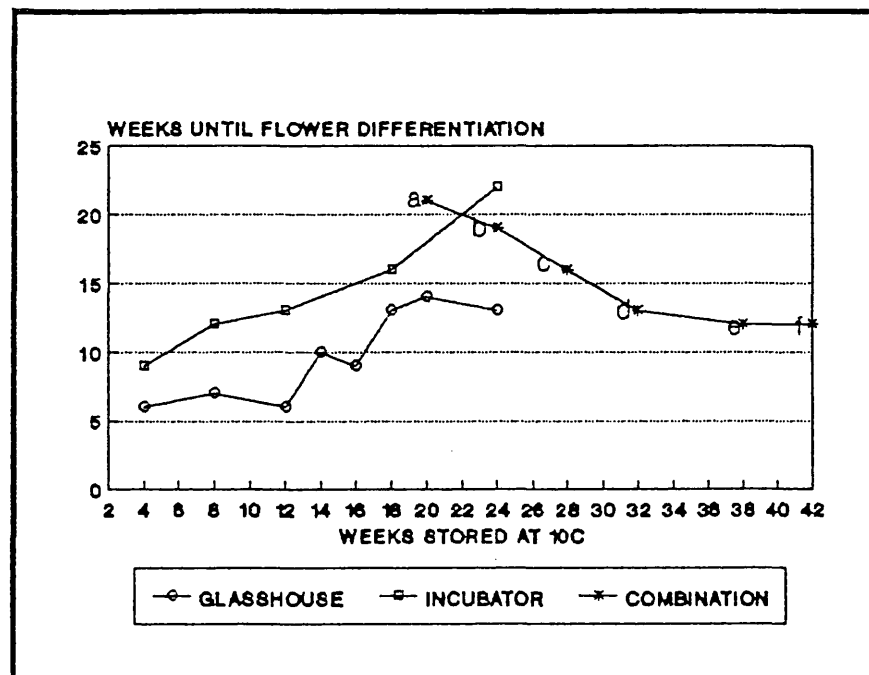


Figure 4.1. The duration of the delayed onset of flower differentiation: After storage at 10 °C of *Lachenalia* cv. Romelia bulbs, the bulbs were transferred to the following conditions:

Experiment I: (★)Bulbs were placed in an incubator at 22 °C for various periods before they were planted in a glasshouse.

- (a) 21 weeks at 22 °C
- (b) 18 weeks at 22 °C and 1 week in glasshouse
- (c) 14 weeks at 22 °C and 2 weeks in glasshouse
- (d) 9 weeks at 22 °C and 4 weeks in glasshouse
- (e) 4 weeks at 22 °C and 8 weeks in glasshouse
- (f) 12 weeks in glasshouse

Experiment II:

- (o) Bulbs were planted in a glasshouse
- (□) Bulbs were put in an incubator (22 °C)

after storage at 10 °C and before they were planted in the glasshouse. Experiment II was designed in order to investigate those results and to determine the influence of the incubator and glasshouse respectively on the after-effect.

Two hundred and eighty flowering size bulbs were stored at 10°C after they were treated with benomyl. Every fourth or second week for 24 weeks, 40 bulbs were sampled. Twenty of these bulbs were placed at 22 °C in an incubator and 20 were planted in a glasshouse. Every second week, starting at the first week in the glasshouse and the eighth or tenth week in the incubator, three bulb samples were taken and studied underneath a dissection microscope for signs of flower differentiation. When flower differentiation was observed in at least two of the three bulbs, the date was noted. Bulbs were left in the incubator until sprouting before they were planted in a glasshouse.

4.3 RESULTS AND DISCUSSION

4.3.1. The effect of 10 °C on flower initiation and flowering date.

A storage temperature of 10 °C completely inhibited flower initiation. Apart from this direct inhibition of flower initiation, 10 °C also delayed the onset of flower differentiation when bulbs were transferred to higher temperatures. The result of Experiment I and II concerning the delayed onset of flower differentiation after storage at 10 °C are illustrated in Figure 4.1.

The duration of the delayed-differentiation period after 10 °C depended on the storage period at 10 °C and the treatment after storage. Bulbs that were planted in the glasshouse, after storage for up to 12 weeks at 10 °C (Experiment II), required 6 to 7 weeks for flower initiation. With periods longer than 12 weeks at 10 °C, a sudden increase in the period of delayed-differentiation was observed with increased storage duration. After a 20-week storage period, a delayed-differentiation period of 13 weeks was noted. It seems as though further increase in the period of delayed-differentiation occurs with increased storage duration, since in Experiment I this delayed action was only 12 weeks after a storage period of 40 weeks at 10 °C.

