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GROWTH AND FLOWERING IN

CYRTANTHUS ELATUS

A thesis presented in partial
fulfilment of the requirements for
the degree of Master of Horticultural
Science at Massey University

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ABSTRACT

Cyrtanthus elatus (Hilliard and Burtt, 1986), commonly called Vallota, is a bulbous plant native to the Southeastern Cape province of South Africa, bearing an inflorescence with several large, bell-shaped, red flowers.

The bulb and flower morphology, plus development of the inflorescence is described and was similar to *Eucharis* and *Hippeastrum*. Sympodial growth of leaves and inflorescences occurred from meristematic cells at the centre of the basal plate. A terminal inflorescence was initiated after 5-7 leaves. Large bulbs (7 cm diameter) had 5 leaves per growth unit and up to 5 inflorescence buds.

Temperature and light intensity influenced growth and development of *C. elatus*. Inflorescences were initiated over a range of temperatures (13-29°C). Vernalization was not required. Floral initiation was optimal from 21-29°C and development to anthesis was optimal at 25°C. Quality of florets was best at 21°C which resulted in larger, brighter, orangey-red flowers. Rates of floral initiation were not affected by shading (50%), however, shading resulted in a high level of inflorescence bud abortion, particularly at warm temperatures (mean 23°C). Inflorescences did not emerge under 50% shade. Scapes were longest at 21-25°C, light intensity 722 $\mu\text{Mm}^{-2}\text{s}^{-1}$. Inflorescence quality was maintained in a simulated home environment and past the macrobud stage, was independent of inflorescence development. Fluctuating warm temperature (17-26°C) and high light intensity (784 $\mu\text{Mm}^{-2}\text{s}^{-1}$) resulted in maximum root, shoot and offset growth.

Good quality plants can be produced year-round under warm conditions (17-26°C), with two inflorescences per year from mature bulbs. Scheduling is complicated by the lack of a vernalization requirement. Shading is not recommended during production. Shipment in the dark at the macrobud stage is possible without deterioration. *C. elatus* is suitable as a patio and as an indoor pot plant.

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CHAPTER 1

INTRODUCTION

1.1 GENERAL

1.1.1 Description

Cyrtanthus (Amaryllidaceae) is a genus of about 40 species of bulbous plants, natives of southern and tropical East Africa, but found mainly in the Southeastern Cape Province. About 25 species are recorded there, 7 from the southern Cape province and 10 from the Transvaal (Reid and Dyer, 1984). The highest concentration of species occurs where there is year round rainfall (i.e. the Southeastern Cape Province).

The generic name is derived from *kyrtos* meaning curved and *anthos*, a flower. The flowers of many of the species hang down from the summit of the scape. A few species, including *C. elatus* have erect flowers. Most species of *Cyrtanthus* have a perianth tube which is longer than the free parts of the perianth (the segments) and which is roughly cylindrical. A few species, including *C. elatus* and *C. sanguinias* have a wide, tapering perianth tube which is shorter than the free segments.

Cyrtanthus species have flowers of a range of colours, including white, cream, yellow, pink and red. The flowers of *C. elatus* are scarlet. There are two mutants, 'alba' (white) and 'delicata' (shell pink) (Chittenden, 1951).

A comprehensive description of *C. elatus* is given by Dyer (1954). The bulb is ovoid with a membranous brown tunic. Dyer gives a size of up to 5 cm in diameter but in this research bulbs grew to 7-8 cm in diameter. Leaves are 4-12 from a bulb, linear lanceolate in shape with smooth margins. They are 20-45 cm long, 2-6 cm in width. The hollow scape is stout and longer than the leaves. There are two lanceolate spathe valves, 2-5 cm long. Two to nine (usually 5 or 6) flowers are borne in an umbel. The perianth is erect or sub erect, trumpet shaped and scarlet in color. The perianth is 7-10 cm long, the tube triangular in shape and shorter than the segments which are equal and spreading. The stamens are inserted at the mouth of the tube, about 2 cm shorter than the lobes. The anthers are small and yellow and attached dorsally. The red-flushed style is almost as long as the segments; the stigma trilobed. The triquetrous ovary is 8-12 mm long. On maturing, the dehiscent locules release black, membranous, winged seeds.

1.1.2 History

Cyrtanthus elatus was discovered in South Africa in 1773 by Karl Thunberg. Masson, a Kew gardener who accompanied Thunberg, took bulbs back to London and grew them at Kew Gardens. From Britain the plants were introduced to Europe, being grown first of all in the Royal Gardens of Shoenbrun, outside Vienna (Dyer, 1954). Plants were illustrated by Jaquin, 1797, under the name *Amaryllis elata*. A colour illustration appeared as *Amaryllis purpurea* in Curtis's Botanical Magazine of 1812. The plant was placed in the genus *Cyrtanthus* by Herbert in 1829, but he later established a new genus *Vallota* for it. This name was given in honour of the French botanist, Pierre Vallot. The name *Vallota purpurea* had become firmly established for it as it was recognised by Baker in *Flora Capensis*, 1896 (Dyer, 1954). Hutchinson, in his book "A botanist in Southern Africa" (1946) refers to the plant as *V. speciosa* as does R.A. Dyer in "Flowering plants of Africa" (1954). The plant was later transferred to the genus *Cyrtanthus* as *Cyrtanthus purpureus* (Traub in *Plant Life* 19: 58 (1963). The name *C. speciosus* was already in use for another plant (Reid and Dyer, 1984) as was 'sanguineas', another appropriate name. However, it is claimed that the epithet *purpureus*, which Traub used, was illegitimate in its original application by Herbert (Hilliard and Burtt, 1986). A new name has been sought. As Jaquin originally called this species *Amaryllis elata* in 1797, this is thought to be the earliest legitimate epithet available for the species. Hilliard and Burtt (1986) believe that the best course is to use *C. elatus*. In this thesis the name *C. elatus* is used.

The name 'vallota' is one of many common names which include George Lily, Kynsna Lily, Berg Lily (describing the native habitat in S. Africa) and Scarborough Lily. It is reputed that during the early 1800's a dutch ship carrying bulbs was wrecked near the Yorkshire town of Scarborough. Bulbs found washed up on the beach were cultivated in the nearby town. Hence the name 'Scarborough Lily' (Simpson, 1985). Another story is that a sailor sent bulbs to his girlfriend in Scarborough (Warren, 1988).

1.1.3 Horticultural potential

C. elatus is a plant of increasing economic importance, both in New Zealand and overseas. It is grown mainly as a cut flower with some potential for pot plant production. Growers in New Zealand produce live plants and bulbs, both for the domestic market and for export.

Total flower exports from New Zealand have increased from NS \$5 m in 1984, to just over NZ \$20 m in 1990 (Steven, 1990). Total exports of bulbs and tubers has increased from 1% of flower exports in 1984 to 13% in 1989 (worth NZ \$2.3 m). Japan is the major market, taking 56% of our flower exports in 1989(NZ \$10.3 m). Other important markets include Europe (12%), the U.S.A. (10%) and Canada (8%).

Japan is a potential market for export of live plants and bulbs of *C. elatus*. The cut flower market is described as "an excellent foreign exchange growth opportunity" (Report of the N.Z. Trade and Development Board, 1990). Annual sales of all plants exceed NZ \$9 billion. Although imported cut flowers represent only 3% of total sales in Japan, the market is expanding rapidly.

One of the reasons for this expansion is because there is a tendency for younger Japanese people to enjoy 'non-Japanese' flowers. They show an interest in 'new' varieties. One of the strategies we can adopt to increase our export options to Japan (and other countries) is to broaden our product range by exporting 'new' species such as *C. elatus*. The success of Calla Lily exports supports this point. The value of this relatively 'new' export commodity has almost doubled every year since 1986 (Kepner and Welsh, 1990), while growth of orchid exports since 1987 has been almost nil.

1.1.4 Present knowledge of *C. elatus*

Considerable information is available concerning the growth and flowering of bulbous plants of significant commercial importance, for example tulip, narcissus, hyacinth, iris and lily. Very little, however, is known about most other geophytic plants including *C. elatus*. Growers need to be able to schedule crops both in New Zealand and potential importing countries. Bulbs may be accelerated to flower or delayed by forcing conditions in greenhouses, although genetic factors impose some limits on these manipulations. Knowledge of environmental factors affecting growth and development is essential before effective treatments can be applied.

Very little work has been published on *C. elatus*. Most of the literature describes the external appearance of the plant, together with cultural information for gardeners pertaining to soil type, amount of irrigation needed, frost hardiness and pest control. Some of the recommendations for best growing environments are conflicting. In general, the genus is

said to prefer light shade or full sun in the morning only (Duncan, 1990). For *C. elatus* in particular, a "certain amount" of shade (Reid and Dyer, 1984) or part-shading from hot afternoon sun (Redgrove, 1987; Warren, 1988) is recommended. Other workers, however, state that the plant grows best in full sun (Bailey, 1947; Eliovson, 1967; Duncan, 1990), although Eliovson believes that a semi-shaded position is desirable in cold or dry areas. Shading results in longer stem length and less flower colour (Warren, 1988). However, the effects of varying light intensity, light quality or photoperiod on the physiology of the plant are not well known.

Eliovson and Redgrove consider the plant does not flower regularly. It is suggested that this may be due to root disturbance (Eliovson, 1967), to ravages of the Narcissus fly (Redgrove, 1988) or to being kept too dry in winter (Bailey, 1947). Duncan (1990) suggests that crowding and competition from the large number of daughter bulbs produced may restrict flowering.

The effects of temperature on growth of *C. elatus* are not well documented. Effects of three temperatures (14, 18 and 22 °C) on vegetative growth and flower quality were investigated (van Nes and Vonk Noordegraaf, 1977). Effects of higher temperatures are not known. Anatomical features of bulbs are described by van Nes and Vonk Noordegraaf (1977). Numbers of leaves between inflorescence initials are not affected by temperature. However, there is no information about stages of flower development and developing flower morphology.

Although *C. elatus* is described as making an excellent pot plant (Simpson, 1985), the response of the potted plant to short or long term exposure to low light intensity conditions experienced in retail outlets and the home environment has not been researched.

1.2 MORPHOLOGY

1.2.1 Morphology of bulbous plants in general

A bulb, in the strict botanical sense, can be described as a storage organ consisting of a short stem bearing fleshy leaf bases or scale leaves enclosing next year's bud. More loosely, the word 'bulbous' is used by amateur gardeners to include plants with other types of storage organ - corms, rhizomes and tubers.

No single bulb structure describes all (Rees, 1972). *Hippeastrum* (Amaryllidaceae) is typical of the simplest structure. This plant grows in tropical and subtropical America where environmental variation is low. *Hippeastrum* is evergreen, the leaves emerging in succession throughout the year. The bulb, composed entirely of leaf bases, is a sympodial branching system. When an inflorescence is initiated, a lateral bud on the side of the axis away from the last leaf, continues the growth, the first leaf and the inflorescence being on the same side. Each growth unit or growth cycle is composed of four leaves and a terminal inflorescence (Fig. 1.1). The youngest or innermost leaf of the four has a semi-sheathing base, the bases of the other leaves sheath the growing point entirely. The emerged leaves present on the plant at any time belong to more than one growth unit. Six units may be present in large, mature bulbs. The older two have no living green leaves, two have emergent leaves and two units have no emerged leaves (Rees, 1972).

Berghoef and van Brenk (1983) showed that *N. bowdenii* and *Hippeastrum* are structurally similar. Each growth unit is composed of 5-10 leaves and a terminal inflorescence. A difference, however, is that the first leaf of a growth unit (i.e. the leaf innermost to the inflorescence) is $\frac{1}{2}$ circular and has no emergent blade. This feature is found in *N. flexuosa alba* (Fortanier *et al.*, 1979) and in *N. sarniensis* (Warrington and Seager, 1988).

N. flexuosa alba has 4-15 leaves per cycle with 5-6 occurring most frequently (Fortanier *et al.*, 1979), 5-9 leaves/cycle were found in *N. sarniensis* (Warrington and Seager, 1988). *N. flexuosa alba* has growth flushes year round and can initiate four or more inflorescences in one growing season (Fortanier *et al.*, 1979), while only 2 inflorescences are formed per growing season in *N. bowdenii* and *N. sarniensis*. These latter species produce flowers only in the autumn or late summer.

Narcissus has a different bulb type. The bulb is made up of special storage scales as well as leaf bases. A mature bulb is formed of a number of annual increments called bulb units. A bulb unit is comparable to a growth unit of *Hippeastrum* but there are some differences. Only one bulb unit is produced each year by the apical meristem. Each bulb unit is made up of three or four storage scales, two or 3 leaves and an inflorescence. The innermost leaf has a semi-sheathing base as in *Hippeastrum* and *Nerine*. There is some disagreement as to whether the flower is lateral or terminal (Rees, 1972). The flower primordium rapidly dominates the apex, with the vegetative apex remaining quiescent until later.

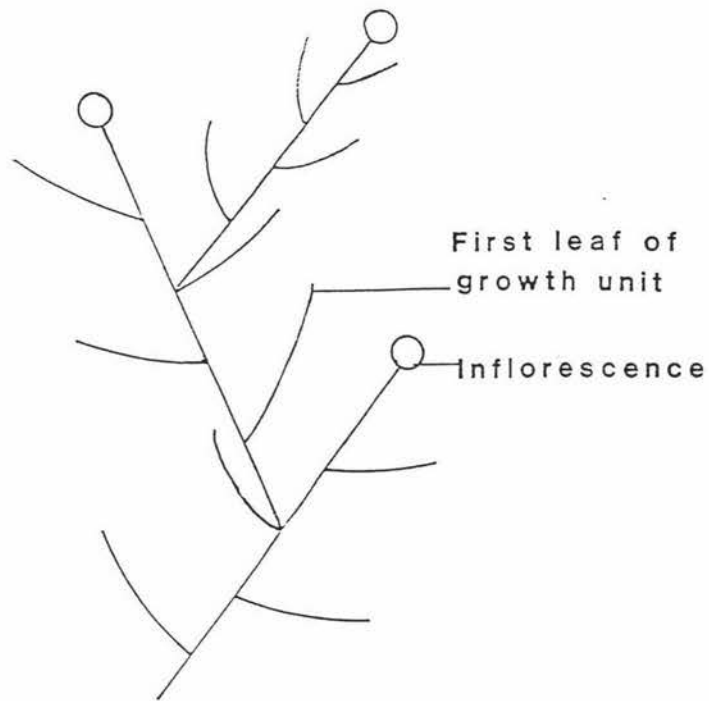


Fig. 1.1 Diagram to show sympodial branching system of *Hippeastrum*. Three growth units shown.

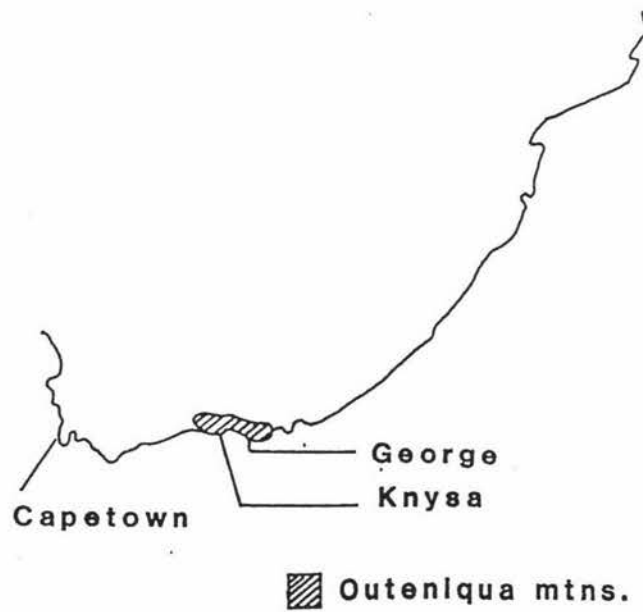


Fig. 1.2 Location of the Outeniqua mountains in the South-eastern Cape Province.

The tulip bulb is another 'type'. It is composed entirely of scales (i.e. leaf-like organs making up the bulb, other than the bases of photosynthetic leaves). In the centre of the bulb, enclosed by the scales, is an axis bearing leaves with a terminal flower. As the stem emerges, the green leaves are carried out clear of the bulb. Thus this bulb differs from the others described, in that more than one internode elongates. Daughter bulbs arise in the scale axils. Another difference is that the mother bulb dies after senescence of the above ground parts during the summer and is replaced by daughter bulbs.

1.2.2 Morphology of *Cyrthanthus elatus*

There is some knowledge about the internal structure of the bulb of *C. elatus*. Photographs of a dissected bulb appear in a paper by van Nes and Vonk Noordegraaf (1977). They reveal numbers, sequence and types of leaves within the bulb. Seven leaves between inflorescences are shown.

1.3 ECOLOGY

1.3.1 Introduction to bulbs

Higher plants are thought to have evolved in tropical climates where the lack of a cambium in monocotyledonous plants led to continuous vegetative growth (Rudnicki, 1974). Migration to a temperate climate, with marked seasonal variation in temperature and moisture, led to the development of a geophytic habit. Seasonal climate changes favoured the development of growth patterns which enabled them to survive periods unfavourable to growth in a quiescent or dormant state (Rees, 1972). Flowering can occur annually or several times during the year depending on species and climate. Flowering time is related to cycles of dormancy and shoot emergence.

Most bulbous plants are adapted to a climate with hot, dry summers and cool, wet winters. Vegetative growth, followed by flowering, occurs in autumn, winter or spring, the bulbs being dormant in summer (Rix, 1983). This is the Mediterranean type climate found around the Mediterranean sea, Western Asia, Cape of South Africa, California and Western Australia. Other bulbous plants, however, grow and flower during summer where this season is hot and wet. Plants are dormant during the cool, dry winter. This type of climate is found in tropical and subtropical regions of central America and southern Africa.

Dormancy has been defined as the temporary suspension of visible growth in any plant structure containing a meristem (Lang, 1987). Where the physiological factors regulating the dormancy are within the dormant structure itself, the term 'endodormancy' is used, where outside the structure 'paradormancy' is the accepted term. Where environmental stress imposes the dormancy it is called 'ecodormancy'. A period of cold may be necessary to overcome dormancy and/or to initiate flowers. In *Narcissus* and tulip there is some physiological dormancy but it is comparatively shallow and easy to overcome (Kamerbeek *et al.*, 1972). A period of cold is necessary for completion of flower development and stem elongation. Tulips originate in the mountains of Asia Minor and the N.W. Himalayas. They require more chilling than *Narcissus* which is native to warmer Mediterranean regions.

Periodicity within the genus *Nerine* varies with species, each having become adapted to survival during unfavourable growth periods in their local environment. The genus, indigenous to S. Africa, has approximately 30 species. The predominant growth types are exemplified by the following. *N. sarniensis* grows in southern regions where summers are hot and dry. Foliage emerges in winter when rainfall predominates. Plants are said to be 'summer dormant'. Flowers emerge at the end of summer before foliage appears. In contrast, *N. bowdenii* and *N. undulata* grow in more northern regions where rainfall predominates in the summer. The plant is dormant in winter, foliage emerging in summer, flowers in autumn (Warrington and Seager, 1988). *N. flexuosa alba* grows in a region where conditions are hot and dry (Fortanier *et al.*, 1979; Warrington and Seager, 1988). Rainfall is evenly distributed throughout the year. Foliage appears year round in flushes with flowers emerging independently of this. *Nerine* species show 'ecodormancy' with water and temperature stress imposing a quiescent state. *N. sarniensis* dormancy is not strictly ecodormancy (Bertaud, 1990, personal comm.). Rising temperatures and drier conditions in spring may impose dormancy, but once imposed, it is overcome fastest by conditions unfavourable to growth, i.e. 30°C (comparative to chilling in winter dormant species). However, if kept too long at high temperatures, a transition to ecodormancy occurs, where a lower temperature is required for growth.

The genus *Hippeastrum* originates from central and southern areas of S. America. Experiencing little seasonal variation in temperature and moisture, plants are normally evergreen. However, some periodicity can be imposed by the environment either by lowering the temperature or withholding water (Rees, 1984) - another illustration of ecodormancy.

1.3.2 Ecology of *C. elatus*

C. elatus is recorded in the South-eastern Cape Province (see Fig. 1.2). Although rare, plants are seen along mountain streams in Tsitsikamma and Outeniqua mountains (Moriarty, 1982). The plant is abundant near the coastal town of George, above the tree-line on the south facing slopes of the Outeniqua mountains (Parsley, 1989, personal comm.). It is also found in the area of the Knysa forests (a rare remnant of native forest) growing above the tree line at a height of about 900 m above sea level. Year round rainfall and mountain mist enables the growth of a fairly lush vegetation on the south facing mountain slopes while on the northern slopes the climate is dry with predominantly xerophytic and succulent vegetation.

The vegetation in the region where *C. elatus* is found is mountain fynbos. This includes grasses and small shrubs growing to a maximum height of 5-6 ft. Although this vegetation provides some shelter from the wind, the cover is open. *C. elatus* is found growing in seepage areas with plentiful water and good drainage. Soil type is probably humus formed from recently decayed plant material.

The plants flower during the hottest part of the summer in January and February. Temperatures at this time typically reach a daily maximum of 25°C with short periods up to 30°C. Night temperatures fall to around 17°C. Growing on south facing slopes results in the plants being exposed to full sun at mid-day but being in the shade during the morning and also in the afternoon when temperatures are the highest level. Snow falls on the peaks of the mountains during the winter months, but only about once every five years on the slopes where *C. elatus* grows, although air temperatures may fall below freezing point (Swart, 1989, personal comm.). Plants are reported to be able to stand up to 6°C of frost (Redgrove, 1987).

Environmental stress appears to impose dormancy on *C. elatus*. As the plant experiences year round rainfall in its native habitat, temperature stress rather than water stress is most likely to be the most important environmental factor. Although like *Hippeastrum*, it is potentially evergreen, meristematic activity is slowed or temporarily suspended by low winter temperatures, a few leaves remaining but none emerging during winter (Parsley, 1987, personal comm.).

1.4 ENVIRONMENTAL PHYSIOLOGY

1.4.1 Effects of temperature

Temperature is usually considered the most important of environmental factors influencing growth and development of bulbous plants (Hartsema, 1961). Temperature is influential not only in the control of cycles or dormancy and shoot emergence as previously discussed, but appropriate temperatures may also be important for flower initiation and/or development, photosynthesis, vegetative growth and partitioning of food reserves. Flower quality may also be affected.

1.4.1.1 Floral initiation and development

Low temperatures are important for flower initiation in bulbous iris and Easter lily (Mediterranean species), while high temperatures are necessary for flower formation in *Eucharis* of tropical S. American origin. In other Mediterranean species, e.g. tulip, narcissus and hyacinth, temperature is important for flower emergence. South African species closely related to *C. elatus*, such as *Nerine* spp. and *Amaryllis* spp., unfavourable temperatures adversely affect flower development, while in *Hippeastrum* (S. American), which like *C. elatus* is evergreen, temperature affects the rate at which flowers are initiated.

Vernalisation is required for flowering to occur in bulbous iris (Rees, 1972) and Easter lily (Weiler and Langhans, 1968). Easter lilies do not flower when kept continuously above 21°C. However, all plants flower after 6 weeks at 7.2°C. Iris requires a period above 25°C followed by a period of below 13°C for floral initiation. In its native habitat dormancy is induced by summer temperatures above 25°C (Kamerbeek *et al.*, 1972). Such temperatures are necessary to ensure flowers will be initiated later (Rees, 1985). Subsequent low winter temperatures (9-13°C) are required for initiation to occur. In their native habitat flowers reach anthesis in the spring.

In contrast, *Narcissus*, *Tulipa* and *Hyacinthus* initiate flowers in the summer; they do not have a low temperature requirement for floral initiation. Optimum temperatures for flower initiation in *Narcissus* and *Tulipa* are between 17 and 20°C (Rees, 1972). Warm temperatures are required to complete floral organogenesis. Subsequent flower development in these species, however, does have a chilling requirement. Low temperatures (1-9°C for *Tulipa* and *Narcissus*, 9-13°C for *Hyacinthus*) are required to promote scape

and leaf elongation (De Hertogh, 1974). Further exposure to warm temperatures is needed for development of the flower to anthesis. A maximum of 20°C is better for tulip forcing in the greenhouse, 13-18°C is recommended for *Narcissus* and 23°C give optimum *Hyacinthus* development (De Hertogh, 1974).

Growing temperatures above 25°C result in flower abortion in tulip, daffodil and bulbous iris (Doss, 1986). Late flower abortion is seen in *Narcissus* where the bud fails to develop beyond the goose neck stage. This is related to excessively high greenhouse temperatures (De Hertogh, 1974).

Flower initiation in the genus *Nerine* appears to occur over a wide range of temperatures, unfavourable temperatures affecting flower development rather than initiation (Rees, 1985). *Nerine bowdenii*, originating in regions of cool dry winters, initiates flowers approximately 24 months before anthesis. Flower abortion occurs a year after growth at 25°C (Berghoef and van Brenk, 1983). Repeated glasshouse cultivation in the Netherlands decreases flowering percentages. Lower outdoor temperatures improve flowering. Temperatures above 21°C reduce flowering in the following growth period (i.e. more than 1 year later). Dissections confirm flower abortion occurs a year after growth at 25°C. Berghoef and van Brenk suggested that high temperatures result in increased competition between the vegetative apex and the developing flower buds, vegetative growth being much increased at high temperatures. At 25°C fewer flower primordia form within the inflorescence bud. Stamens and pistils also failed to form. Thirteen to 17°C provided the maximum level of flowering during the growing season (Berghoef and van Brenk, 1983).

Flower abortion occurs at low growth temperatures (c. 14°C) in *N. sarniensis* (Warrington *et al.*, 1989). A high proportion of aborted unemerged flower buds are found in the outer bulb position compared with very few at 22°C. High temperatures (above 25°C) during the late summer and autumn period result in delayed flowering until temperatures fall.

This work with *N. bowdenii* and *N. sarniensis* suggests that low flowering percentages due to growth at unfavourable temperatures is due to flower abortion rather than a failure of flower initiation. The difference in optimum growing temperatures for the two species reflects different environmental conditions of their native habitats. For floral initiation and development in *N. flexuosa alba*, 9-10°C is optimal (Fortanier *et al.*,

1979). No flowers result after growth at 17 and 21°C. Although *N. flexuosa alba* grows in hot dry regions, Norris (1973) in his description of the collection expedition, says that *N. flexuosa* was found deeply embedded in shale, growing on steep cliffs facing due south, receiving little direct sunlight and presumably was not adapted to warm winter soils.

Amaryllis belladonna, a native of S. Africa, is summer dormant like *N. sarniensis*, flowers appear before the leaves. Flowers are initiated in summer after the initiation of 8-10 leaf primordia and emerge during the autumn of the following year (Hartsema, 1961). Flowering in *A. belladonna* is influenced by dry storage temperatures. Hartsema found 23°C was optimum. A few flowers were initiated at 17°C but no flowers formed at 9, 13 or 31°C. It seems likely that 23°C treatment is similar to that experienced in its native habitat during summer.

The genus *Hippeastrum* includes 50-60 species of bulbous plants from S. America. Their distribution is from sub-tropical central America south to Brazil and Argentina (Rees, 1985). In an environment with little seasonal variation in temperature, plants remain evergreen, regularly producing four leaves and an inflorescence, occurring 3 times per year per bulb. Rees stated that this plant shows "autonomous induction" with inflorescences being produced at equal intervals throughout the year. Temperature, however, does influence flowering in *Hippeastrum hybridum* (Hyashi and Suzuki, 1970). High temperatures (28/23°C) promotes leaf growth but only 66% of potential flowers are initiated in the standard portion of the fourth leaf, 12% being formed after 5 leaves and 12% after six. Cooler temperatures (23/18°C) give better flower initiation. However, high storage temperatures (30°C) for 30 days gave a maximum number of leaves, daughter bulbs and flowering stems (Bose *et al.*, 1979). Lower temperatures (5, 10 and 17°C) had adverse effects on these characteristics. It appears that although this plant has the potential to produce flowers regularly after every fourth leaf has been initiated, the internal control mechanism can be modified by environmental influences.

Eucharis spp., like those of *Hippeastrum*, originate in tropical regions of central and southern America (Rees, 1985). *E. grandiflora*, the Amazon Lily, is evergreen with fragrant white flowers. Flower production in the Netherlands is influenced by temperature and time (Adams and Urdahl, 1971, 1973). Three weeks at 19.4°C is the threshold time/temperature for induction. Best results (89% plants flowered) followed 16 days at 29.4°C with 83% plants flowering after 21 days at 20.6°C. There were similar findings for *E.*

grandiflora by van Bragt and Sprengels (1983). Treatment of 4 weeks at 27°C followed by 90-95 days at 21°C gave 80-100% flowering (plants kept continuously at 21°C remained vegetative). It seems likely that high temperatures experienced in its native habitat trigger the flowering process so that flowers emerge after a subsequent period of cooler temperatures.

Cyrtanthus elatus flowers during the hottest part of the year in its native habitat (Parsley, personal comm.). In New Zealand it has the potential to produce 2 inflorescences per year (Warren, 1988). The main flush over summer is between December and March with a smaller flush in October.

Effects of temperature on flowering of *C. elatus* are not well documented. Growth temperatures of 14, 18 and 22°C were tested over a period of 2 years (van Nes and Vonk Noordegraaf, 1977). Bulbs were lifted and stored at 9°C over winter. The higher temperatures resulted in more florets per inflorescence (flowers/stem).

Low flowering percentages (60-80% for 12-14 cm bulbs) were reported of *C. elatus* grown under controlled temperature conditions (van Nes and Vonk Noordegraaf, 1977). Roberts, however, claimed 100% flowering from his field grown bulbs in New Plymouth (39.04° S Lat.) (personal comm., 1988). These were mature bulbs 11-15 cm circumference. Only 60% flowering was reported for smaller 10-12 cm bulbs from greenhouse grown plants (Auckland 36.52° S Lat.) (McKenzie, personal comm., 1988). It is difficult to make comparisons in these cases as factors other than bulb size and location are involved. Van Nes and Vonk Noordegraaf's bulbs were stored over winter with consequent root disturbance, while those of Roberts overwintered in the field. Van Nes and Vonk Noordegraaf also reported trouble with bulb rot (*Fusarium* sp). Other factors not monitored include planting density, fertiliser and irrigation regimes.

As *C. elatus* is potentially evergreen, like *Hippeastrum*, it is possible that flowers are initiated in a regular sequence at any temperature which permits growth. Temperature may affect subsequent flower development as in *Nerine* spp. with flower abortion occurring if temperatures are too high.

It is clear from these examples of plants described in this section that different stages of flower development from initiation to anthesis may have different temperature

requirements. These temperatures are different in different species, reflecting the different environmental conditions experienced in their native habitat.

1.4.1.2 Effect of temperature on photosynthesis

Both reproductive and vegetative growth of plants are affected by the availability of photosynthate. This may depend on current photosynthetic rate and/or on reserves in storage organs. Photosynthesis is affected by temperature in both bulbous and non-bulbous plants. In most plants temperature optima lie between 10°C and 35°C. For all plants this is a broad range; for each species it may be a narrow temperature band. Unfavourable temperatures may inhibit photosynthesis by adversely affecting photosynthetic apparatus (Berry and Björkman, 1980).

Higher plants show adaptation to particular habitats both in their temperature response and in their ability to function at temperature extremes. Desert species have higher optima than arctic species. *Tidestromia oblongifolia*, a C⁴ plant growing in hot areas, has a higher temperature optimum (ca. 45°C), than does *Atriplex glabriuscula*, a C³ plant native to cool areas. The temperature optimum for this plant is ca. 25°C (Berry, 1975).

Some plants show seasonal acclimation to temperature. Apricot in Israel has a higher temperature optimum in August (c. 38°C) than in March (c. 24°C) or September (c. 27°C) (Lange *et al.*, 1974). Plants from regions where temperatures vary considerably during the growing season tend to acclimate over a wider range of temperatures than do plants with relatively stable temperatures (Berry and Björkman, 1980).

C. elatus is likely to show some acclimation to temperature as it grows over a wide range of temperatures in its native mountain habitat.

Low temperatures during exposure to high light intensity can result in injury to chloroplasts (photoinhibition). This is due to the absorption of light in excess of that which can be utilised.

Temperature affects respiration rate, and the light compensation point (LCP). Changes due to temperature may be dependent on the genetic and adaptive features of shade tolerant and shade intolerant species (Grime, 1965). In the latter, high respiration rates result in a larger depression in photosynthetic rate. Depletion of carbohydrates at high temperatures should be more rapid in plants not adapted to shade.

C. elatus might be expected to show some shade adaptation. Growing on the southern side of mountain slopes in S. Africa it is exposed to sun mainly at mid-day, being in shade during other parts of the day.

1.4.1.3 Leaf growth

Temperature influences the rate at which leaves are produced. In timothy grass a leaf is produced every 9.3 days under glass c.f. 13.5 days outside (Humphries and Wheeler, 1963). Moderately high temperatures (mean 22.5°C) increase rates of leaf initiation in *N. sarniensis* (Warrington and Seager, 1988). There is a more rapid production of growth units at this temperatures compared with 20° (mean) and 10°C. Increasing temperatures (up to 25°C) result in more leaves in *N. flexuosa alba* (Fortanier *et al.*, 1979). Similarly development of tulip leaves is closely related to temperature - warmer spring weather results in earlier and faster leaf expansion (Rees, 1972). Leaf development was stimulated at 21°C (mean temperature) compared with 15.5° and 11.5°C in *Lilium longiflorum* (Wang and Roberts, 1983). Growth at 22°C resulted in more leaf production than 18° or 14°C in *C. elatus* (van Nes and Vonk Noordegraaf, 1977).

It is difficult to separate temperature effects on leaf growth from those on flower development as the latter may be dependent on the former. Tulip scapes and flowers are the strongest sinks for current photosynthate (Ho and Rees, 1975, 1976). Adequate leaf growth is necessary, therefore, for flower development. More rapid vegetative growth is associated with better flowering in the bulbous iris 'Wedgewood' (Rees *et al.*, 1987). Leaves develop first, utilising mother bulb reserves. Rapid inflorescence growth at emergence uses assimilate produced by the leaves, mother bulb reserves being depleted at this time.

There is, however, some evidence that leaf growth competes with flower development. The number of leaves initiated at 25°C in *N. bowdenii* was greater than at 21°C. The number of emerging flowers, however, was decreased at the higher temperature, due to flower abortion thought to be induced by competition with developing leaves (Bergheof and van Brenk, 1983). Similarly, high temperatures (25°C) delay flower initiation in *Freesia* while resulting in the initiation of more leaves at the apex (Berghoef *et al.*, 1986). High temperatures (mean 25.5°C) promoted leaf growth in *Hippeastrum* also (Hayashi and Suzuki, 1970), while bulb development and flower initiation were inhibited. At these high temperatures the number of leaves between flowers was increased in 34% of the bulbs, whilst mean temperatures of 20.5°C did not result in such an increase. Moderately high mean

temperature (22.5°C) did not affect numbers of leaves between flowers in *N. sarniensis* (Warrington and Seager, 1988) or in *C. elatus* (van Nes and Vonk Noordegraaf, 1977).

1.4.1.4 Partitioning

Temperature influences the accumulation of reserves in bulbs and hence affects dry weight.

Studies with *Narcissus* (Rees, 1972) show that after planting, the mother bulb loses dry weight until photosynthesis starts, when weight increases. The initial rate of dry weight loss is faster in warmer areas probably due to higher soil temperatures resulting in high respiration rates and greater use of stored material. Subsequent weight increase occurred earlier and more rapidly in warmer compared with colder climates.

In *N. sarniensis* bulb dry weight, but not diameter, was greater after growth at 14° than at 22°C. This was due possibly to a greater accumulation of reserves in leaf bases. bulbs grown at 30°C had reduced diameter and dry weight values compared with the lower temperature treatments (Warrington *et al.*, 1989). Similarly, bulb weight of *N. flexuosa alba* was less at 25°C than at lower temperatures, 13°C being optimal (Fortanier *et al.*, 1979).

Offsets develop in the axils of the leaf bases of many bulbs including *Nerine* spp and *C. elatus*. These bulbs develop independently when they reach the outer part of the bulb. Temperature affects numbers and dry weights of offsets. More offsets/mother bulb were produced by *N. sarniensis* growing at 22° than at 30° with similar numbers at 14° and 30°C (Warrington *et al.*, 1989). Total dry weights of offsets/bulb was lower at 30° than at 14° or 22°C. Seventeen degrees was optimal for bulblet production in *N. flexuosa alba*. Inhibition occurred at 25°C (Fortanier *et al.*, 1979).

1.4.1.5 Temperature effects on flower quality

Flower quality depends on such characteristics as stem length, flower size and shape, number of flowers/stem, flower colour and flower longevity.

Temperature affects stem length in a number of bulbous plants. Twenty two degrees results in longer stems than 14° or 30°C in *N. sarniensis* (Warrington *et al.*, 1989). Outdoor grown flowers of *N. bowdenii* have shorter stems than those grown under glass (Systema, 1975).

Low temperatures, normally experienced during winter in their native habitat, are necessary for stem extension in tulip, narcissus, iris and hyacinth, even though flowers emerge later, during warmer spring temperatures. Lower temperatures are required by tulip than for iris and hyacinth (de Hertogh, 1974) reflecting the different temperatures of their native environment.

Flowers of *C. elatus* emerging during cooler spring weather had shorter stems than summer emerging flowers (van Nes and Vonk Noordegraaf, 1977).

Temperature affects flower size in tulip (Dosser and Larsen, 1981). Growth at 26/22°C results in smaller flowers than at cooler temperatures (22/18° or 18/14°C). Cool optimal temperatures probably reflects spring time conditions in mountain areas where tulips originate. In *N. sarniensis* 22°C is optimum for inflorescence fresh weight. Thirteen and 30°C give smaller flowers (Warrington *et al.*, 1989). Flowers of *C. elatus* emerging in spring were smaller than those emerging during warmer late summer temperatures (van Nes and Vonk Noordegraaf, 1977).

Flower size is affected by temperature in some non-bulbous plants. Temperatures above 27°C result in smaller flower size in roses (Salinger, 1987). Kohl and Mor (1981) report that cool night temperatures (7.1°C mean) gave heavier chrysanthemum flowers than "normal" night temperatures (15.6°C min.). However, with hydrangea warmer temperatures (24°C) gave larger flowers than 18°C (Bailey and Weiler, 1984).

Flower life is reduced by higher temperatures. Such temperatures and consequent higher rates of respiration, lead to an increase in processes which lead to senescence of flower tissue, e.g. an increase in membrane permeability and leakage of ions (Halvey and Mayak, 1979). High rates of respiration lead to a rapid depletion of respiratory substrate, especially in cut flowers. It has been suggested that the respiratory substrate content of cut carnation flowers may indicate the potential keeping life of the flower at a specific temperature (Nichols, 1973). Hence the importance of supplying sucrose containing preservatives to cut flowers.

High temperatures increase the rate of production of endogenous ethylene, a hormone implicated in the control of flower senescence (Halevy and Mayak, 1981). There is a close correlation between endogenous ethylene production and senescence changes in petals of

Phalaenopsis and *Dianthus* (Woltering, 1989). A wide range of flowers is sensitive to ethylene, resulting in a decrease in longevity, plants responding with typical symptoms (Halevy and Mayak, 1981). Examples include 'sleepiness' (an inrolling of petals of carnation) (Nichols, 1968), fading and inrolling of *Ipomoea* petals (Kende and Baumgartner, 1974) and the fading of the petals of Vanda orchids (Akamine, 1963). Although the literature deals mainly with non-bulbous plants, the wide range of plants affected suggests that responses are general.

Temperature influences number of florets per inflorescence (flowers/stem) in some bulbous plants. More flowers/stem resulted from 2.5 months storage of bulbs of *N. flexuosa alba* at 21°C than at 13°C (Fortanier *et al.*, 1979). These treatments followed 8 months growth periods at 9° and 13°C. More flowers/stem formed in *C. elatus* when inflorescences emerged in late summer compared with those emerging in cooler spring weather (van Nes and Vonk Noordegraaf, 1977). In contrast, floret number per inflorescence was not influenced by temperature in *N. sarniensis* (Warrington *et al.*, 1989).

Temperature affects the synthesis and/or stability of both anthocyanins and carotenoids. These are pigments found in the corolla or many bulbous plants, including *C. elatus*.

Anthocyanidins are flavanoid compounds sharing a basic C₆ - C₃ - C₆ structure. They normally occur as glycosides known as anthocyanins. The actual colour of the flowers is dependent on a number of factors such as the pH of the cell sap, the presence of metal ions and co-pigmentation with other flavanoids (Halevy and Mayak, 1979). Colours range from red to blue.

High temperatures markedly decrease the stability of anthocyanins (Jurd, 1972). Red coloured spathes of *Zantedeschia* hybrids grown outdoors (10-19°C) have stronger reddish hues than those grown in heated greenhouses (12-22°C) (Funnell *et al.*, 1987). A higher content of anthocyanins was found in 'black petals' of outdoor grown 'Baccara' roses in winter compared with 'normal' red petals from greenhouse grown flowers (Zieslin and Halevy, 1969). Prolonged high temperatures decrease the anthocyanin content of flower buds and cause 'blueing' of petals of 'Baccara' roses (Biran *et al.*, 1972).

Carotenoid pigments give the orange colour to many flowers. Over 300 different carotenoids are known (Goldschmidt, 1980). The complement of pigments and hence the observed colour, differs greatly from species to species. High temperatures can inhibit carotenoid formation (Tomes, 1965). The colour of tomatoes and carrots comes largely from two carotenoids, lycopene and β carotene. (These and related pigments may well colour the petals of many bulbous plants). Temperatures above 25°C inhibit formation of lycopene and a number of other carotenoids (Tomes, 1965). High temperatures have similar effects on carotene content of other plants. Narcissus plants with orange coloured coronas develop more intense colour at low temperatures (Rees, 1972). Carotene content of 'valencia' orange rind increases substantially at a mean of 17°C compared with 22.5°C (Coggins *et al.*, 1981).

1.4.2 Effect of light

Plant growth and development is influenced by photosynthetic rate which is dependent on quantitative light energy. Photosynthate availability may affect not only vegetative growth of bulbous plants but also flower initiation, flower development and flower quality.

1.4.2.1 Photosynthetic rate

Short term photosynthetic response curves show rates increased linearly up to a light saturation point beyond which there is no further increase. The light saturation point of a single leaf does not determine maximum photosynthetic rate of the whole plant (Flore and Lakso, 1989). Outermost leaves may be light saturated but an increase in light intensity will increase the rate of photosynthesis of shaded leaves. Hence the light saturation point of a whole plant may be higher than that for a single leaf.

Many plant species can adapt to changing levels of photosynthetically active radiation (PAR). Adaptation has been shown to occur with changes in anatomy, morphology (Fails *et al.*, 1982a; Pass and Hartley, 1979) and in physiology (Fails *et al.*, 1982a; Pass and Hartley, 1979; Grime, 1965). Leaves of *Ficus benjamina* grown in shade are larger, thinner and flatter than those grown in full sun (Fails *et al.*, 1982a). Shade grown plants may have fewer but larger leaves, resulting in a similar light intercepting area. Average areas of young peach trees are increased 18, 30 and 20% by 36, 21 and 9% shade respectively (Kappel and Flore, 1983). Chloroplasts of shade grown *Ficus* leaves are larger and more irregularly dispersed, while chloroplasts of sun grown plants are aligned primarily along radial cell walls. Such anatomical differences appear to be mechanisms for increasing the collection of low light in shaded situations.

Adaptations to changing light intensity also occur at the physiological level. The irradiance at which photosynthesis balances respiration is called the light compensation point (LCP), and is lower for those species adapted to low light situations (Berry, 1975; Pass and Hartley, 1979).

McCree and Troughton (1966) proposed that gross photosynthesis per unit leaf area is the same for sun and shade grown plants, changes in net photosynthetic rates being due to a reduction in dark respiration. In white clover, decreasing the light intensity from 70 to 11 Wm^{-2} results in a 50% reduction in respiration rate. Changes occur within 24 hours which allow the adapted plants to grow at 10 Wm^{-2} . This light level is below the compensation point for unadapted plants (18 Wm^{-2}). Large decreases in dark respiration occur in *Ficus benjamina* (Fails *et al.*, 1982b) and in *Brassica actinophylla*, *Epipremnum aureum* and *Nephrolepis exaltata* during seven weeks acclimation to low light (Pass and Hartley, 1979).

There are structural and physiological differences in chloroplasts of plants adapted to low irradiance. Shade plants have a greater area of thylakoid membranes with more thylakoids per granum and a higher ratio of appressed to non-appressed membranes (Anderson *et al.*, 1988). On a weight basis, shade leaves have more chlorophyll, especially chlorophyll b, so that a/b ratios are lower. Conover and Poole (1979) found higher chlorophyll levels in *Ficus benjamina* grown under 60% shade than in plants grown under 30% shade. Light intensity increase results in changes in the electron transport components and in the cytochrome b/f complexes (Anderson *et al.*, 1988). ATP synthase activity is greater in sun-grown plants.

Compositional differences evoked by the sun/shade response result in variations in leaf photosynthetic capacity. In low irradiance, the light harvesting capacity of photosystems I and II increase, allowing maximum use of the limited amount of light striking the leaves. However, low light conditions do not require large amounts of electron transport components, ATP synthase and stromal CO_2 fixation enzymes. Under high light, however, such electron transport steps are limiting factors. Acclimation to full sunlight leads to changes resulting in faster rates of electron transport and photophosphorylation (Boardman, 1977; Anderson *et al.*, 1988).

Plants adapted to conditions of low light not only have lower LCPs but they saturate at much lower irradiances (Berry, 1975; Kappel and Flore, 1983). Shade plants grow slowly but

survive under conditions where unadapted plants are unable to photosynthesise effectively and can not compete.

Boardman (1977), concludes that the range of adjustment to low light intensity varies widely with different genotypes and reflects genotypic adaptation to light conditions prevailing in the native habitat. For example, clones of *Solidago virgaurea* from sunny habitats are able to photosynthesise at higher rates under high light intensity conditions, while clones native to shaded habitats are not capable of such adjustment (Björkman and Holmgren, 1963, 1966; Holmgren, 1968). At high light intensities sun clones show increase RuDP carboxylase activity and increased mesophyll conductance to CO₂. However, shade-grown clones grown under low light have a 27% higher photosynthetic efficiency at limiting light intensities than do sun clones. The greater efficiency of shade grown clones appears to be due to higher light use efficiency (Holmgren, 1968).