Bulbs that were transferred to an incubator at 22°C, after storage at 10°C (Experiment

II), reacted quite similarly to those planted in the glasshouse after storage. The delayed-differentiated period in the incubator, however, lasted much longer than in the glasshouse. A gradual increase in delayed-differentiated period was noticed until a storage period of 16 weeks. Thereafter a sudden increase in delayed-differentiation period was observed until a storage period of 20 weeks. As was the case with the delayed-differentiation period in the glasshouse, it seemed to stay constant from this point onward.

Under the glasshouse conditions the delayed-differentiation period was much shorter. The maximum delayed action in the incubator was about 21 weeks, while in the glasshouse it was only 13 weeks. From the combination of incubator and glasshouse it is also clear that the glasshouse conditions shorten the delayed-differentiation period. It is not clear which conditions in the glasshouse caused this shortening of the delayed-differentiation period. It can be ascribed to either the fluctuation between day and night temperature, or the watering. It is most likely that it was the watering, since it is well-known that water initiates growth. Stuart (1954) noted that a low moisture content of peat in which lily bulbs were planted, caused significant delays in flowering.

The delayed-differentiation period is an important factor to take into consideration when manipulating the flowering period of *Lachenalia*, since it can delay the flowering date significantly. No reference to such a delayed-action was found in the literature. Hartsema (1961) reported that tulips and hyacinths formed normal flowers as soon as the bulbs were removed from a low inhibition temperature to a suitable initiation temperature.

In Table 4.1 a summary is given of the temperature treatments that were applied and monitored in Experiment I to achieve flowering out of season. The mean date of differentiation commencement and flowering date are also noted in Table 4.1. In order to elucidate and implement the results, it is important to know the time of commencement of differentiation and to know what temperatures prevailed during the development of the inflorescence.

By inhibition of flower initiation at 10 °C, it was possible to achieve flowering out of season (Table 4.1). This inhibition temperature could be used not only to obtain late flowering in October to January, but also 'early' flowering in February to May. By using cold stored bulbs of the previous season, the flowering date could be shifted to the season

Table 4.1: Summary of the treatments and environmental conditions during flower formation and results concerning the date of commencement of differentiation and flowering of *Lachenalia* cv. 'Romelia' at Rooddeplaar.

Treatment no.	Weeks at 10 °C	Weeks at 22 °C	Weeks in glasshouse until differentiation started	Temperature regimes when differentiation commenced		Mean date of commencement of differentiation	Mean date first flower opened	Weeks from the start of differentiation till flowering
				Night	Day			
(Control) 1	0	18	-	22 °C	22 °C	30/12/1989	03/06/1989	22
2	20	22	-	22 °C	22 °C	21/8/1989	22/11/1989	14
3	24	18	1	10-15 °C	20-30 °C	8/9/1989	13/12/1989	14
4	28	14	2	10-15 °C	20-30 °C	11/9/1989	11/1/1990	17
5	33	9	4	10-15 °C	20-30 °C	27/9/1989	25/1/1990	17
6	38	4	8	15-20 °C	25-30 °C	12/11/1989	30/3/1990	20
7	42	0	12	15-20 °C	25-30 °C	13/11/1989	5/4/1990	21

before the natural flowering season. Shoub and Halevy (1971) also used bulbs which inflorescences were inhibited during of the previous season to obtain 'early' flowering.

4.3.2 The influence of the environmental conditions on differentiation rate.

An important aspect of commercial flower production, is the time-lag between planting and flowering. A short time-lag is desirable, since the delay drastically affects production costs (Moolman, 1991, personal communication). From Table 4.1 it is evident that the glasshouse temperatures influenced the differentiation rate of the inflorescence. During the cool spring months, the period between the start of differentiation and flowering was significantly shorter (14 or 17 weeks) than in the hot summer months (22 weeks). This corresponded with previous results. In Chapter 3 it was found that differentiation and elongation occurred much quicker at 15 °C than at 20 °C or higher temperatures.