1.4.2.2 Light intensity and flowering

Reduction in light intensity, as a result of the use of shade cloth in greenhouses for example, may have a detrimental effect on various aspects of the flowering process.

Light is an important factor affecting successful flower development in a number of geophytes, including Easter lily (Einert and Box, 1967; Mastalerz, 1965), gladiolus (Schillo and Halevy, 1976) and bulbous iris (Mae and Vonk, 1974). In Easter lily 50% shade reduces flower initiation and increases flower abortion. Complete darkness results in a high rate of flower abortion, particularly at high temperatures. Light stress causes flower abortion in gladiolus. Flower abortion in winter in Israel is due to reduced PAR, daily sum irradiance being approximately 50% of that prevailing in summer. Bud abortion in bulbous iris also is common during winter forcing.

Light affects flower development in species of plants other than geophytes, including roses (Van den Berg, 1988), geranium (White and Warrington, 1988), African violet (Conover and Poole, 1981) and *Aphelandra squarrosa* (Heide, 1969). All elongating rose shoots have the potential for flower development (Halevy, 1985). There is a greater tendency for flower abortion in the low light of winter, increasing light intensity increases the percentage of flowering shoots (Cockshull, 1975; De Vries *et al.*, 1982). In geranium, flowering will not occur below a daily light integral of 3.3 mol-day⁻¹ m⁻². Flowering ceased in African violet after transfer from the greenhouse to low light conditions (Conover and Poole, 1981).

Interaction between light and temperature has been found in a number of plants. In Easter lily, high temperatures (within the range 15-24 °C) require higher minimum light intensity for successful flower development (Kamberbeek, 1969). Similarly, flowering in *Aphelandra squarrosa* is promoted by high temperatures under summer light conditions, but in low light (3,500 lux) flower initiation can take place only when temperature is low (Heide, 1969).

Temperature may affect the light compensation point. For example, a certain amount of light is necessary for flower formation in *Aphelandra squarrosa* but this requirement is reduced as temperature decreases. Reduced temperatures lower the respiration rate and the light compensation point with a consequent reduced demand on carbohydrate reserves (Heide, 1969).

Carbohydrate availability may be a limiting factor in flower bud survival. A developing flower bud is a relatively weak sink in its early stages of development (Ho and Rees, 1976). Growth rate and consequent carbohydrate demand are high, so the flower bud may starve if carbohydrate levels are low. In the short term, production of leaves rather than flowers would be of advantage.

In the tulip, certain minimum rates of starch degradation within the bulb scales are required before sucrose is translocated from the bulb scales to the shoot - a requirement for normal flower development (Hobson and Davies, 1978). Starch must be utilised at a rate exceeding 80 mg/bulb/day for satisfactory flower development during forcing. Injecting bulb scales with a compound CEPA, which inhibits sucrose translocation, induced tulip bud abortion (Moe, 1979).

Longer dark periods and higher temperatures increase the percentage of bud abortion in Easter lily. This may be due to greater carbohydrate depletion under these conditions (Mastalerz, 1965). At low temperatures the rate of bud development is slow and carbohydrate levels are adequate to prevent deterioration of immature bud tissue.

Although low light inhibits flowering of African violet, plants gradually acclimatise to low light intensity. This is highly correlated to new leaf production and may be due to increased carbohydrate availability (Conover and Poole, 1981).

In addition to effects on carbohydrate reserves, environmental factors also affect growth regulator levels. A number of plant growth regulators have been implicated in the flowering process, including GA₃, IAA, cytokinins and ethylene (Larsen, 1985). GA₃ and IAA hastened differentiation of floral primordia in *Gladiolus* (Tonecki, 1980) while kinetin retarded it. Flower abortion, however, was hastened in GA₃ treated plants grown under low light intensity. Higher levels of GA₃, cytokinins and auxin were found in glowering shoots of roses, while non-flowering shoots had higher levels of ABA (Zieslin and Halevy, 1976). Cytokinins applied to bulbous iris plants during dark treatment increase flowering percentages (Mae and Vonk, 1974). Foliar application of IAA, GA₃ and cyclocel increased the number and size of *Hippeastrum* flowers (Bose *et al.*, 1980).

Growth regulators play an important part in nutrient mobilisation and the establishment of sinks (Weaver and Johnson, 1985). GA₃, IAA and kinetin significantly affect the distribution of sugars and free amino acids in both under- and over-ground parts of *gladiolus* (Tonecki, 1980). This suggests that growth regulators may play a significant part in controlling responses to environmental factors, possibly via the distribution of metabolites.

The effects of CEPA were overcome by GA_{4/7} and/or kinetin in tulip (Moe, 1979). The growth regulators partially eliminated the CEPA-induced floral bud abortion. Moe concluded that the sink capacity of the flower bud is weakened by CEPA and strengthened by the GA_{4/7} treatment.

1.4.2.3 Light and flower quality

Some aspects of flower quality, including stem length and flower colour, are influenced not only by light quantity but also by light quality. The colour and/or form of a plant can be influenced through photomorphogenesis, the photoreceptor being a blue-green pigment called phytochrome. This pigment can exist in two spectral form Pr and Pfr. The inactive form (Pr) is converted to the active form (Pfr) when it absorbs red light. This induction is photoreversible, Pfr converts to Pr with far-red light. Phytochrome responses are characterised by red light induction and far-red reversibility (Kuhlemeier *et al.*, 1987). Hence red light is responsible for inducing the expression of genes controlling development.

Some photomorphogenic phenomena, referred to as high irradiance reactions (HIR), are controlled by prolonged illumination (Rau, 1980). There are two spectral regions with

high quantum efficiency - far-red light (wavelength = 710-720 nm) and blue-to-near-U.V. light (wavelength = 340-480 nm). Not all action spectra have a peak in the F.R. region, some have a maximum in the R part of the spectrum. Phytochrome is thought to be the receptor for the far-red and red regions (Rau, 1980), with cryptochrome and U.V.-B. photoreceptors absorbing blue and U.V. light respectively (Gilmartin *et al.*, 1990).

Effects of light quality on flower colour

Major pigment groups involved in flower colour are flavanoids and carotenoids. Rate of flavanoid synthesis is regulated by light as well as by temperature. Action spectrum studies for brief irradiation treatments indicate maxima around 660 nm with reversibility in FR (730 nm). This demonstrates some capacity of the low energy phytochrome system to control flavanoid synthesis. Continuous irradiation has shown peaks in the blue, red and far-red regions, indicating that the high irradiance reaction (HIR) system is also involved (Smith, 1972). High irradiance reactions are responses to long periods of high light intensity and depend on light quality and quantity (Cosgrove, 1986).

Light induces activity in phenylalanine ammonia lyase (PAL), an enzyme which regulates anthocyanin synthesis. A good correlation exists between PAL activity and anthocyanin accumulation (Grisebach, 1980). Light also stimulates the formation of PAL and there is some evidence that this may be a phytochrome mediated response (Walker, 1975).

Promotion of flavanoid synthesis by light is found in apples (Heinicke, 1966; Jackson *et al.*, 1971) and roses (Biran and Halevy, 1974). Anthocyanin synthesis in apple peel was one of the first systems used to show the action of phytochrome - red promotes and far-red suppresses production (Siegelman and Hendricks, 1958). The degree of exposure to sunlight of 'red delicious', 'Mc Intosh' (Heinicke, 1966) and 'Cox's orange pippin' apples (Jackson *et al.*, 1971) is directly related to colour development. Such results, usually attributed to effects of light intensity, may be related to differences in light quality, as light beneath a tree canopy is richer in far-red light (Smith, 1971).

Low light intensity during the period of maximum pigmentation (75% shade - 1.8 m W cm⁻²) results in the blueing of 'Baccara' roses (Biran and Halevy, 1974).

Anthocyanin production depends on the supply of sugars (Blank, 1958). Net photosynthesis may therefore affect anthocyanin synthesis. Blueing of rose petals was

associated with low concentrations of CO₂. High temperature induced blueing was reduced at high light intensities when CO₂ levels were increased. In low light, increased CO₂ levels did not reduce blueing (Biran *et al.*, 1972).

These findings suggests that low light reduced photosynthetic rate, and prolonged high temperatures increased respiration rate, both reduce sugar supply and that this limits anthocyanin synthesis.

Carotenoid synthesis is also photoregulated. Blue light stimulates formation in fungi (Rau, 1980). In *Sinapis* synthesis is thought to be mediated by phytochrome (Schnarrenberger and Mohr, 1970).

Work with tomato fruits suggests that phytochrome is involved with the synthesis of lycopene (Thomas and Jen, 1975). The accumulation of lycopene is induced by R and reversed by FR light. β carotene, the other major carotenoid present, reaches similar levels in both R and FR light, suggesting that phytochrome is involved in synthesis of lycopene but not of β carotene. A reduction in light intensity caused by heavy shading (60% and 80%) of *Leucospermum* by shade cloth, results in poor colour development (Jacobs, 1983). Flowers fail to develop the natural orange colour and are greenish in colour. This may be due to an effect on photosynthesis or possibly the HIR is involved.

The effect of low light intensity on colour development in flowers of *C. elatus* is important if pot plants are marketed at a stage prior to complete pigmentation of the perianth segments.

Scape length

Scape length is modified by light quantity and quality. Photosynthesis provides raw materials for growth but photomorphogenic pigments appear to modulate and control the growth processes.

Brief irradiation with red light inhibits scape elongation in many plants. This is reversible with far-red light, indicating the involvement of phytochrome. However, plants in natural environments are exposed to long periods of high intensity light. Scape growth responses are more striking compared with responses to brief irradiation. Such responses indicate involvement of the HIR system.

Scape length of a number of bulbous plants is affected by light. Einert and Box (1967) report that in USA, Easter lily, for example, there is a 20% increase in stem length with 50% light reduction. In *N. sarniensis*, 55% shade resulted in a greater increase in stem length than 33% shade (Warrington *et al.*, 1989). Tulips grown under a range of light intensities produced the longest stems in 37% full sunlight and shortest stems in full sunlight (Wassink, 1965, cited by Rees, 1972). Shorter stems resulted from 12% full sunlight than from 37% full sun. Rees (1972) suggests that stem length may be a compromise between available assimilates and the photomorphogenic effects. This idea is supported by similar observations made on *Caladium bicolor* (Conover and Poole, 1973). Shade levels of 0, 40, 60 and 80% were tested and found plant height greatest in the 60% shade treatment. Larger stem length with reduced light intensity has also been found in *Calendula officinale* (Armitage *et al.*, 1987), *Pelarganium hortorum* (Craig and Walker, 1963), *Gladiolus* spp. (Monselise, 1957), and *Zantedeschia elliottiana* (Funnell *et al.*, 1987).

In very low light and/or low temperatures the supply of photosynthate may be a limiting factor. A high rate of respiration at high temperatures will also reduce carbohydrate levels. Net photosynthetic rate is likely to interact with photomorphogenic effects. It seems probable that *Cyrtanthus elatus* will show increased stem length with moderate shading. However, too much reduction in light intensity or extremes of temperature may reduce growth owing to an effect on net photosynthesis.

Flower size

There is little information pertaining to effects of light on flower size in bulbous plants. Reducing photosynthetic photon flux density (number of photons (400-700 nm) incident per unit time on a unit of surface) from 695-315 $\mu\text{mol m}^{-2}\text{s}^{-1}$ had no influence on flower fresh weight of *N. sarniensis* (Warrington *et al.*, 1989). However, continuous light increased the diameter of hydrageas at 24°C but not at 18°C (Bailey and Weiler, 1984). A 4-fold increase in PAR increased total dry weights of chrysanthemums but only if supplementary light was applied during the long day treatment (Hickleton, 1984).

Flower life

There is little specific information on effects of light on longevity of flowers of bulbous plants. Reduced irradiance adversely affects flower longevity of Easter lily (Miller and Langhans, 1989). Preharvest low light conditions affect the postharvest behaviour of some cut flowers (Halevy and Mayak, 1979). Carnation and chrysanthemum flowers age

more rapidly if produced during periods of low light intensity. If cut flowers are supplied with sugars this effect can be abolished, suggesting that the preharvest low light conditions exert their effect by reducing carbohydrate levels.

Environmental stress imposed by low light levels may increase endogenous ethylene production (Tingey, 1980), thus hastening the onset of flower senescence.

Stress-induced ethylene may also result in bud or flower abortion, or in the shedding or petals "shattering" of pot plants. Most (83%) calceolaria flowers abscised when plants were placed in the dark for 4 days (Cameron and Reid, 1983). Only 22% of flowers abscised on plants treated with silver thiosulphate (STS), an ethylene action inhibitor (Beyer, 1976). Continuous lighting during storage of poinsettia plants results in lower leaf and bract abscission compared with plants kept in darkness (Scott *et al.*, 1984). The duration of dark storage on poinsettias was found to be important (Scott *et al.*, 1982).

Light intensity levels during production of cut flowers of *C. elatus* may be important for maximum flower longevity. Transfer of pot plants to the low light intensity of the retail outlet and home environment may result in early flower senescence or in bud or flower abortion.

Effect of photoperiod

Photoperiod is the duration of light within a 24 hour day/night cycle. Photoperiodism is the ability of a plant to respond differently to different photoperiods. The response of flower initiation results in flowers reaching anthesis during favourable times of the year. The two forms of phytochrome are involved, long and short day plants reacting differently to the Pr-P_{fr} balance, in order to produce the same flowering stimulus.

Flower initiation in bulbous plants has been reported to be unaffected by daylength (Hartsema, 1961). Flowers can be initiated out of normal times of the year in narcissus, tulip and iris without photoperiodic treatment (Rees, 1972), whilst in *Hippeastrum* flower initiation occurs regularly throughout the year. Photoperiod is reported to have no effect on flowering in *N. flexuosa alba* (Fortanier *et al.*, 1979). However, flower formation is influenced by photoperiod in some geophytic plants. Flowering in gladiolus is thought to be affected by both light intensity and daylength (Schillo and Halevy, 1976), flowering fails if daylength is too short, probably due to lack of current photosynthate. Long days facilitate

flowering in Easter lily (Bahadur and Blaney, 1968). In bulbous iris, however, if temperatures are high, long days result in bud abortion (Elphinstone *et al.*, 1986). In long photoperiods daughter bulbs are stronger sinks. At lower temperatures this photoperiodic effect is less obvious. This response ensures that flowering ceases before the onset of hot summer temperatures. Bulbing in iris is similar to that on onion, which is promoted by long photoperiods, the critical daylength decreasing as temperatures rise. Similarly, a combination of photoperiod and temperature, controls flowering in *Sternbergia clusiana* (Gutterman, 1990). Low temperatures and long days give higher flowering percentages and earlier flowering. This is of ecological importance, ensuring flowering occurs before the onset of the rains.

As in iris and onion, bulbing is increased by long days in tulip, narcissus and iris (Rees, 1972), rapid growth starting in early spring even though soil temperatures are low.

1.4.2.4 Light intensity and vegetative growth

Reduced photosynthate accumulation may result in lower bulb weight, a factor detrimental to successive crops. Bulb dry weight of *N. sarniensis* is reduced by 20-30% under 55% shade (Warrington and Seager, 1988). Weights of bulbs and offsets of *N. bowdenii* were lower after late planting compared with those planted earlier, probably as a result of lower light intensities during part of the growing period of the late planted bulbs (Systema, 1971). Light quantity is reported to have had only a little effect on growth of *N. flexuosa alba* (Fortanier *et al.*, 1979). More and longer leaves were produced in 8 h of light/day (113 J cm^{-2}) than in 16 h (226 J cm^{-2}). Bulb weight, however, was greater in 16 h light at temperatures below 25°C . After flowering tulip bulbs are completely replaced by daughter bulbs formed in the axils of old scale leaves. Weight of tulip daughter bulbs under 12% full sunlight was only 40% of bulbs grown under full sun (Rees, 1972), suggesting that daughter bulb weight is dependent on photosynthetic rates. Seventeen percent of starch in daughter bulbs is derived from the mother bulb, 83% from current photosynthesis (Ho and Rees, 1974). Dry matter accumulation of corms and leaves of gladiolus decreases with decreasing illumination (Monseliese, 1957). Shaded plants have a slower rate of leaf development.

Cyrtanthus elatus

Seasonal growth patterns in *C. elatus* may be somewhat different from those of *N. bowdenii* and *N. sarniensis*. In these plants rainfall, in addition to temperature, appears

to be an important influence on periods of dormancy which occur during dry seasons. *C. elatus* grows in regions where rainfall is plentiful year round. Cold winter temperature in the mountain habitat is likely to be the most important environmental factor influencing seasonal growth. Meristematic activity is slowed or temporarily suspended during winter, a few leaves remain, but none emerge at this time (Parsley, 1989, personal comm.).

The native environment of tulip may also be compared with that of *C. elatus*. Both plants experience winter cold, although in the mountains of Iran and neighbouring regions this is likely to be more intense. Physiological dormancy of the tulip is likely to be deeper than the ecological dormancy of *C. elatus*, requiring intense cold to overcome. Summers are hot and dry in Iran. Spring flowering and leaf growth is followed by the dying down of overground parts during summer, although flower initiation and some development occurs during this time. On the south-facing slopes of the Outeniqua mountains summer temperatures are not so high (mean = 25°C approximately) and water is plentiful. Plants of *C. elatus* flower in the summer, producing more than one inflorescence and leaf growth at this time. Most *Hippeastrum* species grow in regions with little seasonal variation and remains evergreen year round. *C. elatus* behaves in a similar manner provided temperatures remain high enough. It is possible that *C. elatus* may have evolved from species native to more equable climates.

Flower initiation occurs over a wide range of temperatures (9-25°C) in *Nerine* spp. in spite of seasonal variations in temperatures and moisture in their native habitat. It is known that *C. elatus* initiates flowers at 14, 19 and 22°C (van Nes and Vonk Noordegraaf, 1979) although effects of higher temperatures are not known. Temperatures above 25°C result in flower abortion in *N. bowdenii* with 30°C temperatures inhibiting flower emergence in *N. sarniensis* (Warrington and Seager, 1988). High temperatures are less likely to inhibit emergence of flowers of *C. elatus*. Flowers of *N. sarniensis* emerge in cooler autumn temperatures while flowers of *C. elatus* emerge during the heat of summer. Effects of high temperatures on flower abortion of *C. elatus* are not known.

The effect of low light intensity on flower initiation and development of *C. elatus* are not documented. Growing on the south facing slopes of mountains with some shade from surrounding vegetation, the plant is likely to show some shade tolerance. However, heavy shading, particularly if temperatures are high, might induce flower abortion or delay flower emergence, owing to low photosynthate availability.

Light effects on vegetative growth, owing to their effect on photosynthetic rates are likely to be similar to those of other bulbous plants growing in a partially shaded habitat.

C. elatus may well show some acclimation to temperature differences in relation to photosynthetic rates, as it grows over a wide range of temperatures in its native habitat (i.e. in spring, summer and autumn). Temperatures up to 25°C are likely to stimulate leaf production as these emerge during summer which may also stimulate bulb growth and offset production as these are dependent on photosynthate availability.

Low temperatures necessary for scape extension in tulip are not necessary for *C. elatus*. Tulip produces one flower each spring after experiencing low winter temperatures while *C. elatus* flowers in spring and later in summer. Summer-produced-flowers experience warm temperatures for several months before emergence so that a cold requirement for scape extension is unlikely.

Environmental effects on aspects of flower quality, e.g. colour, size and longevity, are not known. Colour and size are likely to be affected in a similar way to other bulbous plants, owing to the general nature of light and temperature effects on these characteristics. However, the longevity of summer produced flowers of *C. elatus* may be affected differently by temperature compared with spring flowering tulip, narcissus and hyacinth and with autumn flowering *Nerine* spp.

1.5 HORTICULTURE

From a horticultural viewpoint there are two possible niches for *C. elatus* - one as a pot plant, the other as a cut flower. Some qualities are desirable for both cut flower and pot plant production. These include production time, disease control, attractiveness of the flower and colour availability (Sachs *et al.*, 1976).

1.5.1 Production time

Relatively low production costs and consequent price of the marketable product, is important. This is affected partly by time necessary to obtain forcing size. *C. elatus* flowers in about 4 years from seed (Reid and Dyer, 1984). Daughter bulbs (offsets) normally flower

after two years (Warren, 1988). Tissue cultured explants purchased in October, grown under glass until the following February and planted outdoors under 30% shade, flowered during the following February (Sax, P., 1989, personal comm.). This production time compares well with some other bulbous plants, e.g. *Lilium* and hyacinth which requires 3-5 years of field production before forcing.

For *C. elatus* there may be no need for either daylength control, or chilling, both of which delay the production process.

1.5.2 Pest and Disease

The most serious pest of *C. elatus* is the Narcissus fly *Merodon equestris* (Roberts, E., 1988, personal comm.; Warren, 1988). In early spring the female lays its eggs in the neck of the bulb, the grub eats the bulb completely destroying the inside of it. Protection by the use of insecticides should begin before November in New Zealand. Greenhouse-grown plants need protection as insects fly through vents.

Another serious pest is thrips. Careful spraying into the crown of the plant is needed, particularly during bud emergence. Thrips inside the flower bud result in deformed blooms.

Stagonosporopsis curtisii is one of the main fungal diseases (Pennycook, 1989). Regular spraying, particularly in wet, humid conditions is recommended (Warren, 1988).

Infection by *Fusarium* spp. results in bulb rot (van Nes and Vonk Noordegraaf, 1977).

Virus

Narcissus mosaic virus is thought to be present in most plants in New Zealand (Pennycook, 1989).

1.5.3 Colour availability

Most cultivated plants of *C. elatus* have scarlet flowers. However, there are more rare white and delicate pink forms. Importation of these stocks into New Zealand and/or breeding to obtain more colour variety for this plant is desirable.

1.5.4 Pot plants

Qualities desirable for pot plants include foliage appearance and size, flower size and longevity, plus the ability to tolerate the low light of a wide range of interior environments.

The persistent foliage of *C. elatus* will give a year-round display, unlike periodic bulbs, for example tulip, narcissus and hyacinth. The dark green, strap-like leaves, however, may not be regarded as attractive by many people. The presence of numerous offsets may make the pot plant look untidy. These may be removed if repotting, although root disturbance is not recommended for members of this genus (Duncan, 1990).

For pot plants, height and diameter should be suitable for growth in a small container (Sachs *et al.*, 1976), a h/d ratio of 1:5 is recommended as 'ideal'. Leaf dimensions of *C. elatus* are said to be "rather variable" (Duncan, 1990). It is probable that this is light regulated. Environmental conditions might be manipulated to improve foliage dimensions. Inflorescence scapes are usually a little longer than the leaves so that flowers are displayed just above the leaves, a desirable quality in a pot plant. The effect on flower stem length in the low light of an interior environment needs investigation, as there may be some undesirable etiolation.

The attractiveness of flowers of *C. elatus* is unquestioned. The bright scarlet flowers would complement colour schemes of many rooms, particularly lounge rooms, studies or hallways. However, it is possible that flowers developing in a low light interior environment will not develop full colour or be reduced in size. The stage of inflorescence development at which plants are marketed may be important in this respect. Similarly, pot chrysanthemums sent to market before flowers are fully open are smaller than those maturing in the greenhouse (Crater, 1980). Poinsettias leaving the greenhouse with immature bracts require bright light to acquire full pigmentation (Shanks, 1980).

The number of florets which open concurrently is important for attractiveness of display. Mature bulbs produce inflorescences with 5-8 flowers/stem, usually 3 of these are open at any one time (Redgrove, 1987).

Flower longevity of *C. elatus* in an interior environment is not documented. Premature abscission of buds or flowers in low light may present a serious problem. Stress-

induced endogenous ethylene production may hasten senescence. The stage of inflorescence development at which the plant is marketed may also influence longevity. Transferrance of potted *Zantedeschia* plants to a post production room at a late, compared with an early, stage reduced flower longevity by 10 days (Plummer *et al.*, 1989).

1.5.5 Cut flowers

For high grade cut flowers, adequate stem length is important. The influence of shading on stem length of *C. elatus* needs investigation. Shading is known to increase stem length in a number of bulbous plants.

Information on vase life (longevity) of cut flowers of bulbous plants is relatively sparse (Doss, 1986). Variability in different studies may be due to different climatic conditions during growth and/or harvest time. Low storage temperature and the use of keeping solutions influence vase life of daffodil, tulip and iris (Doss, 1986) and will probably be effective for *C. elatus*.

1.6 OBJECTIVES

The main objectives of this research were to investigate bulb and flower morphology, to find the influence of temperature and light on growth, and to assess horticultural possibilities.

1.6.1 Morphology

The aim was to determine the pattern of primordial differentiation at the apex, to define stages in the development of the inflorescence from initiation to anthesis and to describe the morphology of the bulb and flower.

1.6.2 Environmental influences

The effects of temperature and light on flower initiation, flower development, flower quality and vegetative growth were to be investigated. As little is known about temperature requirements of this species, low (13°C), cool (17°C) and warm (21°C) temperatures were

examined initially. Similar temperatures were tested on *C. elatus* (van Nes and Vonk Noordegraaf, 1977) but little detail of growth was presented. The importance of low temperatures for flower initiation in Easter lily and bulbous iris, and cool temperatures for optimum development of the flower buds of *N. bowdenii* (Berghoef and van Brenk, 1983) were taken into account. Subsequently, higher temperatures (21°, 25° and 29°C) were required to determine the optimum for flower and vegetative growth. The influence of light on vegetative and floral development was investigated to determine if shading increased stem length and if there were any undesirable effects. Photoperiod influences are rare in bulbous plants and were thought to be unlikely to affect growth on *C. elatus* and were therefore not investigated.

1.6.3 Horticultural possibilities

The suitability of *C. elatus* as an indoor pot plant was assessed. Low light intensities of indoor environments may result in unattractive elongation of stems and/or in abortion/abscission of buds or flowers. The best stage of inflorescence development for marketing is also to be investigated.

CHAPTER 2

BULB AND FLOWER MORPHOLOGY AND INFLORESCENCE DEVELOPMENT

The aims were to investigate bulb and flower morphology, to determine the pattern of growth at the apex and to define the stages of inflorescence development from initiation to anthesis of the first floret. An understanding of the normal processes of the origin and development of the flower within the bulb is necessary to deal with many problems in the culture of bulbous plants (Beyer, 1942). A system for comparison of bulbous crops was developed by Beyer (1942) and this was used to compare *C. elatus* with other known bulbs. The terminology used was suggested by Beyer and used also by Salinger (1987) (Table 2.1).

Table 2.1 Symbols used for flower development in bulbous plants (From Salinger, 1987).

Stage symbol	Originating word	Stage of development
I	-	Leaf formation stage. Apex flat or slightly convex.
II	-	Apex becoming domed. Onset of flower formation.
Pr	Primordium	1st flower initial of inflorescence formed.
Sp	Spathe	Spathe leaf of flower or inflorescence formed.
Br	Bract	Bract initial formed.
Bo	Bracteole	Bracteole initial formed.
P ₁	Perianth	1st whorl of tepals.
P ₂	Perianth	2nd whorl of tepals.
A ₁	Androecium	1st whorl stamens.
A ₂	Androecium	2nd whorl stamens.
G	Gynaecium	Carpel primordia.
Pc	Paracorolla	Corona primordium.

2.1 MATERIALS AND METHODS

2.1.1 Experiment I: Bulb morphology and pattern of growth at the apex

Bulbs were dissected during the course of the experiments described in Chapter 3. Number of leaves formed before the first flower and in each growth unit and number of

inflorescence buds formed were noted. Information was recorded as drawings and/or photographs.

2.1.2 Experiment II: Development of the inflorescence

Apical meristems with inflorescence primordia were viewed as fresh samples with a binocular microscope, or were prepared for light or scanning electron microscopy (SEM). Meristems were fixed in glutaraldehyde (3%, v/v) with 0.1M phosphate buffer (pH 7.2), stained with osmium and dehydrated in a gradient acetone series. For light microscopy, specimens were infiltrated with acrylic resin, 1 μ m sections were cut with an ultramicrotome, mounted on glass slides and stained with toluidine blue. For the SEM, specimens (1 - 10 mm in length) were critical point dried, mounted on aluminium stubs, sputter coated with gold and examined with an SEM (Cambridge Model No. 250, Mark 3). Once inflorescences had emerged from the bulb they were dissected at various stages and recordings made in the form of drawings and photographs.

2.2 RESULTS

2.2.1 Morphology of the bulb

Bulbs of *C. elatus* were composed of leaf bases which enlarged to form food storage scales. Sympodial growth of leaves and inflorescences occurred from meristematic cells at the centre of the basal plate. The vegetative apex became reproductive at the end of a growth cycle. Further vegetative and floral growth was from a lateral bud which developed on the opposite side of the axis from the last leaf. The first leaf of the new growth cycle was a scale leaf which had its abaxial surface against the inflorescence (Fig. 2.1). Each growth unit was composed of 5 - 7 leaves and a terminal inflorescence. The last leaf of a growth unit had a half-sheathing base, all other leaves had a base which completely surrounded the growing point. The first leaf of the new cycle never bore a lamina. In the juvenile stage, 12 or 13 leaves were initiated before the apex became reproductive. Thereafter 6 or 7 leaves followed by an inflorescence were initiated and the growth cycle of the mature bulb was established. In older bulbs > 4.5 cm in diameter, 5 or 6 (rarely 7) leaves/growth unit were found. As young green leaves emerged from the centre of the crown, the outer leaf blades senesced, leaving the fleshy leaf bases. The storage materials in these leaf bases were gradually

withdrawn so they became brown and papery, forming the membranous tunic. Eventually they were sloughed away and rotted in the soil.

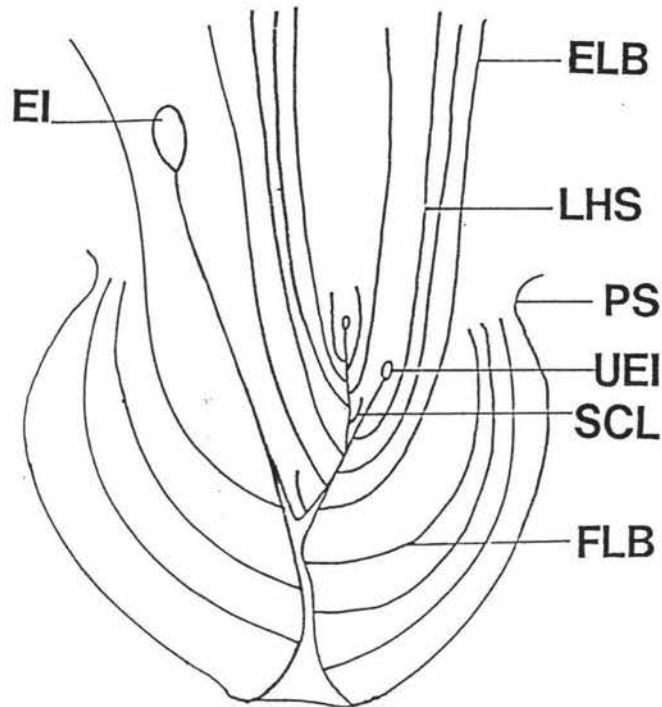


Figure 2.1 Diagram to illustrate the structure of a bulb of *C. elatus*. (Adapted from Rees, 1972). Papery scale (PS), fleshy leaf base (FLB), leaf with half-sheathing base (LHS), emerged leaf blade (ELB), scale leaf (SCL), unemerged inflorescence (UEI), emerged inflorescence (EI).

The structure of the bulb of *C. elatus* could also be described from bulb dissections. A typical bulb (4.0 cm in diameter) after flowering in March 1978, was dissected and described on 17 June 1988 (Table 2.2; Figs 2.2 and 2.3; Plate 2.1).

Offset 'buds' were visible in the axils of the older leaf bases. Leaves emerged from offsets while still enclosed by the outer leaf bases. Offsets are pushed off the basal plate as new leaves were initiated on the central meristem and became independent of the mother bulb.

The number of inflorescence buds in bulbs of *C. elatus* depended on bulb size (Fig. 2.4). Larger bulbs had more.

Table 2.2 Organs present in bulb of *C. elatus*. Numbering of organs commences from the outside of the bulb. Structures 7-13 (and 14-20) constitute a growth unit.

Organ number	Description
1	One papery leaf base (fully-circular).
2-4	Three fully-circular fleshy leaf bases with desiccated leaf blades.
5	One half-circular leaf base with emergent green leaf blade.
6	Inflorescence scape with withered inflorescence.
7	One fleshy, fully-circular scale leaf with no leaf blade.
8-11	Four leaves with circular fleshy leaf bases and emergent green leaf blades.
12	One leaf with half-circular base and emergent leaf blade.
13	One inflorescence bud and scape, 15 mm long with 2 white bract-like structures at the side.
14	One fleshy, fully-circular scale leaf - no leaf blade.
15-18	Four leaves with fleshy circular bases (leaf blades not yet emerged).
19	One half circular leaf base (leaf blade not yet emerged).
20	Inflorescence bud 1.5 mm long (+ 2 bract-like structures).
21	One fully circular scale leaf.
22-24	Three leaf initials. Innermost 0.2 mm long.

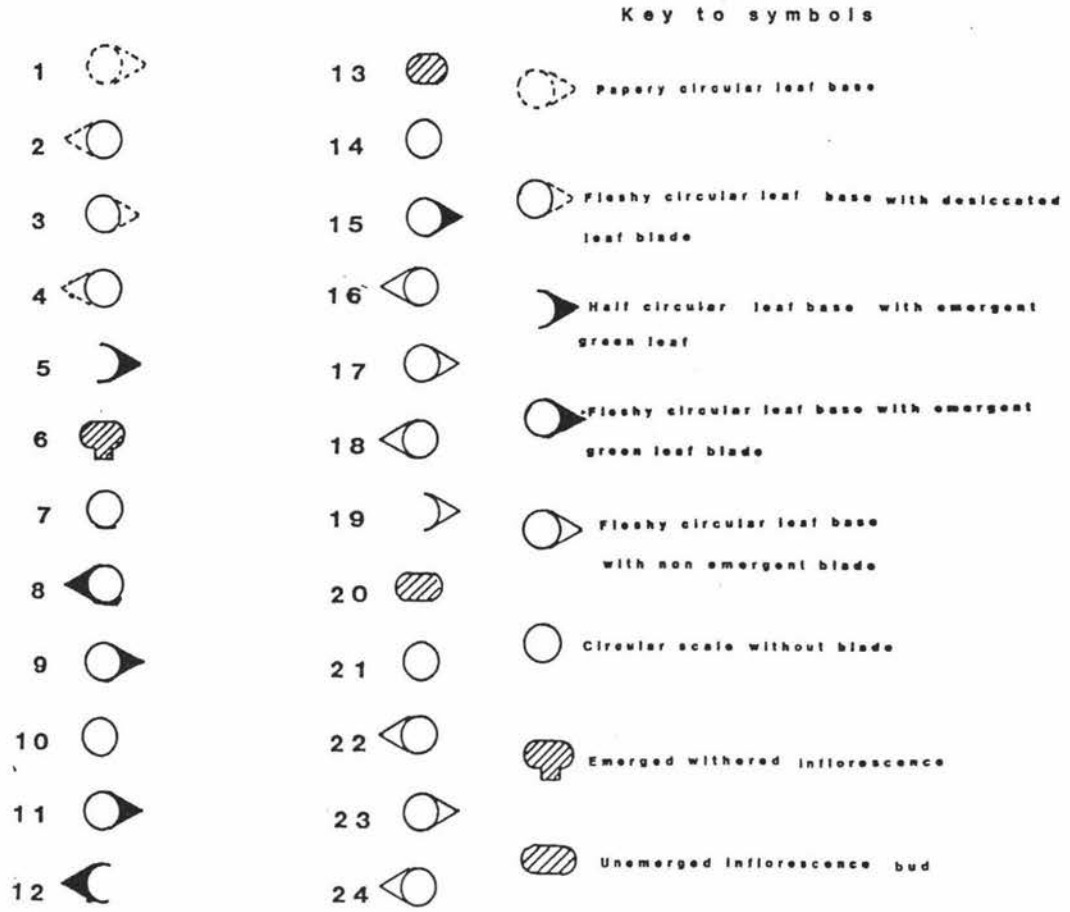


Figure 2.2

Diagram of organs present in bulb of *C. elatus*. Refer Table 2.2.

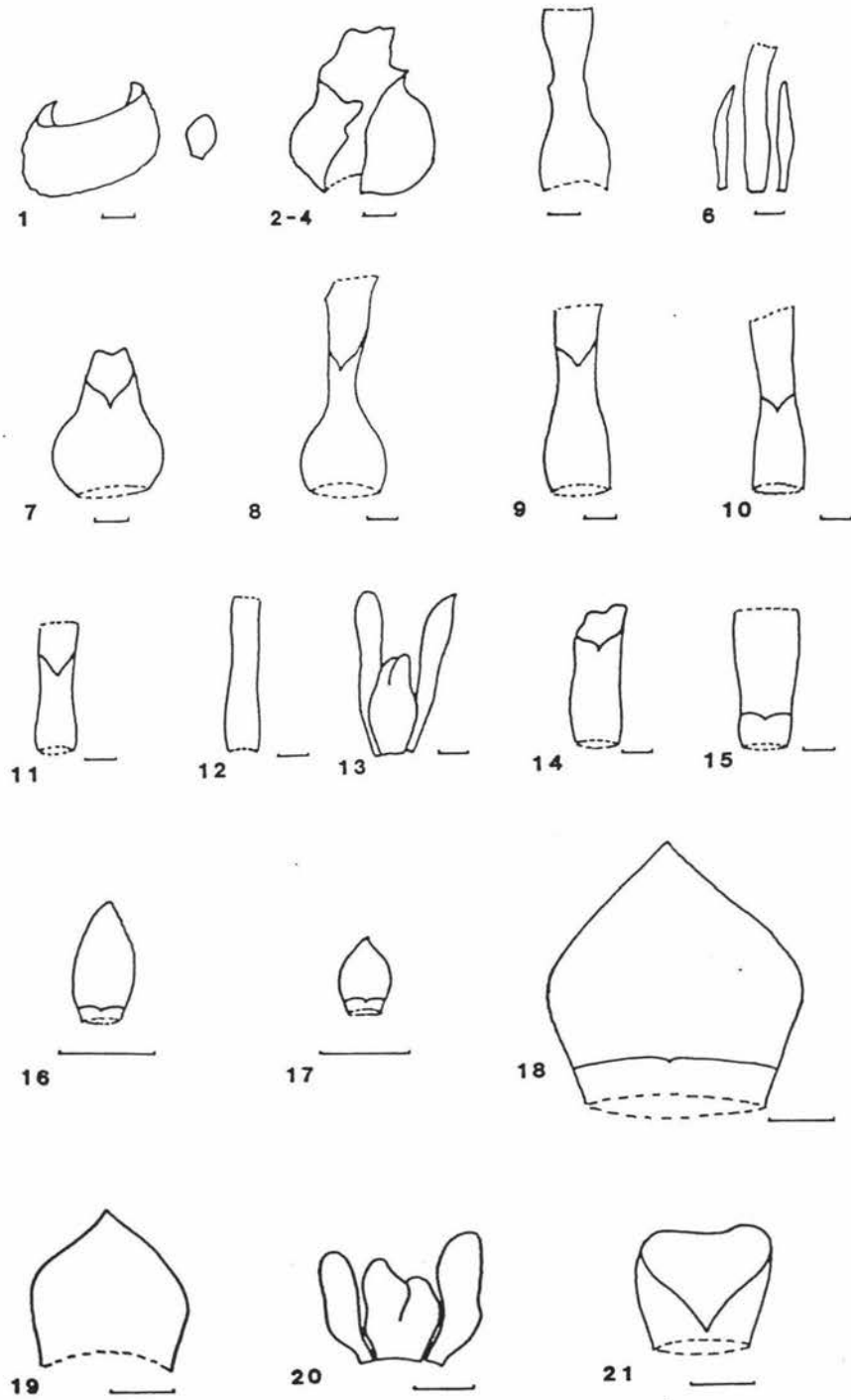


Figure 2.3

Organs present in bulb of *C. elatus*. Refer Table 2.2 and Fig. 2.2 (Organs 22-24 not shown in Fig. 2.3). Bar = 1 cm for organs 1-17. Bar 1 mm for organs 18-21.

Plate 2.1

Types of leaves and inflorescence bud of *C. elatus*. (a) Fleshy, fully-circular scale leaf with no leaf blade, (b) Leaf with half-circular base and emergent leaf blade, (c) Leaf with fleshy, fully-circular base and emergent leaf blade, and (d) Inflorescence bud with two adjoining bract-like structures.

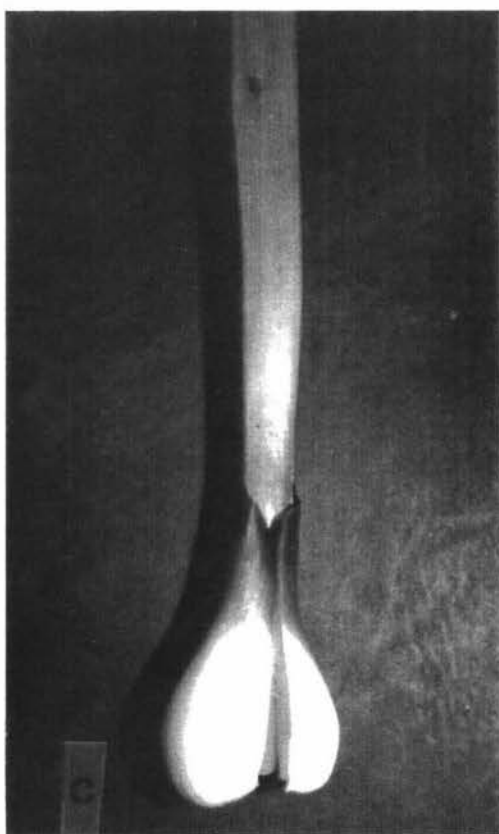
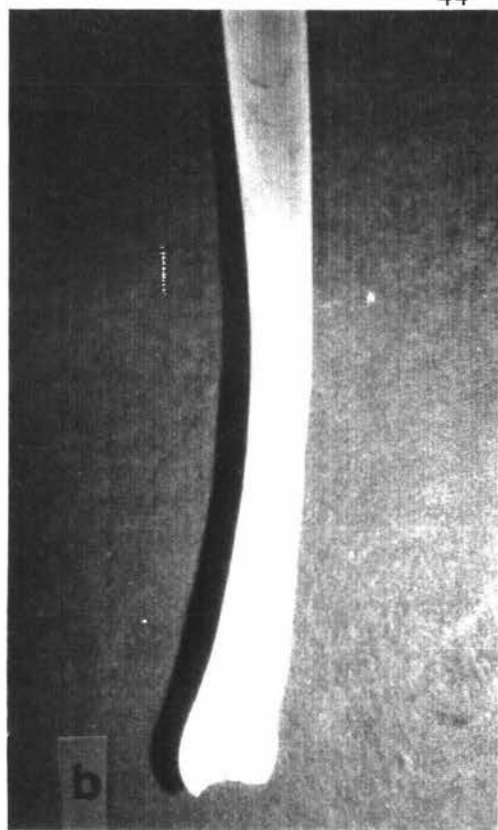
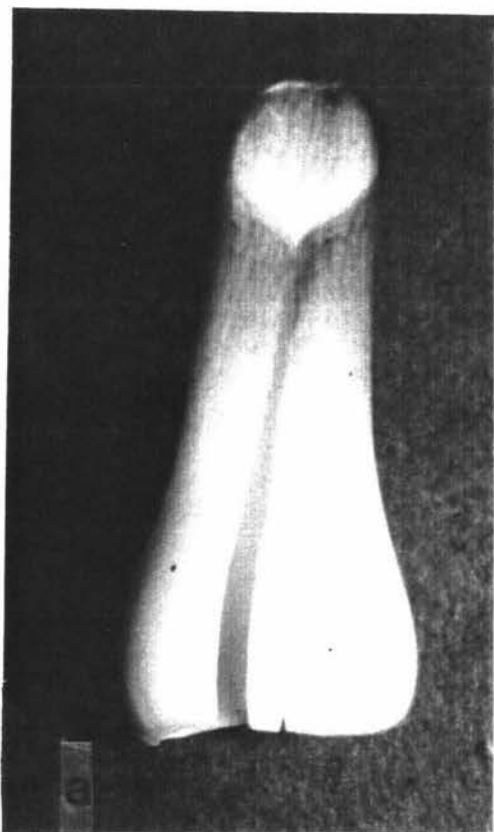


Plate 2.1

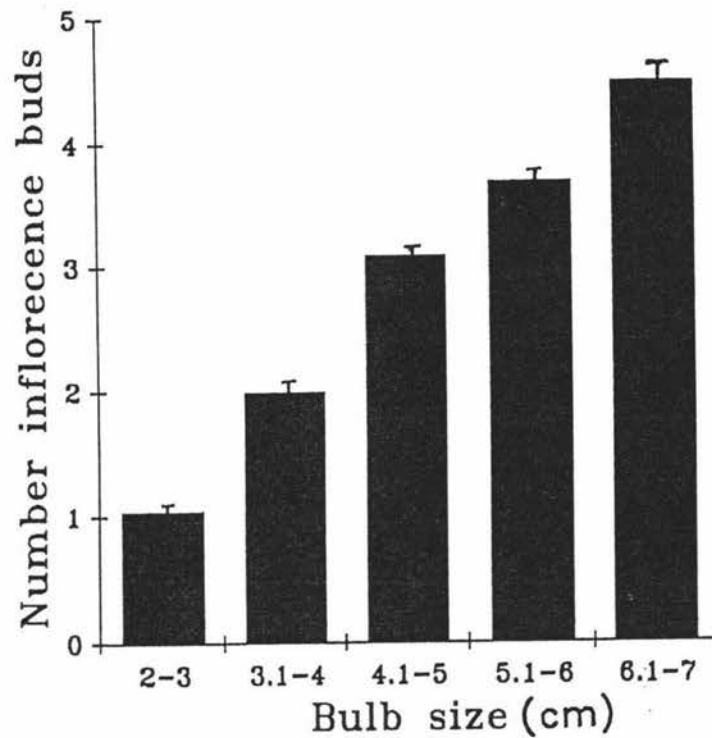


Figure 2.4 Number of inflorescence buds in relation to bulb size (diameter) of *C. elatus*.