4.3.3 Flower quality

It is important that flower quality is not negatively influenced when the flowering date is shifted. In Table 4.2 a summary of the quality parameters is given for the different treatments in Experiment I. Differences between the treatments with regard to floret number, rachis length, peduncle length, number of secondary inflorescences and keeping ability of the inflorescence were detected. There was no significant difference in peduncle cross section and compactness of the inflorescence, between the treatments. The only bulbs that produced good quality inflorescences, that corresponded with the control (Treatment 1), were those stored for 20 weeks at 10 °C, followed by 22 weeks at 22 °C before being planted in the glasshouse (Treatment 2, Table 4.1).

Although flower quality with regard to floret number and secondary inflorescences for the rest of the treatments were significantly lower than the control, there was no decline in quality with increased storage duration at 10 °C. It seemed therefore as though it was not the storage period at 10 °C that caused this poor flower quality. To elucidate these results the time of differentiation commencement and the temperature regimes during differentiation, as given in Table 4.1, must be considered. The only difference between those bulbs that produced good quality inflorescence and those that produced poor quality, was the temperature during the time of flower differentiation. Good quality inflorescences

Table 4.2: Summary of the inflorescence quality parameters at the different treatments^a of *Lachenalia* cv. 'Romelia' at Roodeplaat

Treatment no.	Number of plants	Weeks at 10 °C	Weeks at 22 °C	Number of florets	Rachis length (mm)	Peduncle length (mm)	Days inflorescence was acceptable	Number of sec. inflorescence
1	26	0	18	22a	153a	138a	32a	2,5a
2	26	20	22	22a	142a	97c	26b	2,6a
3	72	24	18	18b	105bc	98c	21c	1,4b
4	74	28	14	-	115b	97c	21c	1,5b
5	86	33	9	-	94c	104bc	26b	1,4b
6	61	38	4	16bc	113bc	116b	34a	1,4b
7	67	42	0	16bc	107bc	124ab	32a	1,6b

^a Values not followed by same letter are significantly different at the 1% level.

were produced only when differentiation commenced at a constant 22 °C in an incubator (Treatments 1 and 2). When differentiation commenced in the glasshouse (Treatments 3 to 7), flower quality was unacceptable. The temperatures that prevailed in the glasshouse during differentiation commencement are summarized in Table 4.1. Night temperatures lower than 20 °C resulted in poor quality inflorescences (Table 4.1 & 4.2, Treatments 3 to 7). These results corresponded with those in Chapter 3. In experiments described in Chapter 3 good flower quality was only obtained with bulbs that differentiated flowers either in the incubator at 25 °C or in the glasshouse, when the temperatures at the time of differentiation were 20 °C (night) and 30 °C (day).

From these results it seemed as though it was the temperature during and directly after the commencement of differentiation that played the major role in flower quality. This statement is made since differentiation was only slightly more than a week in progress at 22°C in Treatment 2, when the bulbs were planted in the glasshouse at lower temperatures. The lower glasshouse temperatures accelerated the differentiation rate, since a period of only 13 weeks was observed between commencement of differentiation and flowering (Treatment 2, Table 4.1). Flower quality was not negatively affected. These results also correspond with those in Chapter 3.

In this experiment there was a significant difference between peduncles that elongated during winter (Treatment 1, 6 and 7) and those that elongated during summer (Treatment 2 to 5, Table 4.2). Higher light intensities and temperatures during the summer months resulted in shorter peduncles than in winter. These results are in accordance with those in Chapter 3.

The short keeping ability of the inflorescences under certain treatments (Treatment 2 to 5), was probably caused by high temperatures that reigned in the glasshouse during flowering (25 - 35 °C day and 20 - 25 °C night). Inflorescences that flowered in the cool autumn months (Treatments 1, 6 and 7) lasted significantly longer (Table 4.2).

Bulbs that were previously stored for a long period at 10°C before being transferred to an incubator at 22°C (Experiment II), differentiated inflorescences, but did not have the ability to elongate the inflorescence to sprout under these conditions. These bulbs have to be planted and watered in order to elongate and sprout. It is possible that bulbs that were

stored for a long period did not have enough reserve water to support elongation.

It is possible to shift the flowering date of *Lachenalia* cv. 'Romelia' out of season, without losing flower quality. The temperature during differentiation is, however, important in order to retain good flower quality.

4.4 CONCLUSION

The flowering date of *Lachenalia* cultivar 'Romelia' can successfully be manipulated to flower out of season without losing flower quality. Flower initiation can be inhibited completely by 10°C for as long as 42 weeks. When these bulbs were shifted to an initiation temperature of 22°C in an incubator, a prefloral period of at least 8 weeks existed before differentiation commenced. This prefloral period extended to 21 weeks after bulbs were inhibited for 20 weeks at 10 °C. By planting bulbs in a glasshouse the after inhibition effect could be reduced to 13 weeks. Although it is not clear which factor in the glasshouse was responsible for the quick upliftment of the after-effect, it was probably the provision of water. The glasshouse temperatures were, however, not always optimal for flower differentiation. It is thus not a practical solution to use high cost glasshouse space for the purpose of reducing the after-effect elongation. This after-effect has to be taken into consideration when manipulating flowering since it can influence the flowering date considerably.

The temperature during the first part of inflorescence differentiation was of utmost importance. It appeared that a night temperature lower than 20 °C was unfavourable for flower differentiation. Bulbs that were inhibited for 20 weeks at 10 °C differentiated inflorescences with acceptable quality after 22 weeks at 22 °C. These bulbs had to be planted after differentiation of the flower parts, since the inflorescence failed to elongate in an incubator after a long storage period at 10 °C.

Until the factor in the glasshouse that was responsible for the quick release from the after-effect is identified, the following procedure is recommended: After storage at 10 °C, the bulbs must be transferred to an incubator at the optimum temperature of flower initiation and differentiation, namely 25 °C. Taking Figure 4.1 into consideration, samples will have to be taken in order to determine when flower differentiation commences. A period

of at least 4 weeks of differentiation must be allowed in order to produce good flower quality. Thereafter the bulbs must be moved to a glasshouse with a temperature regime of 10 - 15 °C (night) and 20 - 25 °C (day) for further development and flowering. This procedure, however, still has to be tested.

4.5 REFERENCES

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GENERAL DISCUSSION AND CONCLUSION

In order to develop a forcing programme for *Lachenalia*, it was necessary to examine the life cycle of *Lachenalia* and the process of flower initiation and development. The morphological development of *Lachenalia* closely resembles that of *Ornithogalum arabicum*. The only difference is that in *Lachenalia* cv. Romelia the vegetative bud produces no additional leaves during storage before it becomes transformed into a flower bud.

The stage in the life cycle at which flower initiation occurs, is an important aspect to take into consideration in the forcing of bulbs. *Lachenalia* initiated flowers during storage after harvesting. *Lachenalia* can thus be grouped together with *Tulipa*, *Hyacinthus*, *Ornithogalum* and *Iris reticulata* in this regard.

The developmental stages of the inflorescence of *Lachenalia*, are in accordance with that of another member of the Hyacinthaceae family namely, *Hyacinthus*. The transitional phase of *Lachenalia* was very short and was therefore missed. The prefloral phase was the first sign of the reproductive stage. The meristem proceeded through eight stages as described for *Hyacinthus*, the last of which is commonly known as stage 'G'. At this stage, the primordia of six perianth leaves, six anthers and a trilobed gynoecium are visible in the oldest flowers.

The temperature requirements of *Lachenalia*, as for other bulbs, are closely linked to the temperatures that prevail in their natural habitat. The early flowering *Lachenalia* cv, Romelia differs from other bulbous species which have a warm-cold-warm developmental cycle. *Lachenalia* cv. Romelia has a warm-cool developmental cycle, since flowering already occurs during the low temperature of June. *Lachenalia* bulbs are dormant during the high temperatures in summer. During this period, flower initiation and differentiation occur. A decrease in temperature during autumn coincides with elongation of the flowering stalk and flowering occurs during the low temperatures of winter.

As with most other bulbous plants, flower initiation occurs over a range of temperatures, from 15 to 30 °C. Flower initiation and commencement of differentiation is first completed at 20 and 25 °C. A storage temperature of 15 and 30 °C retards the initiation

process and temperatures of 10 and 35 °C inhibit flower initiation completely. There is thus an optimum, a minimum and a maximum temperature for flower initiation. The optimum temperature for *Lachenalia* is high, as for most other bulbs.