2.2.2 Development of the inflorescence and flower morphology

Floral initiation

The vegetative apex became floriferous when the bulb had formed 11-13 leaves and was approximately 25-30 mm in diameter. The apex became more convex (Fig. 2.5, 1b) and developed lateral protrusions which were the spathe valve primordia. The spathe valves grew up and surrounded the apical dome (Fig. 2.5, 2). Florets developed from the apical dome. In Fig. 2.5, 4a two developing florets are shown. The three outer perianth segments (tepals) developed first (Fig. 2.5, 3a). The terminal regions were expanded and bore colourless multicellular glandular hairs. They appeared to interlock and their function was possibly to hold the tips of the outer tepals together. Inner tepals developed later towards the centre of the floral apex and were alternate with the outer tepals (Fig. 2.5, 3b). The staminal primordia formed next (Fig. 2.5, 4a, 4b). The carpel primordia were initiated towards the centre of the floral dome (Fig. 2.5, 5). The three carpel primordia united to form the gynaecium.

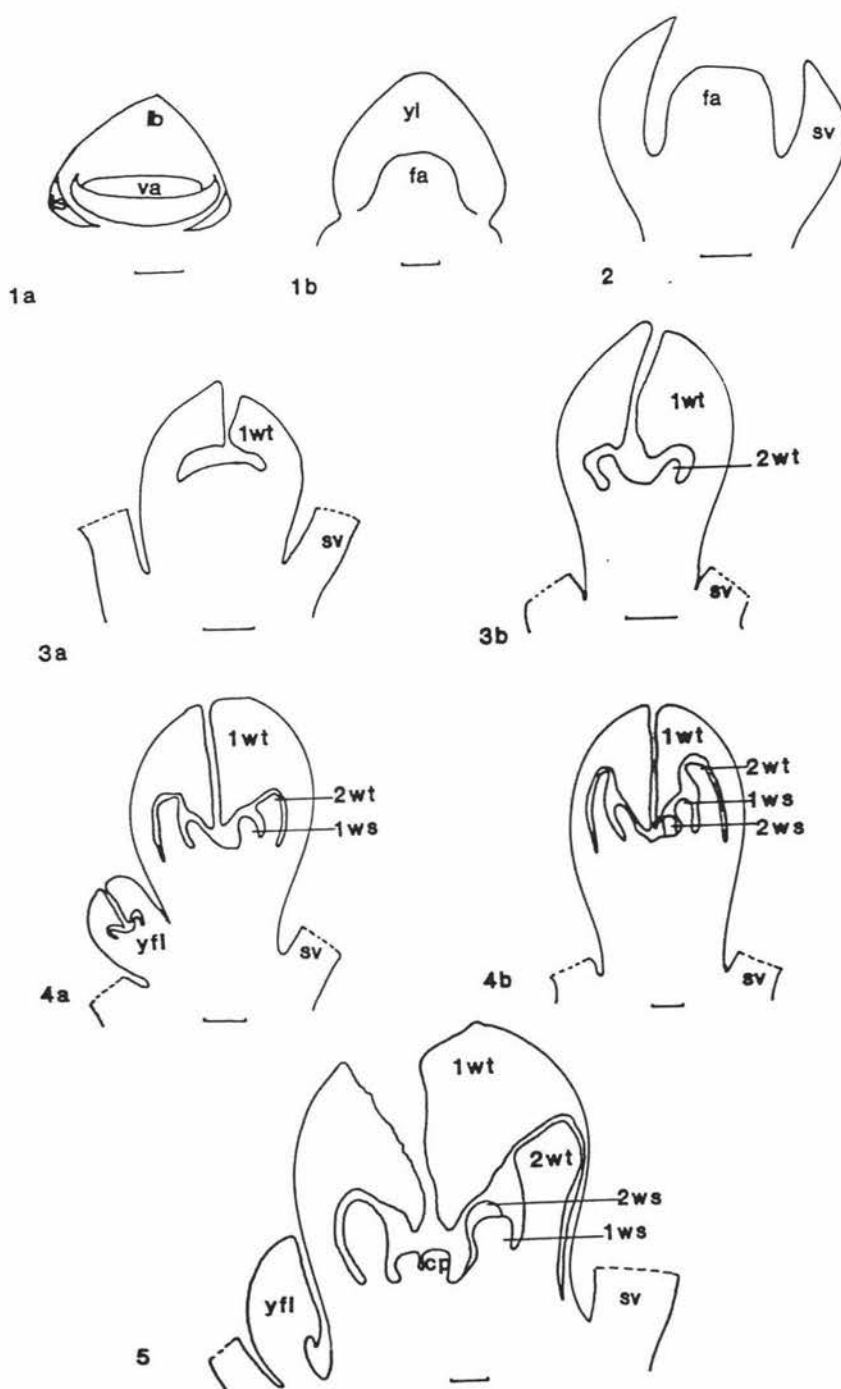


Figure 2.5

Stages of inflorescence development in *C. elatus*. Refer Table 2.3 stages 1-5. Leaf sheath (ls), leaf blade (lb), vegetative apex (va), youngest leaf (yl), floral apex (fa), spathe valve primordia (sv), first whorl tepals (1wt), second whorl tepals (2wt), first whorl stamens (1ws), second whorl stamens (2ws), younger floret (yfl), carpel primordia (cp). Bar = 0.2 mm.

Emergent inflorescence

The inflorescence bud (2-7 florets enclosed by 2 spathe valves) emerged when it was 25-30 mm long (Plate 2.2a). Figure 2.6a shows a half-floret from a macrobud, while Fig. 2.6b illustrates a more elongated floret from an inflorescence with a 10 cm scape (Plate 2.2b). The three stamens, united with the bases of the outer tepals, had shorter filaments than those of the stamens united with the bases of the inner tepals. (Figs 2.6, 2.7). The tips of the outer tepals bore glandular hairs concentrated on swollen, pad-like regions. Florets continued to enlarge as the scape grew in length. When the scape was approximately 20 cm long, the spathe valves separated and the oldest floret protruded and became pigmented at the tip. This was termed the 'Red-tip' stage (Plate 2.2c). Filaments were approximately 13 mm and the style 12 mm long (Fig. 2.6c). At this stage the glandular hairs at the tips of the outer tepals began to dry out and tepals were easily separated. Florets became fully pigmented 2 days later (Plate 2.2d). The style was then equal in length to the longest stamens (Fig. 2.7a). When the scape was approximately 30 cm in length the oldest flower reached anthesis (Plate 2.2e). The style was longer than the stamens (Fig. 2.7b). Florets reached anthesis in sequence as the scape continued to elongate a further 3-4 cm.

Description of the flower at anthesis

Florets were borne on pedicels 1.5 - 4.5 cm long attached to a scape (18-37 cm long). The perianth was erect, scarlet in colour and 7.5 - 10.5 cm long. The filaments of the stamens were attached to the perianth at the mouth of the tube and were 1-2 cm shorter than the segments. The three stamens attached to the base of the outer tepals were approximately 4 mm shorter than those attached to the inner tepals. The anthers were made up of four pollen sacs. They were fixed dorsally to the filaments and were approximately 10 mm long at dehiscence. The inferior ovary was approximately 10 mm long, triangular in transverse section (TS), with three locules and two rows of ovules in each locule. An inflorescence with one floret open is shown in Plate 2.2e.

Plate 2.2

Stages of inflorescence development in *C. elatus* after emergence. Refer Table 2.3, stages 6-10. a - e = stages 6-10, f = first signs of senescence of tepals.

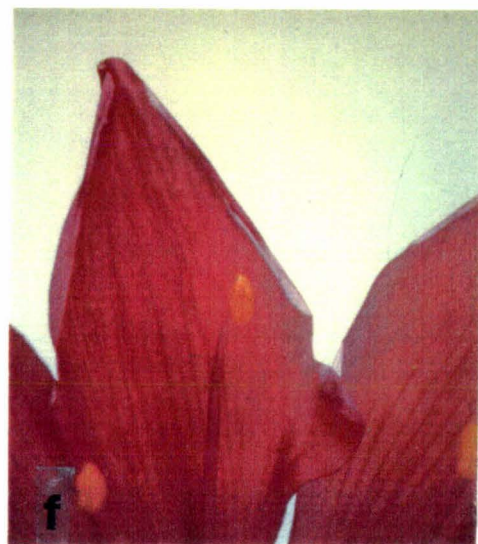


Plate 2.2

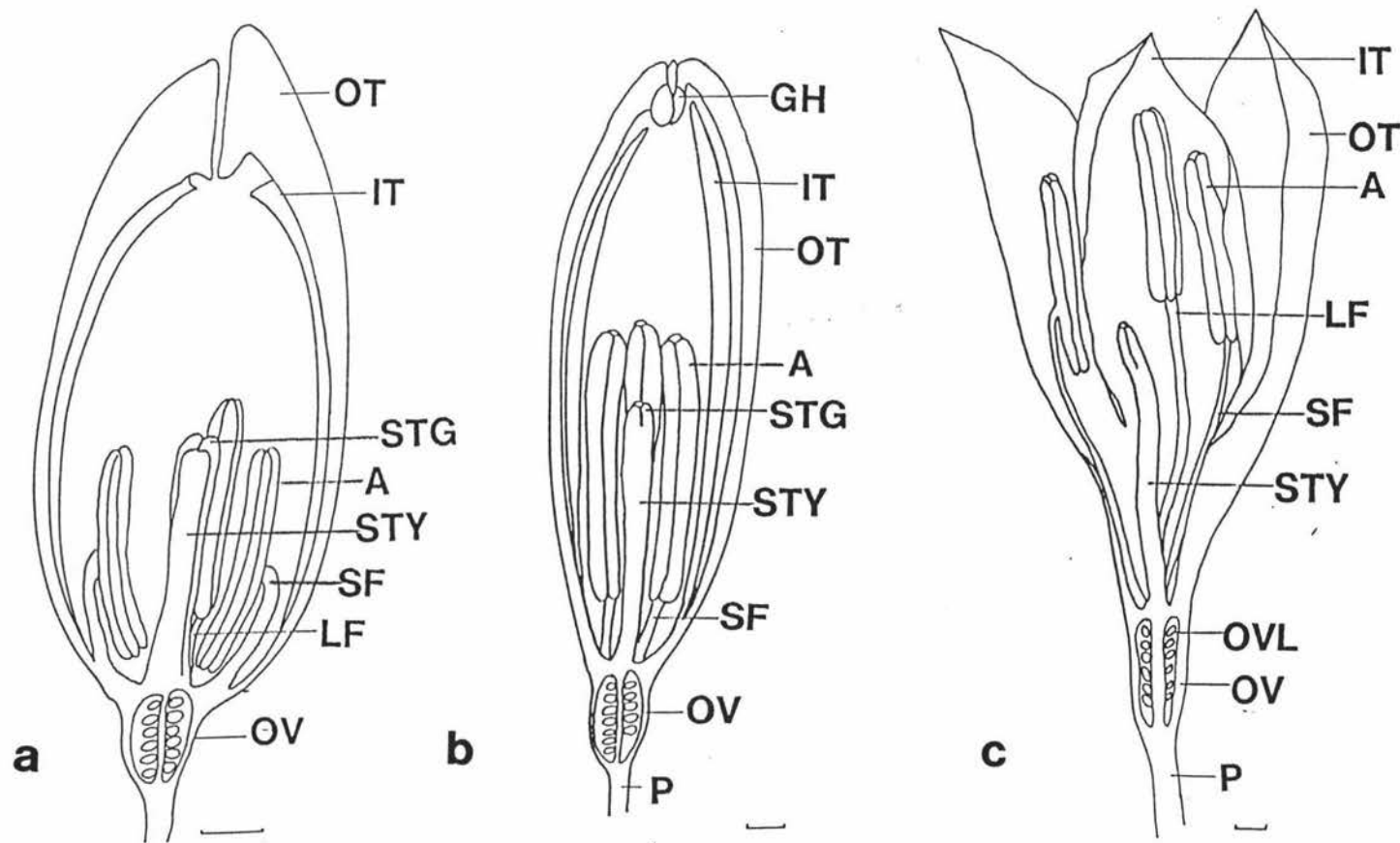


Figure 2.6

Stages 6, 7 and 8 of floret development in *C. elatus* after inflorescence emergence. Outer tepal (OT), inner tepal (IT), anther (A), short filament (SF), long filament (LF), stigma (STG), style (STY), ovary (OV), ovule (OVL), pedicel (P). Bar = 1 mm.

a = stage 6, b = stage 7, c = stage 8.

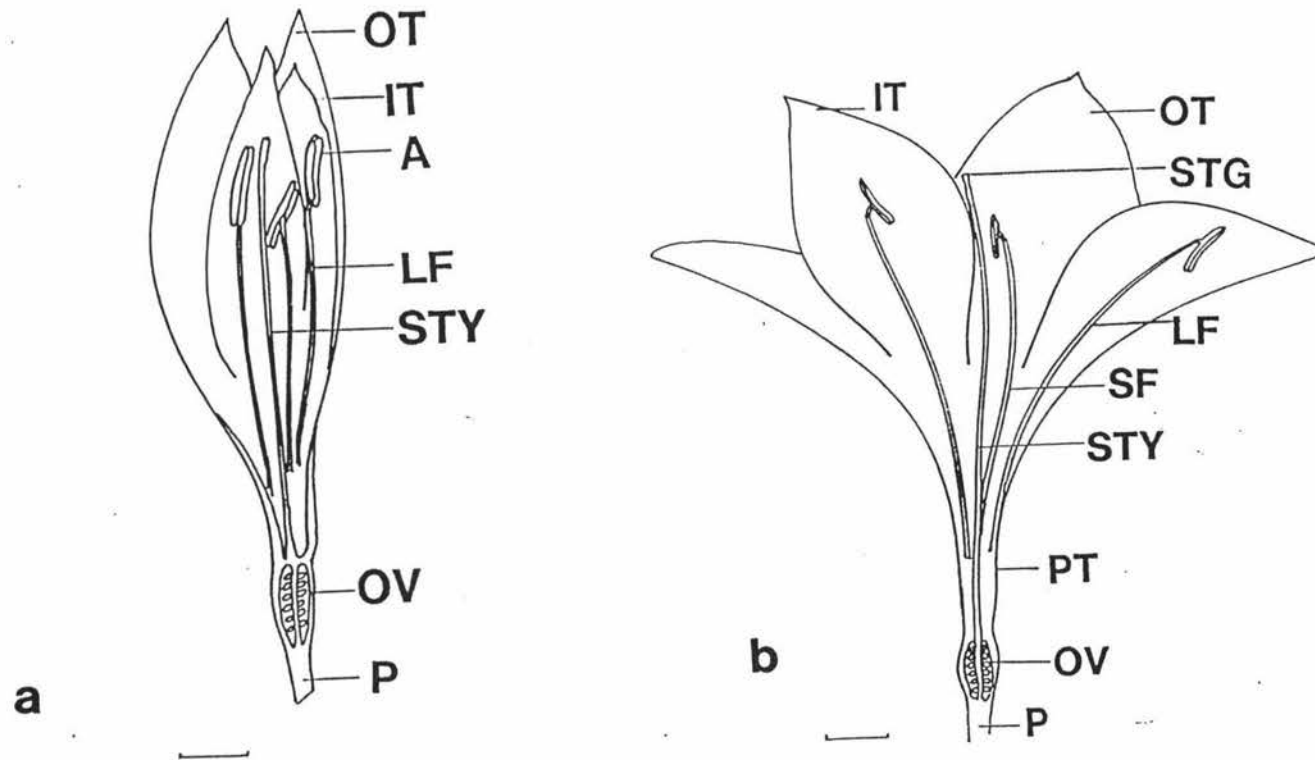


Figure 2.7

Stages 9 and 10 of floret development in *C. elatus*. Bar = 1 cm. Refer Fig. 2.6 for a meaning of labels.

a = stage 9 b = stage 10.

2.3 DISCUSSION

2.3.1 Bulb Morphology

Bulb structure has been defined only in commonly grown commercial cultivars. *C. elatus* had a bulb structure similar to other Amaryllidaceae including *Hippeastrum* and *Nerine*. It was not so similar to *Narcissus* (Fam. Amaryllidaceae) and *Tulipa* (Fam. Liliaceae).

Bulbs of *C. elatus* had much in common with those of *Hippeastrum*. Like *Hippeastrum*, *C. elatus* was evergreen, and leaves emerged in succession throughout the year. Bulbs were composed entirely of leaf bases and showed sympodial growth from the meristem at the centre of the bulb. The inflorescence buds were terminal. Growth was continued by a lateral bud initiated on the side of the axis away from the last leaf. The first leaf of the new growth unit had its abaxial surface lying next to the inflorescence bud (Fig. 2.1). In contrast to *Hippeastrum* however, this leaf did not bear a blade (Plate 2.1a). Growth units of *C. elatus* were composed of 5-7 leaves (5 being more common in larger, mature bulbs) and an inflorescence. Mature *Hippeastrum* bulbs usually have four leaves in each growth unit (Rees, 1972). As in *Hippeastrum*, the youngest leaf in a growth unit of *C. elatus* had a semi-sheathing base (Plate 2.1b), the bases of all other leaves entirely sheathed the growing point (Plate 2.1a and c). A number of growth units were present in mature bulbs, emerged leaves belonging to more than one growth unit (Fig. 2.1). The inflorescence emerged after the leaves of the same growth unit had senesced, so that it occupied a lateral position on the bulb (Fig. 2.1). This feature is seen in *Hippeastrum* also (Rees, 1972). *C. elatus* showed many structural similarities to *Nerine* spp. including *N. bowdenii* which had 5-10 leaves and an inflorescence in each growth unit. Like *C. elatus* (and in contrast to *Hippeastrum*), the first leaf of a new growth unit in *N. bowdenii* is a scale which does not bear a leaf blade. However, this scale leaf is quarter circular (Warrington and Seager 1988), while that of *C. elatus* was fully circular. The two flat, white, bract-like structures found on either side of the inflorescence buds of *C. elatus* (Plates 2.1d, Fig. 2.3, 13) are not described in other Amaryllidaceae although the scale leaf of *Nerine* spp. sometimes has this form (Bertaud 1990, Personal communication).

The number of inflorescence buds in mature bulbs of *C. elatus* (i.e. ≤ 5) was similar to *Hippeastrum*. *N. flexuosa alba* also initiates 4 or more flowers/growing season

(Fortanier *et al.*, 1979). These species originate in regions of year-round rainfall. *C. elatus* and *Hippeastrum* are evergreen while *N. flexuosa alba* produces leaves in growth flushes throughout the year with flowers emerging independently of this. In contrast, only two inflorescence buds/growing season are formed in *N. bowdenii*. The plants are dormant during dry winters, producing summer foliage and emergent inflorescences only in autumn.

The bulb morphology of *C. elatus* had some distinct differences from *Narcissus*. No special storage scales existed in *C. elatus* and more than one growth unit was formed each year by the apical meristem. *Narcissus* form only one bulb unit each year. This probably reflects the fact that *Narcissus* is a periodic bulb, producing leaves and flowers only in the spring.

The tulip bulb shows many differences from *C. elatus*. Not only does it belong to a different family (Liliaceae) but is a periodic bulb requiring winter chilling for completion of flower development and scape elongation (see 1.3.1). In the bulb centre is an axis bearing leaves and a single terminal flower. As the axis elongates, both leaves and flower emerge together. Emerged flowers thus occupy a central position in contrast to *C. elatus* where emerged inflorescences are lateral (Fig. 2.1). The replacement of the mother bulb of the tulip by daughter bulbs (being akin to the growth habit of cormous plants), contrasts with *C. elatus*, *Nerine spp* and *Hippeastrum* where offsets develop in the axils of leaf bases and gradually become independent of the persistent mother bulb. Offsets are pushed off the basal plate by the growth of new leaves on the central meristem.

2.3.2 Floral development from initiation to anthesis of oldest floret

A number of stages in the development of the inflorescence of *C. elatus* from initiation to anthesis of the oldest floret were identified (Table 2.3).

Flower development in *C. elatus* was comparable with other geophytes (Table 2.4). It was most similar to *Hippeastrum*, *Eucharis* and *Narcissus*, all members of the same family (Amaryllidaceae). Particular interest has been focussed on flower formation in *Eucharis amazonica* (van Bragt *et al.*, 1986). In *C. elatus*, as in *E. amazonica*, the youngest leaf formed before an inflorescence did not bear a sheath. Spathe valves formed at the base of the floral dome on which floret initials develop. Thereafter, floral parts were initiated in the same sequence in both plants (Table 2.4). Although bract and bracteole

initials were not observed in sections or in SEM specimens in this research, bracts were observed at the bases of the pedicels in older inflorescence buds. In contrast to *C. elatus*, *Narcissus* develops a paracorolla, a structure characteristic of the genus.

Table 2.3 Stages in development of the inflorescence of *C. elatus* from initiation to anthesis of the oldest floret. Refer Figs 2.5, 2.6, 2.7.

Stage	Description	Length of inflorescence bud	Length of oldest floret (pedicel not included)
1 a	Apex was vegetative	-	-
b	Apex became convex	-	-
2	Spathe valve primordia formed	0.5 mm	-
3 a	Outer tepal primordia of oldest floret formed	2 mm	0.8 mm
b	Inner tepal primordia formed	3 mm	1.1 mm
4 a	Outer whorl of stamen primordia formed	4 mm	1.3 mm
b	Inner whorl of stamen primordia formed	5 mm	2.0 mm
5	Carpel primordia formed	7 mm	2.5 mm
6	Macrobud. Inflorescence just emerged	25 mm	10 mm
7	Scape 10 cm long	33 mm	1.8 cm
8	Spathe valves separated Oldest floret red-tipped	-	3.0 cm
9	Oldest floret fully red	-	7 cm
10	Oldest floret anthesis	-	10 cm

Flower development in *C. elatus* was also similar to that of *Lilium* (Liliaceae) although spathe valves are not formed in the latter genus. Spathe valves which surround and protect developing florets are characteristic of the Amaryllidaceae. In *Lilium* and *Tulipa* (Liliaceae) this function is served by the outer tepals which remain green until just prior to the opening of the flower.

Table 2.4 A schematic survey of flower development in a number of bulbous plants. The corresponding stages are placed in the same vertical row (Adapted from Beyer, 1942) and numbers indicate order of development. Refer Table 2.1 for meanings of stage abbreviations.

Family	Genus	I	II	Sp	Pr	Br	Bo	P ₁	P ₂	A ₁	A ₂	G	Pc
Liliaceae	Tulipa	1	2	-	-	-	-	3	4	5	6	7	-
	Lilium	1	2	-	3	4	5	6	7	8	9	10	-
Iridaceae	Iris	1	2	-	-	-	-	4	5	3	-	6	-
	Gladiolus	1	2	-	3	4	5	7	8	6	-	9	-
Amaryllidaceae	Narcissus	1	2	3	-	-	-	4	5	6	7	8	9
	Hippeastrum	1	2	3	4	5	-	6	7	8	9	10	-
	Eucharis	1	2	3	4	5	-	6	7	8	9	10	-
	Cyrtanthus	1	2	3	4	5	-	6	7	8	9	10	-

Not all stages of flower development seen in *C. elatus* are present in *Iris* and *Tulipa*. A single flower rather than an inflorescence is formed and stages associated with inflorescence formation (i.e. Sp., Pr, Br and Bo - see Table 2.1) are missing. In *Iris* only one set of stamens develop. The developmental sequence also is different in the Iridaceae where stamen primordia develop prior to the perianth segments (Uhring, 1973; Cremer *et al.*, 1974).