Before flower differentiation commenced, a natural period of at least eight weeks passed. Although no histological changes were observed during this period, some physiological processes must have taken place that are a prerequisite for flower differentiation. In this study this period before differentiation commenced is referred to as initiation. A time-lag before differentiation was also observed in *Tulipa*, *Narcissus*, and *Hyacinthus*. At a storage temperature of 10 °C initiation is inhibited in *Lachenalia* cv. 'Romelia', since the time-lag of eight weeks endured after the inhibited bulbs were moved to a high initiation temperature. A high temperature treatment at 30 or 34 °C for a week before moving the bulbs to a flower initiation temperature of 20 °C shortens the initiation period of hyacinths, tulips and daffodils. This treatment will probably have a similar effect on *Lachenalia*, but this still has to be tested.

Differentiation and elongation of the inflorescence followed flower initiation. The most rapid development proceeded at 15 °C; at 30 °C, however, this process was very slow. The optimum temperature for further flower development is thus lower than that for initiation. This tendency was also observed in *Tulipa*, *Hyacinthus* and *Narcissus* and in *Ornithogalum arabicum*, but not in *O.thyrsoides*. Although flower development proceeds most rapidly at 15 °C, this cannot be regarded as the optimum temperature when flower quality is taken into consideration. The high development rate at low temperatures has more influence on elongation of the inflorescence than on organogenesis of the florets. The rapid elongation rate prevents the formation of upper florets on the inflorescence. Good quality inflorescences can be obtained when they are allowed to reach the proper stage of floral development before being transferred to a lower temperature. This stage is cultivar dependent, but most tulip cultivars can be transferred upon reaching stage 'G'. The concept of transferring *Lachenalia* cv. 'Romelia' bulbs to lower temperatures still has to be investigated.

A low temperature treatment is a prerequisite for stem elongation in some bulbs e.g. tulips and hyacinths. In others e.g. *O. arabicum* low temperatures accelerate the elongation and subsequent flowering date, but do not have an effect on the stem length. From results in

this study it appears as though *Lachenalia* will react similarly to *O.arabicum*. A more detailed study on the effect of low temperatures on organogenesis is necessary in order to know whether the high rate of inflorescence development at low temperatures can be ascribed only to elongation.

The temperature that prevailed in the storage room during flower differentiation did affect flower quality. The temperature influenced floret number, rachis length, peduncle length, peduncle cross section, compactness of the inflorescence and occurrence of secondary inflorescences. A storage temperature of 25 °C during flower differentiation gave optimum flower quality; that is compact inflorescences, with high floret numbers, firm peduncles and the occurrence of secondary inflorescences. The duration of the storage is also important. The bulbs must be stored for a period of at least four weeks at 25°C after differentiation has commenced, in order to achieve optimum flower quality. The exact stage of development of the lower florets after this minimum period at 25°C still has to be determined. This developmental stage will be a more accurate indication as to when bulbs can be transferred to lower temperatures for elongation.

Storage temperature did effect peduncle length but it seemed as though light intensity after planting had the greater effect. The higher the light intensity the shorter the peduncle length. Keeping ability of the inflorescence was not influenced by the storage conditions. The keeping ability of the inflorescence was affected by the temperatures in the glasshouse during flowering. The inflorescences lasted longer in cool conditions.

Although the optimum glasshouse temperature for subsequent flowering was not investigated, a relatively cool environment is recommended. This recommendation is given according to the natural environment of *Lachenalia* and from results that were obtained in Chapter 4. In Chapter 4 there was an indication that the period from commencement of differentiation until flowering in the glasshouse is reduced from 22 to 14 weeks. The glasshouse period must be kept as short as possible, since it is a very costly phase in the production of a potplant.

Flower initiation was completely inhibited at 10 and 35°C. Large quantities of bulbs stored at 35°C became dry and rotted. These temperatures are thus not regarded as appropriate temperatures for flower manipulation. Ten degrees Celsius could however be

used to shift the flowering date of *Lachenalia* cv. Romelia to any desirable date. There are, however, certain factors that have to be taken into consideration. Apart from direct inhibition of initiation, 10 °C also resulted in a delay of the onset of flower differentiation after the bulbs were moved to higher temperatures. The duration of this delayed-action depended on the duration of the 10 °C treatment and on the treatment thereafter. When bulbs were moved from 10 °C to 22 °C in an incubator, the delayed-differentiation period lasted up to 20 weeks. When bulbs were moved from 10 °C to a glasshouse where they were exposed to fluctuating day and night temperatures and watered, the delayed-action was counteracted within 13 weeks maximum. It is most probably the water that negates the delayed-differentiation. This delayed-differentiation is an important factor to take into consideration when manipulating the flowering date of *Lachenalia*, since it can delay the flowering date significantly. There is no reference in the literature to such a delayed-action of an inhibition temperature. Flower initiation of tulips and hyacinths was inhibited for 8 months at -1 °C and the normal formation of flowers was reported as soon as the bulbs had been transferred to suitable temperatures.