CHAPTER 3

ENVIRONMENTAL INFLUENCES

Three experiments were set up in order to investigate the influences of temperature and light on flower initiation, flower development, flower quality and vegetative growth.

3.1 MATERIALS AND METHODS

3.1.1 Experiment III: Influence of temperature on floral and vegetative growth

Flowering sized bulbs of *C. elatus* expected to flower for the first time during the summer of 1988/89, were lifted on 16 May 1988. These bulbs had been raised in a greenhouse from tissue culture by Mr B. McKenzie from Topline, Auckland. The tops and roots were trimmed to approximately 5 cm and 4 cm respectively, dipped in insecticide, transported by air to Palmerston North in boxes of damp moss and stored in an outdoor garage until 25 May (temp. approx.: Max. = 20°C, Min. = 9°C).

The diameters of 150 bulbs were measured and means and standard errors were calculated. The bulbs were ovate in transverse section because off-sets form in one plane. The smaller transverse diameters were recorded.

A sample of (15) bulbs was dissected at time 0 (28 May 1988). The remaining 135 bulbs were soaked in 0.2 Ridomil for 10 minutes to control bulb rot and planted in 9.5 cm diameter, 8 cm deep plastic pots. A peat/pumice (80:20, v/v) mix was used in all experiments. This was supplemented with 200 ml m⁻³ Osmocote (long term), N:P:K:: 18:2.6:10, 100 ml m⁻³ Osmocote (short term), N:P:K:: 14:6.1:11.6, 300 ml m⁻³ dolomite and 60 ml m⁻³ Micromax.

Forty-five bulbs were randomly assigned to each of 3 treatment groups and placed in controlled environment (CE) cabinets at constant temperature with a 12 h photoperiod. The three treatment temperatures were 13 ± 1°C (treatment 1), 17 ± 1°C (treatment 2) and 21 ± 1°C (treatment 3) (Table 3.1). Light levels were measured at plant height at 5 different parts of the cabinet and means calculated. Mercury halide lamps were separated from plants by a water and glass layer. These bulbs are referred to as the first set of bulbs in the results and discussion. Bulbs (5) were dissected at 28 day intervals during the course of the experiment (28 May 1988 - 3 March 1989).

Table 3.1 Photosynthetic rates of *C. elatus* under various environmental conditions. (Mean $\pm$ s.e). PAR was measured at 1 pm at plant height over 10 days in Feb-March.

Location	Temperature ($^{\circ}$ C) Feb/Mar			PAR ($\mu\text{Mm}^{-2}\text{s}^{-1}$)	Photosynthetic rate ($\mu\text{MCO}_2\text{m}^{-2}\text{s}^{-1}$)	Daily mean temp. ($^{\circ}$ C) Greenhouse Feb/July Outdoor Feb/May
	Min.	Max.	Daily mean			
Greenhouse shade	17.6 $\pm$ 0.2	31.7 $\pm$ 0.7	24.6 $\pm$ 0.3	324.3 $\pm$ 37.2	7.3 $\pm$ 0.8	22.3 $\pm$ 0.2
Greenhouse No shade	17.6 $\pm$ 0.2	32.7 $\pm$ 1.1	25.1 $\pm$ 0.5	785.3 $\pm$ 100.6	15.8 $\pm$ 1.6	22.5 $\pm$ 0.3
Outdoors shade	13.2 $\pm$ 0.9	28.7 $\pm$ 1.1	21.0 $\pm$ 0.6	613.9 $\pm$ 71.9	13.3 $\pm$ 1.9	16.5 $\pm$ 0.9
Outdoors No shade	12.9 $\pm$ 0.8	29.9 $\pm$ 1.2	20.9 $\pm$ 0.7	1251.1 $\pm$ 146.2	17.6 $\pm$ 0.1	16.9 $\pm$ 0.8
CE ¹ cabinet			17 $\pm$ 1	740 $\pm$ 8.3	8.2 $\pm$ 1.1	
CE cabinet			21 $\pm$ 1	736 $\pm$ 10.4	10.6 $\pm$ 0.6	
CE cabinet			25 $\pm$ 1	722 $\pm$ 9.2	14.0 $\pm$ 0.5	
CE cabinet			29 $\pm$ 1	704 $\pm$ 11.2	10.4 $\pm$ 1.0	

¹ CE = Controlled environment

A further trial involving a second set of bulbs at higher temperatures was later carried out. This was done because it became obvious that the optimum growth temperature had not been reached. On 8 October 1988, one hundred bulbs were received at Massey University, sent by Mr Andrew Warren of "Bloomers Ltd", Tauranga. Mr Warren had received these plants ex tissue culture from "Topline Nurseries", Auckland, in March 1987. They were grown in a greenhouse in polystyrene trays until summer 1987/88, when they were transferred to outdoor soil conditions under 30% shade. They were lifted and sent to Massey University on 7 October 1988.

The bulbs were measured and planted as above. Bulbs were placed in a greenhouse (Temp.: Min. = 18 $^{\circ}$ C, Max. = 30 $^{\circ}$ C) until 13 January 1989, when CE cabinets became available. A sample of bulbs (4) was dissected and the remaining plants were randomly assigned to the following treatments:-

12 plants in 21 $\pm$ 1 $^{\circ}$ C (treatment 3)

37 plants in 25 $\pm$ 1 $^{\circ}$ C (treatment 4)

37 plants in 29 $\pm$ 1 $^{\circ}$ C (treatment 5)

Light was measured at plant height (Table 3.1). Other conditions were as per the earlier experiment.

Table 3.2 Temperature conditions over time of inflorescence emergence (7 April - 14 July). (No flowers emerged in shade). Mean $\pm$ s.e.

Location	Temperature (°C)		
	Min.	Max.	Daily Mean
Greenhouse	17.2 $\pm$ 0.1	25.8 $\pm$ 0.3	21.5 $\pm$ 0.2
Greenhouse shade (50%)	17.2 $\pm$ 0.1	25.9 $\pm$ 0.3	21.5 $\pm$ 0.2
Outdoor	7.5 $\pm$ 0.2	18.5 $\pm$ 1.0	13.0 $\pm$ 0.9
Outdoor shade	8.1 $\pm$ 0.9	18.3 $\pm$ 0.9	13.4 $\pm$ 0.8

A sample of bulbs was dissected from each treatment every 28 days during the course of the experiment (13 January - 12 July 1989). Three bulbs per sampling time were dissected from treatment 3 to confirm previous results and 5 per sampling times from treatments 4 and 5.

Measurements were taken at each sampling time. These included the smaller transverse diameter of the bulb, numbers of leaves initiated between inflorescence buds in the bulb, total number of leaf initials formed after the oldest inflorescence bud, number and length of inflorescence buds and numbers of green leaves which had emerged since the start of the experiment. Dry weights of main bulb, together with roots and leaves and separate dry weights of offsets bearing leaves, were also recorded. (Plant materials was dried at 60°C for 48 hours.)

As the inflorescences emerged, measurements were made at anthesis on pedicel length, flower width and flower length (Fig. 3.1). Scape length was measured daily.

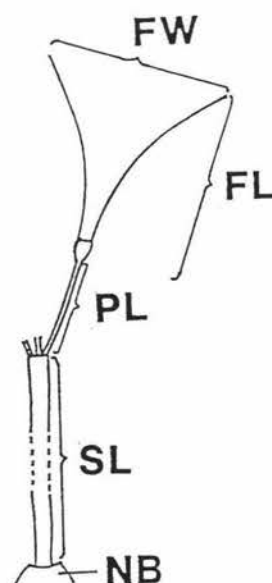


Figure 3.1 Measurements taken on emerged inflorescences of *C. elatus*. Flower width (FW), flower length (FL), pedicel length (PL), scape length (SL), neck of bulb (NB).

Colour of flowers was measured using a chromameter (Minolta chromameter C.R.100). Readings were taken from each tepal at anthesis of the oldest flower of the inflorescence. The area measured was in the centre of the upper surface of the tepal. A chromameter was used in order to eliminate human judgement. Quantifying a colour gives an objective valuation. The L.a.b. system was used, where the output from the chromameter was measured in terms of the lightness/darkness factor (L), the red-green factor (a) and the yellow-blue factor (b), a:b ratios were calculated (Fig 3.2). L.a.b. values are not independent variables and so analyses of data were not carried out (Francis, 1980). Differences in mean values were linked with visible colour and lightness differences.

The life of florets of each inflorescence was recorded. Life was defined as the number of days between anthesis (first sign of pollen shed) and senescence (defined as visible signs of darkening around the edge of tepals). The life of the oldest floret was not recorded as slight damage from the chromameter resulted in premature closing of the floret.

On 13 March 1989, net photosynthetic rates were measured on the youngest leaf longer than 10 cm on plants in treatments 2, 3, 4 and 5. The instrument used was a Li-Cor portable photosynthesis system (Model LI-6200).

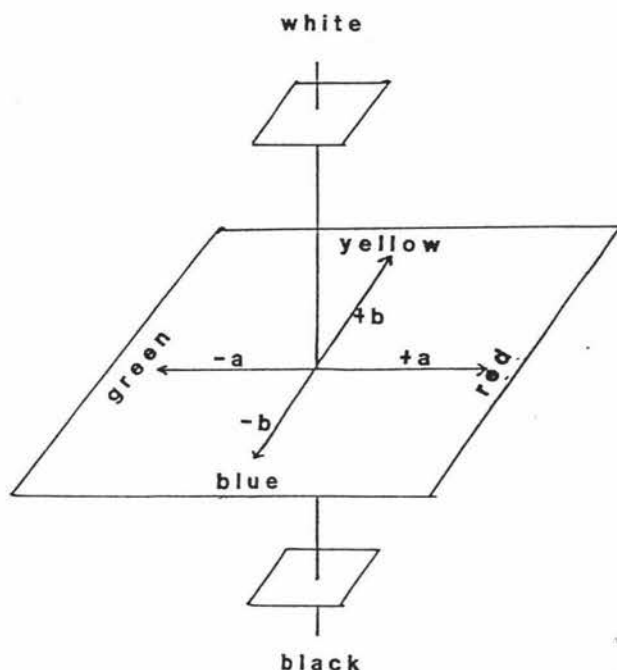


Figure 3.2 Illustration of L.a.b. colour space. L is the lightness/darkness factor, a is the red-green factor, b is the yellow-blue factor.

3.1.2 Experiment IV: The effect of shade and growing environment temperature on growth and flowering

C. elatus bulbs grown commercially for flower production by Mr E. Roberts of New Plymouth were received at Massey on 20 October 1988. The bulbs were mature and had flowered previously. They were soaked in 0.2% Ridomil for 10 minutes and planted in Size 5 Epic PB5 black polythene planter bags. Dasanit, a systemic insecticide (0.3 g/plant bag), was added to the medium to control attack by the Narcissus fly. Plants were irrigated by a capillary watering system.

On 25 January 1988, 84 vegetative plants (i.e. not flowering) were selected for uniformity and randomly assigned in groups of 21 plants to each of four growing environments. Plants were placed in shade and without shade in both a greenhouse and outdoors. In each of the four treatments were three blocks each of seven replicates. The shaded blocks were interspersed with the non-shaded so that no shading occurred on the non-shaded blocks. Shade was provided by enclosing the plants in wire-framed structures covered with shade cloth (50% light reduction). The enclosures were 92 cm high. Other dimensions were 60 cm x 82 cm.

Light intensity, PAR and maximum and minimum temperatures for each growing environment were recorded in February/March (Table 3.1), when plants usually flower in New Zealand (Mr E. Robert's personal communication). Flowering was delayed until April/May in the greenhouse and until June/July outdoors. Therefore daily maximum and minimum temperatures were also recorded during a 16 day period during these months (Table 3.2). Daily mean temperatures were calculated for the greenhouse plants over Feb/May. The low temperatures of winter were not included in calculating the mean over the 6 month period for outdoor plants as relatively little growth might be expected to take place during that time. On a clear sunny day (11 March 1989) rates of net photosynthesis were measured on the youngest leaf longer than 15 cm on each plant. As flowers emerged, measurements were made on scapes, pedicels and flowers as described in Experiment III. Twenty bulbs were dissected at the beginning of the experiment and all bulbs in the treatments were dissected at the conclusion of the experiment starting on 25 July 1989. Measurements included bulb size, root and shoot dry weights, number and dry weights of offsets, number and sizes of inflorescence buds and numbers of leaves initiated within the bulbs.

3.1.3 Experiment V: The influence of post-production environment on flower quality

Sixty vegetative plants of *C. elatus* grown from mature bulbs, supplied by Mr E. Roberts of New Plymouth, were randomly allocated to five treatments and left to grow in a heated greenhouse (Max. 35°C - Min. 17°C). Treatments were the five stages of flower development at the time of transfer to a simulated home environment room (Fig. 3.3). Plants were transferred at stage 6 through to 10. Measurements were made on all inflorescences as described in 3.1.1.

Temperatures were maintained at $20 \pm 2^\circ\text{C}$ with a relative humidity (RH) of $75 \pm 10\%$. Spectral balance was achieved by use of cool white fluorescent tubes with a diurnal cycle of 12 hours day, 12 hours night. Light intensity in the room at the level of the plants on the bench was 12.67 W m^{-2} .

A few plants with inflorescences at stage 6 were placed in complete darkness at a mean temperature of $21 \pm 2^\circ\text{C}$.

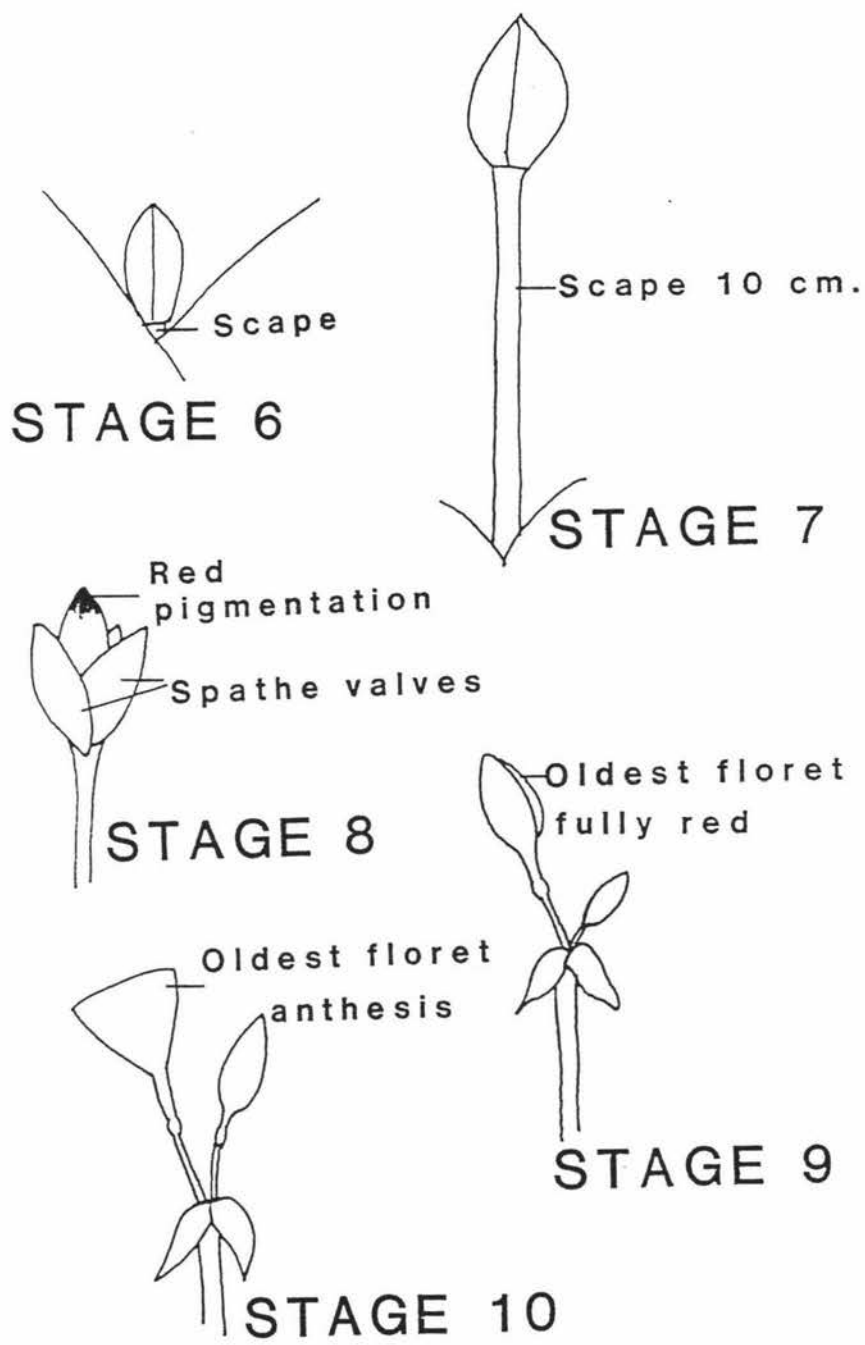


Figure 3.3 Stages of inflorescence development for transfer to a simulated home environment room.

3.2 RESULTS

3.2.1 Experiment III: Influence of temperature on floral and vegetative growth

3.2.1.1 Flower initiation

Flowers were initiated over a wide range of temperatures (13-29°C). Rates of flower initiation were dependent on temperature (Fig. 3.4). In the constant temperature treatments rates were slow at temperatures below 21°C (Fig. 3.4a), but were optimal and similar from 21-29°C (Fig. 3.4b).

3.2.1.2 Flower development

Temperature influenced the development of flowers to anthesis. Flowers continued to develop over a wide range of temperatures but the period between initiation and emergence extended with temperatures away from 25°C.

Growth of the inflorescence bud within the bulb was greatly affected by temperature. Growth at 13°C was very slow, with growth at 21°C being greater than 17°C (Fig. 3.5a). In the second set of bulbs, growth rates for 3 waves of flowering were determined. Rates were similar between temperature treatments (21-29°C, Fig. 3.5b) in the first wave, were slower for 21°C in the second wave (Fig. 3.6a) while 25°C was optimal in the third wave (Fig. 3.6b).

3.2.1.3 Flower quality

Temperature influenced scape and pedicel elongation. Greater elongation occurred under moderate to warm conditions (21-25°C), compared with high (29°C) temperatures (Figs 3.7a, 3.8a). No flowers emerged from small bulbs (3.4-4.5 cm diameter) grown under constant 13° and 17° C conditions, but comparisons of scape and pedicel elongation were made with outdoor, winter-grown, large bulbs (4.5-6.5 cm diameter) where flowers emerged.

Flower size was affected by temperature, with 21°C being optimal for the development of large flowers (Fig. 3.9a). Floret longevity was reduced by increased temperatures (Table 3.3). The number of florets per inflorescence, however, was not influenced by temperature (Table 3.4) but was affected by bulb size. Larger bulbs had a greater number (Table 3.5).

Figure 3.4

The influence of a) low, b) high temperature on the time taken to initiate inflorescences of *C. elatus*. Days = days from planting. Symbols represent the means of 5 replicates.

- = a) 13°C b) 21°C
- △ = a) 17°C b) 25°C
- = a) 21°C b) 29°C

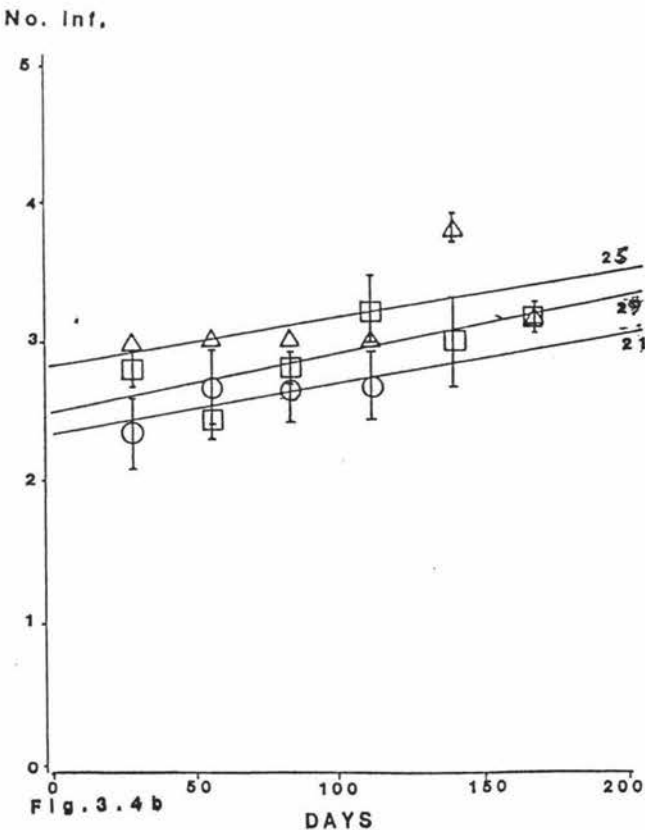
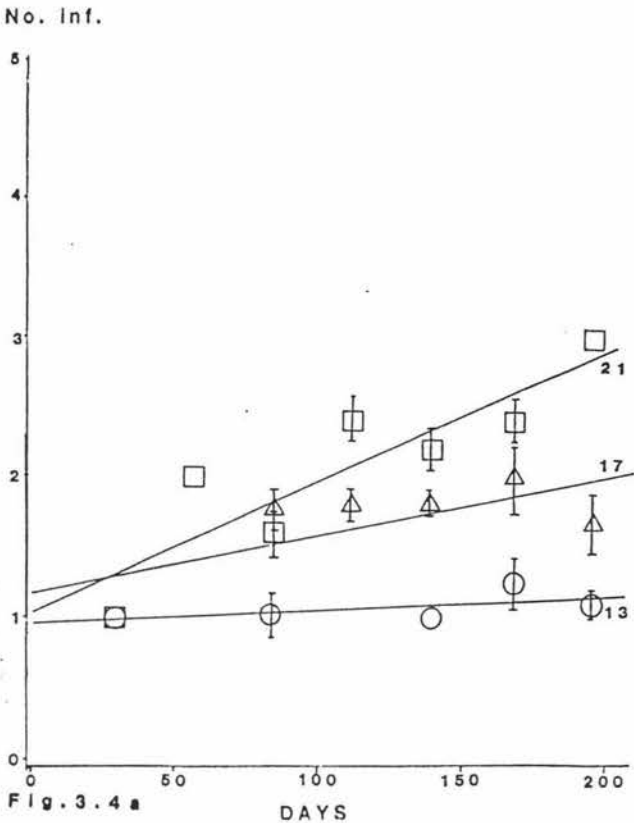
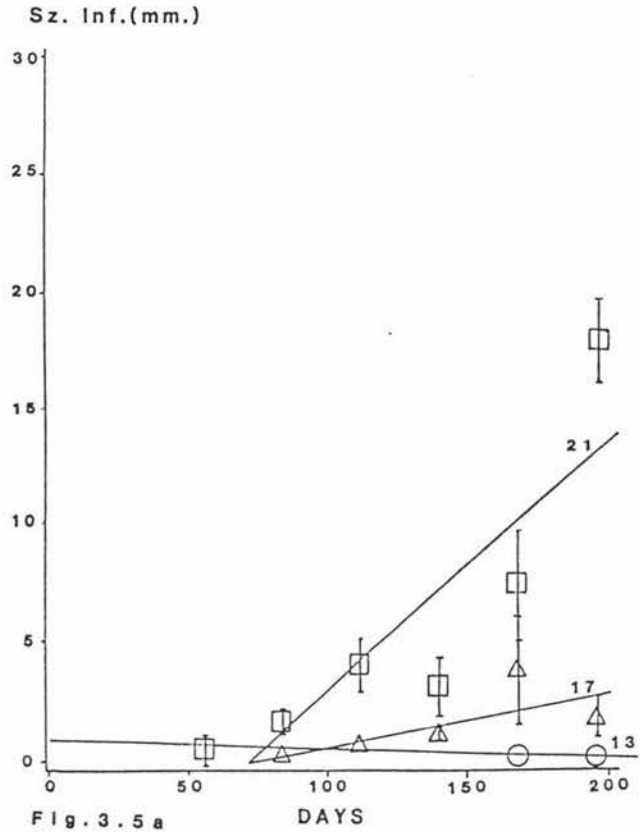


Figure 3.5

a. The influence of low temperature on size increase of the second oldest inflorescence bud of *C. elatus*.

b. The influence of high temperature on size increase of the oldest inflorescence bud for the first wave of flowering of *C. elatus*.