The 10 °C inhibition treatment did not have a negative effect on flower quality. The differentiation temperature after inhibition is, however, of utmost importance to flower quality. The optimum flower differentiation temperature should be used.

In order to shift the flowering date of *Lachenalia* cv. Romelia the following facts have to be taken into consideration:

- The flower initiation process takes at least 8 weeks at the optimum initiation temperature of 25°C.
- When the initiation process is inhibited at 10°C, delayed-differentiation period exists after bulbs are transferred to higher temperatures, in order to calculate the duration of this delayed-action, Figure 3.1 in Chapter 3 should be consulted.
- Optimum inflorescence quality can be obtained if differentiation is allowed to take place at 25°C for at least 4 weeks.
- After inflorescence differentiation the bulbs have to be transferred to lower temperatures (15°C) for elongation of the inflorescence stalk.
- The greenhouse temperatures have to be cool (15°C, night and 25°C, day) for fast growth until flowering.

Table 1. A model for year-round production of flowering potplants of *Lachenalia* cv. 'Romelia.' Storage started on 6 November.

Proposed flowering date	Weeks at 10 °C,	Weeks at 25 °C		Weeks from plant to flower
		For initiation	For differentiation	
1 June	0	8	5	12
1 July	4	8	5	12
1 Aug	9	12	5	12
1 Sept	14	12	5	12
1 Oct	17	13	5	12
1 Nov	18	16	5	12
1 Dec	19	19	5	12
1 Jan	22	21	5	12
1 Feb	26	22	5	12
1 March	30	22	5	12
1 Apr	34	22	5	12
1 May	38	22	5	12

From results obtained in this study, Table 1 was compiled. It must be stated, however, that this table is incomplete and much research still has to be done in order to give comprehensive recommendations. The table was compiled with the following presumptions:

- Storage started 6 November.
- The after-effect at 25 °C will concur with that at 22 °C.
- The period from plant to flower will remain 12 weeks at a glasshouse temperature of 10-15°C (night) and 20-25°C (day).

Certain shortcomings and aspects that needed further research were identified during this study. An important shortcoming of this study is the fact that no attention was given to the leaves. For a potplant both the inflorescence and the leaves are important. The course of inflorescence differentiation was followed at 20 °C, but since 25 °C is the optimum differentiation temperature, it has to be repeated at 25 °C, especially the time-lag between the commencement of differentiation and stage 'G'. The effect of a high temperature (34 °C) directly after lifting might shorten the initiation time-lag, and this needs investigation. The effect of a low temperature treatment, at different stages of the differentiation process, on the time-lag before flowering and flower quality is an important aspect that must still be sorted out. The optimum stage when bulbs must be transferred to the glasshouse and the temperature regimes in the glasshouse need investigation. More research still has to be done on the delayed-differentiation to identify the factor that is responsible for the earlier lifting of this delayed-action in the glasshouse, and to draw a more detailed graph.

OPSOMMING

Bloeiwyse inisiasie, differensiasie en ontwikkeling van *Lachenalia* cv. Romelia stem ooreen met die van 'n tipiese bol. Wat die morfologiese ontwikkeling van die vegetatiewe knop betref, is daar egter 'n verskil. Die vegetatiewe apikale meristem van *Lachenalia* produseer geen vegetatiewe blare tydens opberging voordat dit reprodutief raak nie.

Temperatuur het 'n effek op die tyd van blominisiasie en differensiasie. Blomgrootte bolle is vir verskillende periodes by verskillende temperature opgeberg. Blominisiasie het die vinnigste by 20 en 25 °C plaasgevind. Vyftien en 30 °C vertraag blominisiasie en by 5, 10 en 35 °C het geen blominisiasie plaasgevind nie. Verdere blom differensiasie en verlenging het die vinnigste by 15 °C plaasgevind, terwyl 30 °C die proses baie vertraag het.