Days = days from planting.
Symbols represent means of 5 replicates.



○ = a) 13°C b) 21°C

△ = a) 17°C b) 25°C

□ = a) 21°C b) 29°C

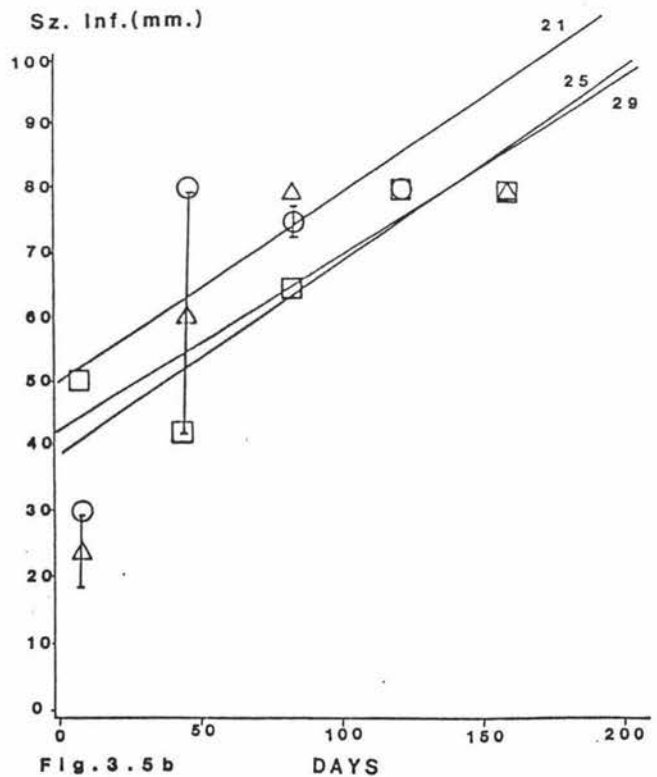


Figure 3.6

The influence of high temperature on size increase of the inflorescence a) for the second and b) for the third wave of flowering. Days = days from planting. Symbols represent means of 5 replicates.

- = 21°C
- △ = 25°C
- = 29°C

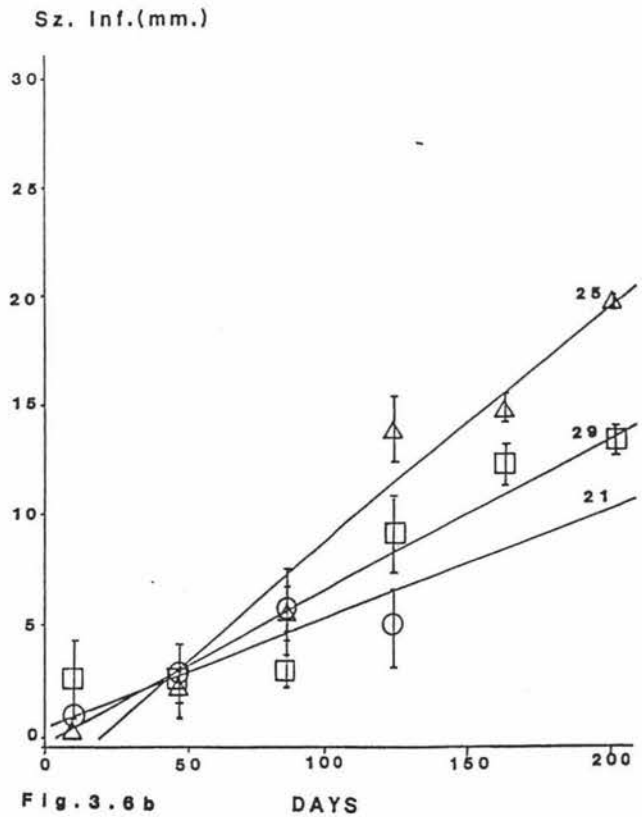
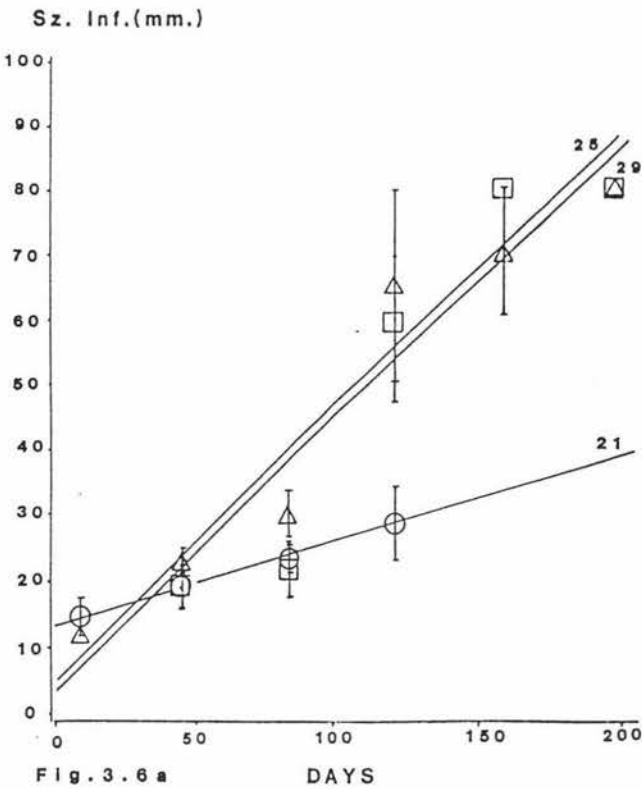


Figure 3.7a

The influence of temperature on final scape length of *C. elatus*. Scares were measured from visible base to base of spathe valves.

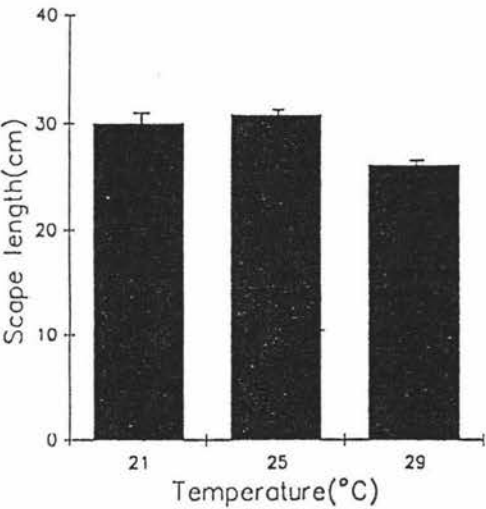


Figure 3.7b

The influence of various environmental conditions on final scape length of *C. elatus*. No flowers emerged under shade (50%) GH = Greenhouse, OD = outdoors S = shade, NS = no shade.

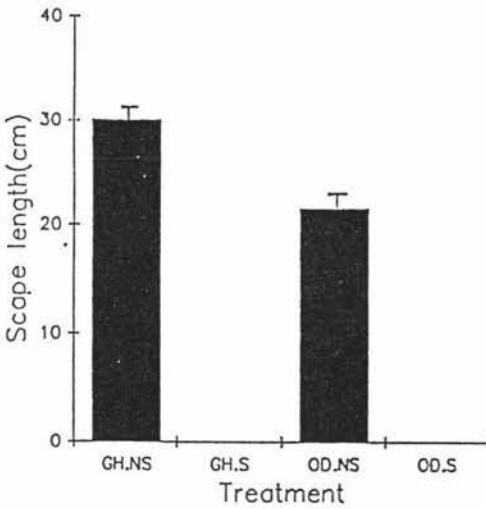


Figure 3.7c

The influence of stage of inflorescence development after transfer to a simulated home environment (Mean temp. 20.3°C, mean light intensity 12.7 Wm⁻², mean PAR 18.3 μMm⁻²s⁻¹) on subsequent final scape length of *C. elatus*.

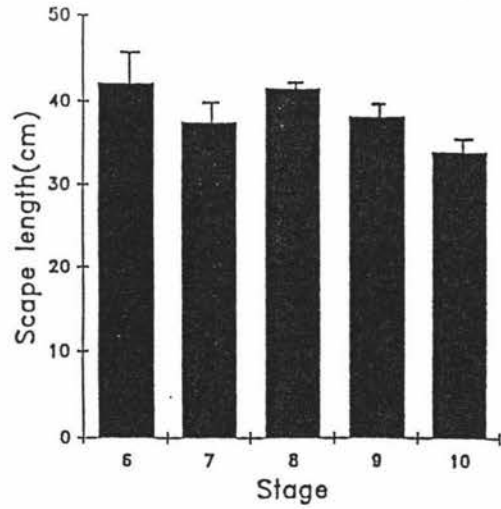


Figure 3.8a

The influence of temperature on pedicel length at anthesis of florets of *C. elatus*.

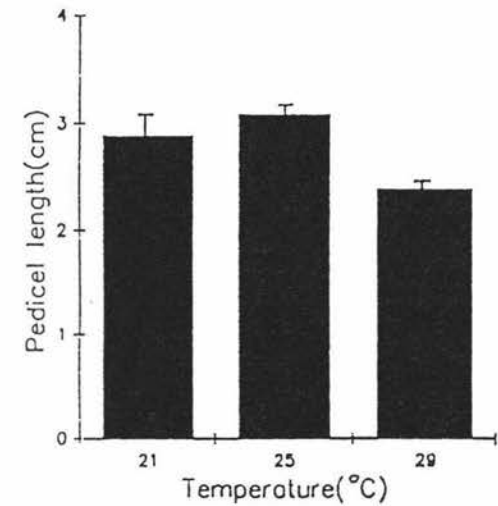


Figure 3.8b

The influence of various environmental conditions on pedicel length of *C. elatus*. No inflorescences emerged under shade (50%). GH = greenhouse, OD = outdoor, S = shade, NS = no shade

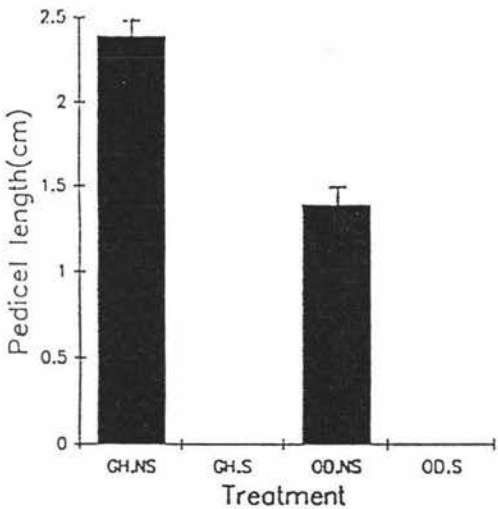


Figure 3.8c

The influence of stage of inflorescence development after transfer to a simulated home environment (Mean temp. 20.3°C, mean light intensity 12.7 Wm⁻², mean PAR 18.3 μMm⁻²s⁻¹) on subsequent pedicel length at anthesis.

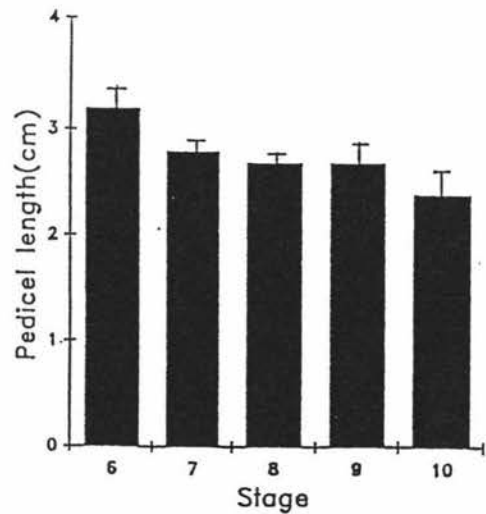


Figure 3.9a

The influence of temperature on flower size in *C. elatus*.

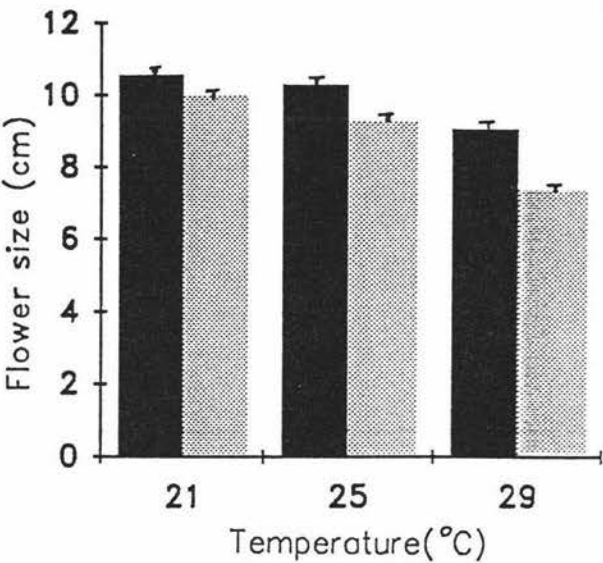


Figure 3.9b

The influence of various environmental conditions on flower size in *C. elatus*. No flowers emerged under shade (50%). gh = greenhouse, od = outdoors.

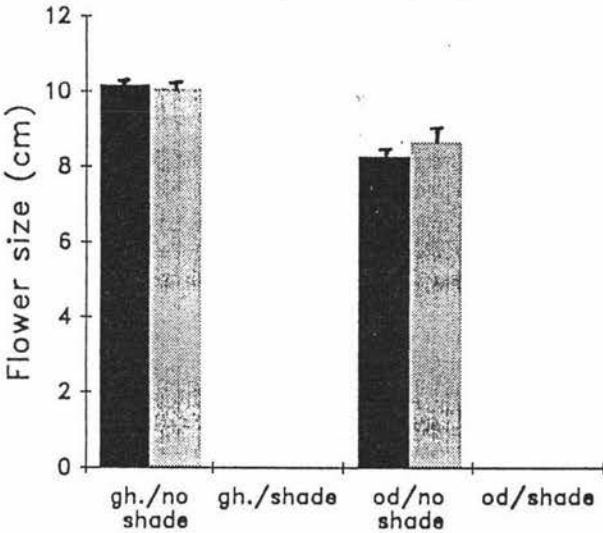
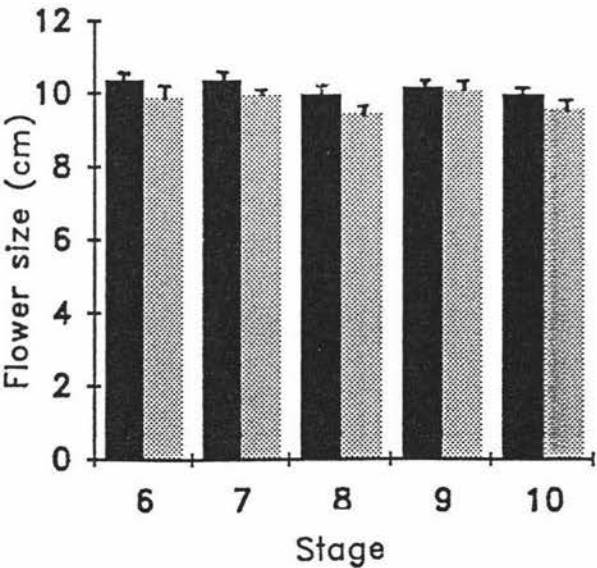
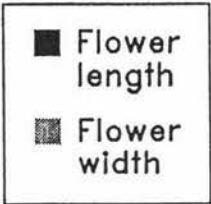


Figure 3.9c

The influence of stage of inflorescence development on transfer to a simulated home environment (Mean temp. 20.3°C, mean light intensity 12.7 Wm⁻², mean PAR 18.3 μMm⁻²s⁻¹) on subsequent flower size in *C. elatus*.



Temperature influenced the colour of the perianth. Moderate temperatures (21-22°C; Tables 3.4, 3.12) resulted in bright orangey-red flowers. At 25°C colour appeared similar to the eye though a little less orange, while at 29°C flowers were a faded red with little orange colour.

Table 3.3 Influence of temperature and light levels on floret longevity and rate of emerged inflorescence growth in *C. elatus* in various environments including controlled environment (CE) cabinets. Dissimilar letters across rows indicate significant differences ($P = 0.05$).

	Outdoor winter	Home Environment room	CE cabinet	Greenhouse autumn	CE cabinet	CE cabinet
Mean temperature (°C)	13	20.3	21	21.5	25	29
Mean P.A.R. ($\mu\text{Mm}^{-2}\text{s}^{-1}$)	-	18.3 ± 0.9	736 ± 10.4	-	722 ± 9.2	704 ± 11.2
Floret life (days)	14.8a	5.7b	8.9c	7.5d	7.2d	4.1e
Time stage 6-10 (days)	25.5a	-	15.6b	15.2b	13.0c	12.6c

Table 3.4 Influence of constant temperatures on floret number and colour. (Mean). Dissimilar letters within columns indicate significant differences ($P = 0.05$).

Temperature (°C)	Floret number (including oldest 2 unemerged inflorescences)	Colour	
		Lightness	a:b
13	0	-	-
17	0	-	-
21 ¹	4.1a	51.3a	0.9a
25	4.0a	50.0a	1.2b
29	3.6a	48.4a	1.3b

¹ Means for 21°C are derived from two sets of bulbs.

Table 3.5 Relationship between bulb size and florets/inflorescence in *C. elatus*. Dissimilar letters across rows indicate significant differences ($P = 0.05$).

	Bulbs used in Experiment III	Bulbs used in Experiments IV and V
Mean diameter at planting	3.2a	4.5b
Mean no. of florets/inflorescence	3.8a	5.5b

3.2.1.4 Vegetative growth

Temperature influenced rates of leaf initiation (Fig. 3.10a,b), emergence (Fig. 3.11a,b) and senescence (Fig. 3.12a,b). Leaf initiation rate was optimal at 21°C under the constant temperature conditions (Leaf initiation = 0.09 days + 8, $r^2 = 80\%$). The rate decreased with reduced temperature below 17°C (Fig. 3.10a). Rates were somewhat depressed at 25 and 29°C (Fig. 3.10b). Leaf emergence rate reflected initiation rate and was lowest at 13°C, similar at 17-25°C and again slightly depressed at 29°C (Fig. 3.11a,b). Rates of leaf senescence increased with increasing temperature (Fig. 3.12a,b). Functional leaf area (Table 3.6) was dependent on numbers of leaves emerging and senescing.

The number of leaves per growth unit (i.e. number initiated between inflorescences) was not affected by temperature (Tables 3.7, 3.8).

Warm temperature (25°C) was optimal for increases in offset dry weight (Fig. 3.13a,b). At 25°C offset dry weight increase = 0.1 days - 1.9, $r^2 = 96\%$.

Bulb diameter increase was optimum and similar at constant 21° and 25°C (Fig. 3.14a,b). Size increase at 21°C = 0.009 days + 0.6, $r^2 = 93\%$, at 25°C = 0.009 days + 0.5, $r^2 = 68\%$. Rates were depressed at 29°C (Fig. 3.14b).

Figure 3.10

The influence of a) high, b) low temperature on time taken to initiate leaves of *C. elatus*. Days = days from planting. Symbols represent means of 5 replicates.

(For 21°C (b) - 3 replicates only).

- = a) 13°C b) 21°C
- △ = a) 17°C b) 25°C
- = a) 21°C b) 29°C

At 21°C (b) leaf initiation = 0.09 days + 8. $r^2 = 80\%$.

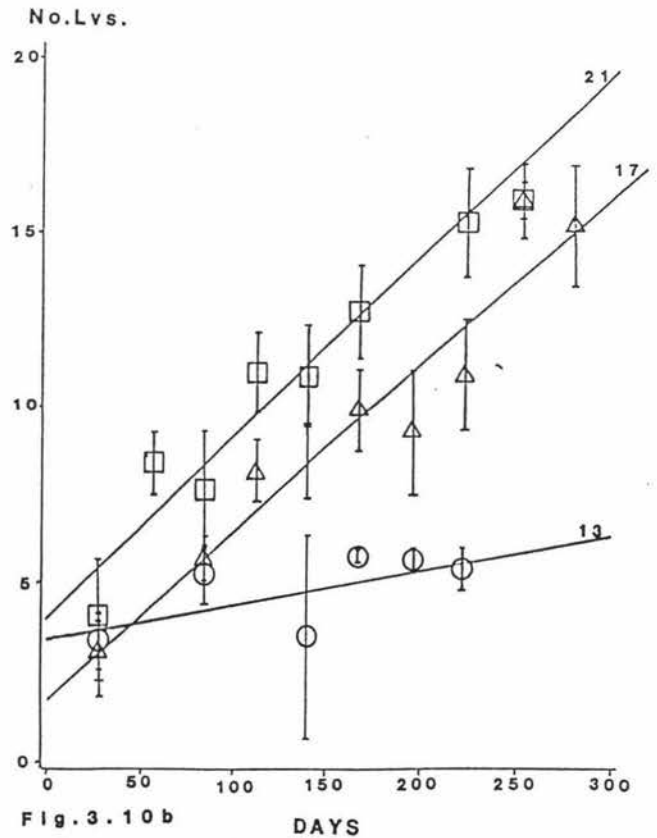
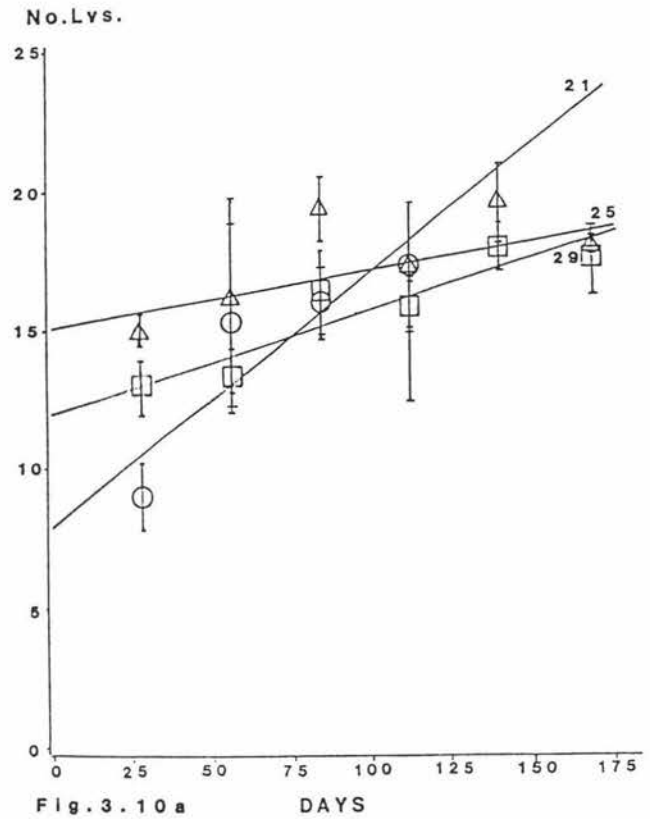


Figure 3.11

The influence of a) low, b) high temperature on the rate of emergence of leaves of *C. elatus*. Days = days from planting. Symbols represent the means of 5 replicates.