Die opbergingstemperatuur tydens blomdifferensiasie beïnvloed bloeiwyse kwaliteit. Die beste kwaliteit is verkry indien blomdifferensiasie by 25 °C plaasvind vir 'n minimum periode van 4 weke. Kompakte bloeiwyses met 'n groot getal blomme en stewige bloeistele is by hierdie behandeling geproduseer. Die opbergingstemperatuur het ook 'n invloed gehad op die getal sekondêre bloeiwyses wat gevorm het. By hoër opbergingstemperatuur is meer sekondêre bloeiwyses waargeneem as by laer temperature. Die lengte van die bloeistele word wel beïnvloed deur die opbergingstemperatuur, maar omgewingsfaktore, na plant, veral ligintensiteit, speel egter 'n belangriker rol in die verband. Hoër ligintensiteite veroorsaak kort bloeistele. Houvermoë van die bloeiwyse word nie deur die opbergingstemperatuur bepaal nie, maar wel deur die omgewingstoestand tydens blom.

Die blomdatum van *Lachenalia* cv. 'Romelia' is vertraag deur die bolle by 10 °C op te berg, aangesien hierdie temperatuur blominisiasie volledig inhibeer. Bolle wat daarna in 'n inkubator by die optimum blominisiasie temperatuur geplaas is, het 'n vertraagde aanvang van bloeiwyse differensiasie getoon deurdat dit, afhangend van die opbergingsperiode by 10 °C, tot 20 weke neem vir differensiasie om 'n aanvang te neem. Hierdie vertraging moet inaggeneem word indien die blomdatum gemanipuleer word met behulp van 10 °C, aangesien dit die blomdatum merkbaar beïnvloed. Daar is gevind dat die vertraging vinniger opgehef word indien die bolle na opberging by 10 °C, in 'n glashuis geplant word. Die omgewingsfaktor wat vir die vinniger opheffing verantwoordelik is, is waarskynlik water.

Uit die studie blyk dit dat 'n lang opberging by 10 °C geen negatiewe effek het op blomkwaliteit nie. Wat wel van belang is, is die temperatuur tydens blomdifferensiasie. Dit is noodsaaklik dat bolle wat by 10 °C geïnhibeer was, daarna by die optimum temperatuur vir blomdifferensiasie geplaas moet word.

SUMMARY

Inflorescence initiation and differentiation of *Lachenalia* cv. 'Romelia' corresponded with that of a typical bulb. There was, however, a difference between *Lachenalia* and most other bulbs with regard to the morphological development of the vegetative bud. The vegetative apex of *Lachenalia* do not produce additional leaves during storage before it transform into a reproductive apex.

Temperature affected the time of flower initiation and differentiation. Flowering size bulbs were stored for different periods at different temperatures. Flower initiation is promoted at 20 and 25 °C. Fifteen and 30 °C retarded flower initiation and at 5, 10 and 35 °C no flowers were initiated. Further flower differentiation and elongation proceeded most rapidly at 15 °C while 30 °C retarded this process.

Storage temperature during flower differentiation influence inflorescence quality. The best quality was obtained when flower differentiation occurred at 25 °C for at least 4 weeks. Compact inflorescences with a high floret number and firm peduncles were produced at this treatment. The storage temperature also influenced the number of secondary inflorescences. More secondary inflorescences were produced after storage at high temperatures, than at low temperatures. Peduncle length was also influenced by the storage temperature. Storage at 15 °C resulted in significantly longer peduncles than the other temperatures. Light intensity, however, played the major role in this regard. High light intensity generated short peduncles. Keeping ability of the inflorescence was not determined by the storage temperature, but by the environmental conditions that prevailed during flowering.

The flowering date of *Lachenalia* cv. 'Romelia' was retarded by storing the bulbs at 10 °C, since flower initiation was totally inhibited at this temperature. When these bulbs were transferred to an incubator at optimum initiation temperature, an after inhibition effect was noticed. This after-effect prevented the commencement of flower initiation for up to 20 weeks. The duration of the after-effect depended on the period at 10 °C. This after-effect must be considered when the flowering date is manipulated, since it has a major effect on the flowering date. When bulbs that were stored at 10 °C were planted in a glasshouse, this after-effect was shortened. The environmental effect that was responsible

for this shortened time period was probably the provision of water.

From this study it was clear that prolonged storage at 10 °C does not have any negative effect on flower quality, provided that flower differentiation occurred at the optimum temperature. Good quality inflorescences were produced when flower differentiation commenced at 22 °C after the bulbs were stored at 10 °C.

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