(For 21°C (b) - 3 replicates only).

- = a) 13°C b) 21°C
- △ = a) 17°C b) 25°C
- = a) 21°C b) 29°C

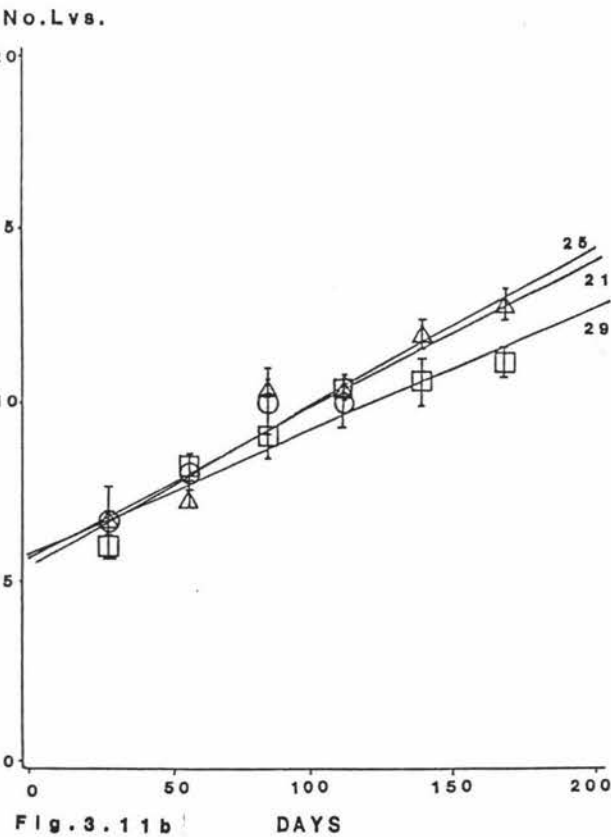
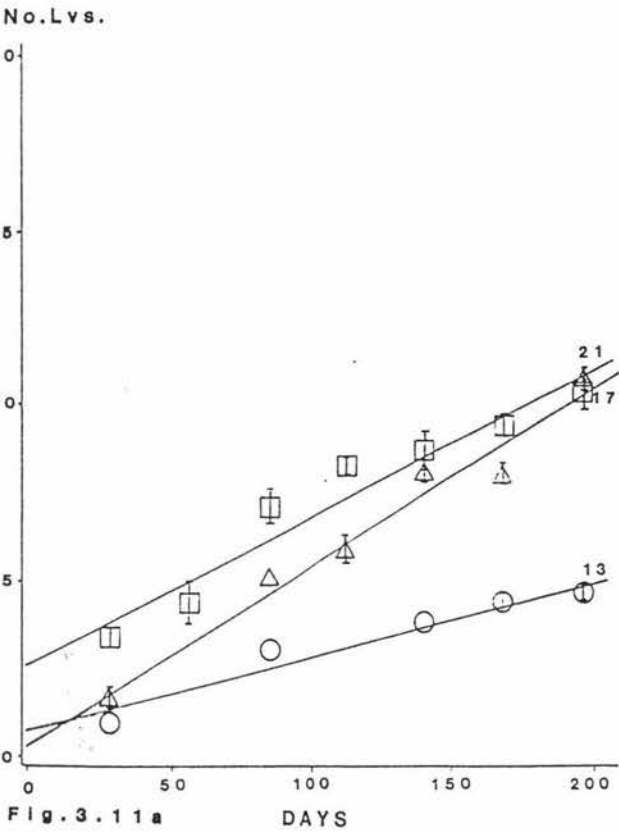


Figure 3.12

The influence of a) low, b) high temperature on the rate of senescence of leaves of *C. elatus*. Days = days from planting. Symbols represent means of 5 replicates.

(For 21°C (b) - 3 replicates only).

- = a) 13°C b) 21°C
- △ = a) 17°C b) 25°C
- = a) 21°C b) 29°C

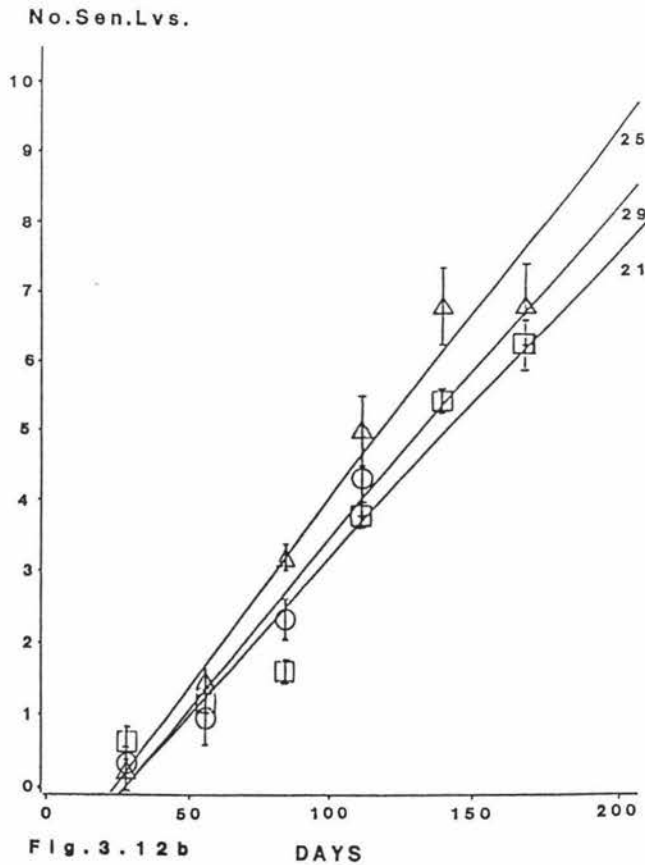
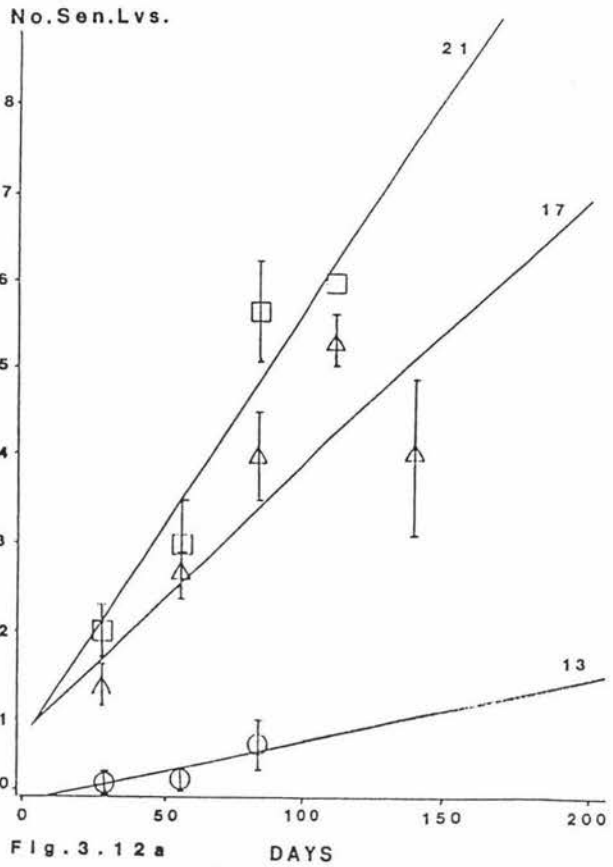


Table 3.6 Influence of environment on leaf area in *C. elatus*. Senescing (yellowing) leaves were not included. Dissimilar letters across rows indicate significant differences (P = 0.05).

	1st set bulbs			2nd set bulbs		
Constant temp (°C)	13	17	21	21	25	29
Leaf area at start of expt (cm²)	0	0	0	210 ± 4	210 ± 4	210 ± 4
Leaf area after 3 months (cm²)	-	-	-	283a	337b	274a
Leaf area after 6 months (cm²)	-	-	-	-	167a	103b
Leaf area after 12 months (cm²)	55a	105b	173c	-	-	-

Treatment	GH ¹ no shade	GH shade	OD ¹ no shade	OD shade
Leaf area at start (cm²)			253 ± 15	
Leaf area after 6 months (cm²)	622a	670a	367b	410b

¹ GH - greenhouse; OD - outdoors

Table 3.7 The influence of temperature on number of leaves initiated between inflorescences (mean). ¹ Expt with first set of bulbs; ² Expt with second set of bulbs.

	13°C ¹	17°C ¹	21°C ¹	21°C ²	25°C ²	29°C ²
Leaves between inflorescences 1 - 2	6.3a	6.8ax	6.4ax	7.0ax	6.9ax	7.1ax
Leaves between inflorescences 2 - 3	-	6.1ay	6.1ay	6.7ax	6.5ay	6.5ay
Leaves between inflorescences 3 - 4	-	-	6.0ay	-	6.0az	6.0az

Different letters across rows (abc) and down columns (xyz) indicate significant differences (P = 0.05)

Table 3.8 Influence of the environment on the number of leaves between inflorescences (Mean). Bulbs had 3 inflorescence primordia at the start of the experiment.

	Outdoor shade	Outdoor no shade	Greenhouse shade	Greenhouse shade
Leaves between inflorescences 1 - 2	6.0ax	6.5ax	5.8ax	6.1ax
Leaves between inflorescences 2 - 3	6.2ax	6.1ax	6.3ay	6.2ax
Leaves between inflorescences 3 - 4	5.7ay	5.4ay	5.6ax	5.4ay
Leaves between inflorescences 4 - 5	6.0ax	5.0 bz	4.9bz	5.1by
Leaves between inflorescences 5 - 6	-	-	5.0bz	5.0by

Different letters across rows (abc) and down columns (xyz) indicate significant differences (P = 0.05)

Figure 3.13

The influence of a) low, b) high temperature on the increase in dry weight of offsets of *C. elatus*. Days = days from planting. Symbols represent means of 5 replicates (3 for 21°C (b)).

- = a) 13°C b) 21°C
- △ = a) 17°C b) 25°C
- = a) 21°C b) 29°C

At 25°C dry weight increase = 0.1 days⁻¹ (r² = 96%).

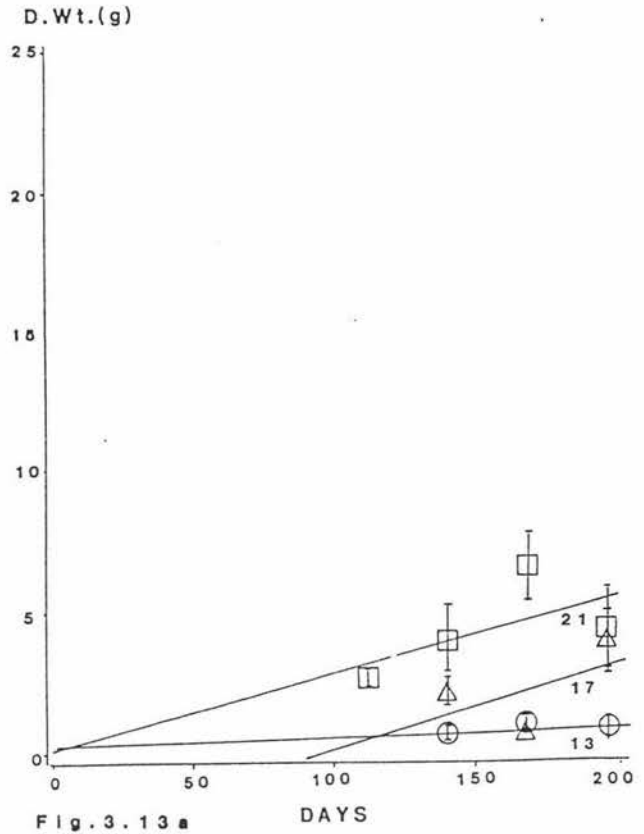


Fig. 3.13 a

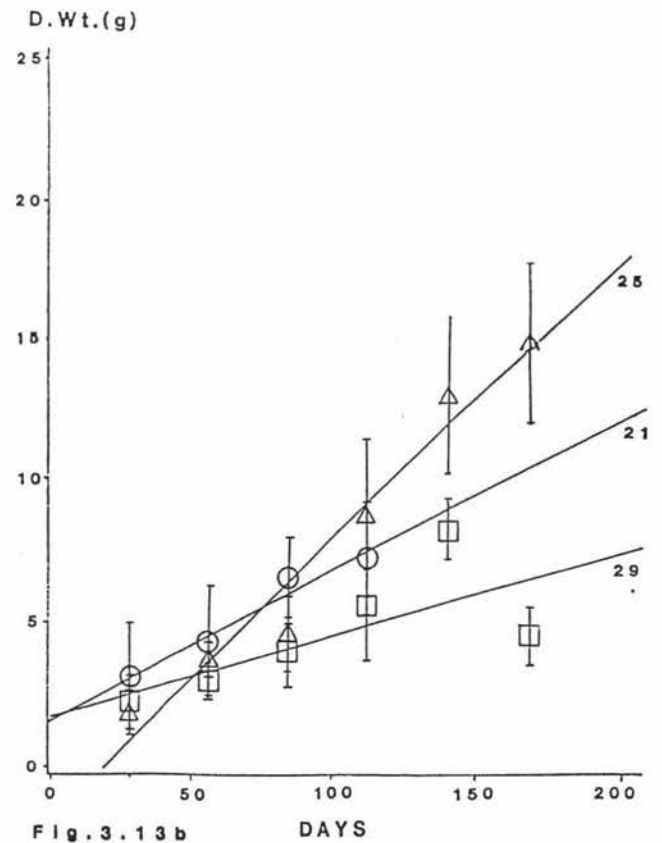


Fig. 3.13 b

Figure 3.14

The influence of a) low, b) high temperature on the change in diameter of bulbs of *C. elatus*. Days = days from planting. Symbols represent means of 5 replicates (3 for 21°C (b)).

- = a) 13°C b) 21°C
- △ = a) 17°C b) 25°C
- = a) 21°C b) 29°C

At 21°C size increase = 0.009 days + 0.6. ($r^2 = 93\%$).

At 25°C size increase = 0.009 days + 0.5. ($r^2 = 68\%$)

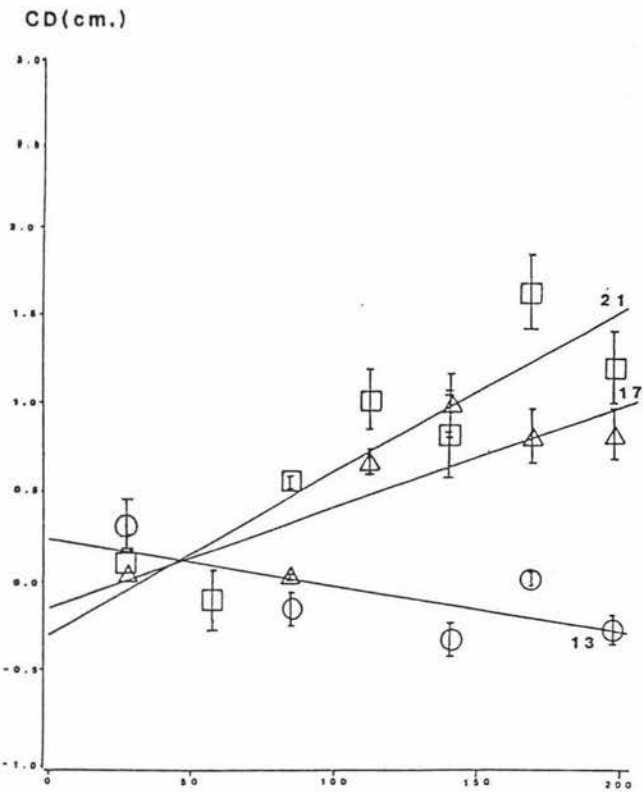


Fig. 3.14 a

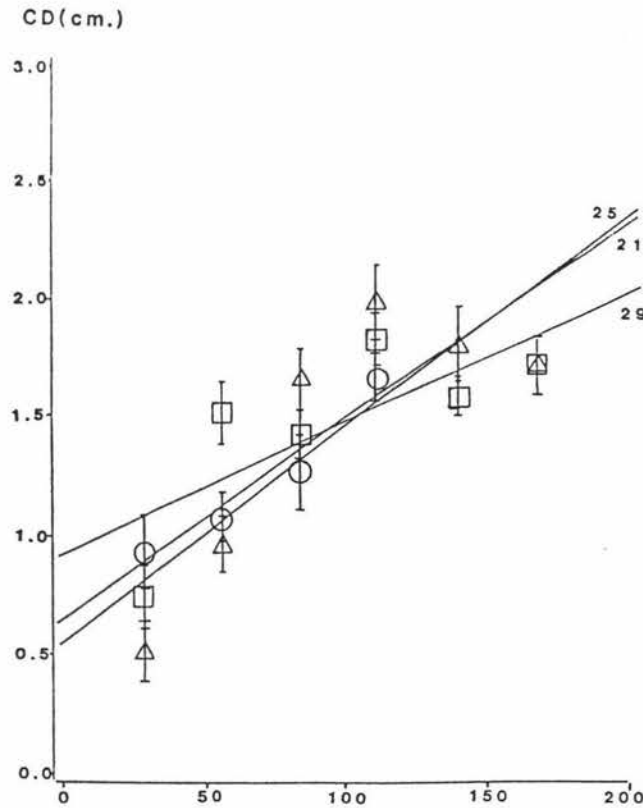


Fig. 3.14 b

Temperature influenced increases in root and shoot dry weights. There was a greater gain in total plant dry weight at constant 21°C compared with all other temperatures tested (Fig. 3.15a,b; increase in dry weight at 21°C = 0.2 days + 4.5, $r^2 = 96\%$). Lowering temperatures from 21° to 17° and 13°C reduced plant growth (Fig. 3.15a) as did increasing constant temperatures to 25° and 29°C (Fig. 3.15b). Separate shoot and root dry weights were not measured in the first set of bulbs grown at constant 13°, 17° and 21°C. However, data from the second set of bulbs showed that shoot growth was optimal at constant 21°C. After 3 months growth at constant temperatures, root growth was greatest at 25° compared with 21° and 29°C (Table 3.9). This was consistent with greater root growth under greenhouse (no shade) conditions compared with outdoors (Table 3.13). Constant high temperature (29°C) reduced root growth considerably (Table 3.9).

Table 3.9 Influence of temperature (constant) on root and shoot dry weights of *C. elatus*. The experiment involving growth at 21°C was discontinued after 4 months. Separate root and shoot measurements were not made for 13° and 17°C treatments. Dissimilar letters down columns indicate significant differences ($P = 0.05$).

Time	Temperature (°C)	Mean shoot dry wt (g)	Mean root dry wt (g)	Root/shoot ratio
After 3 months	21	18.4a	3.9a	0.2a
	25	18.2a	5.3b	0.3b
	29	14.5b	2.1c	0.1c
After 6 months	25	15.7x	7.5x	0.53x
	29	12.2y	2.0y	0.2y

Plants grown at constant 13°C developed bulb rot when over-watered. This was controlled by keeping the medium drier. At constant 17°C most plants showed acute foliar chlorosis, caused by the presence of a virus.

Figure 3.15

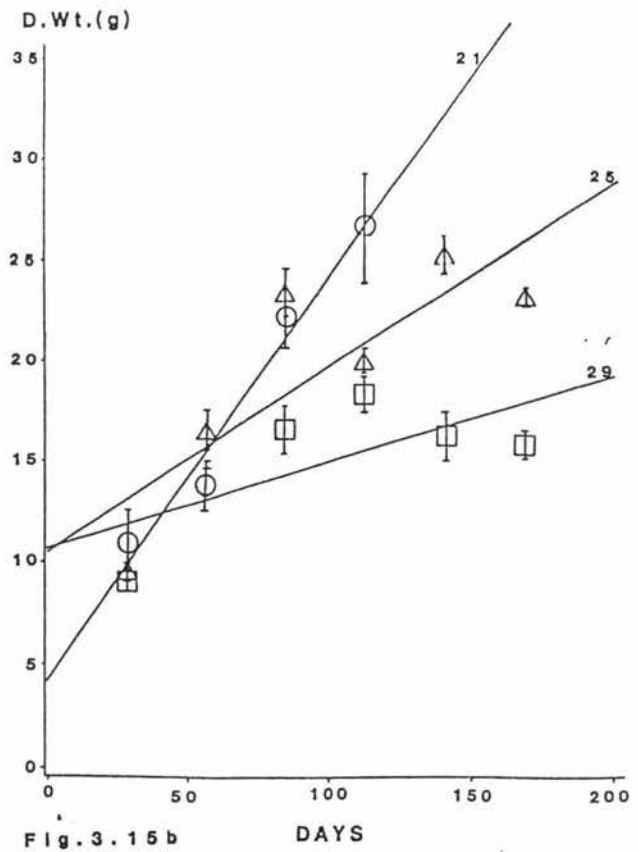
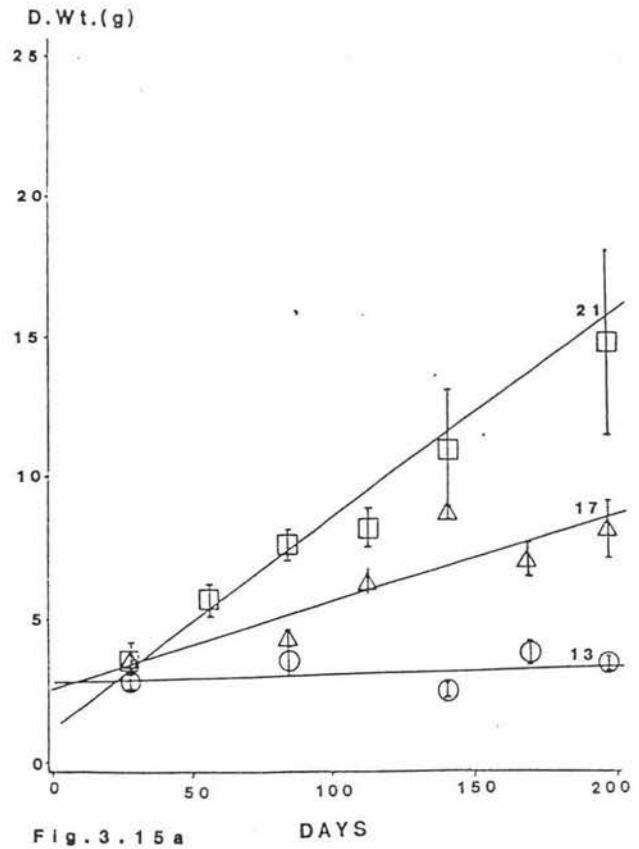
The influence of a) low, b) high temperature on increase in plant dry weight of *C. elatus*. Days = days from planting. Symbols represent the means of 5 replicates (3 for 21°C (b)).

○ = a) 13°C b) 21°C

△ = a) 17°C b) 25°C

□ = a) 21°C b) 29°C

At 21°C dry weight increase = 0.2 days + 4.5. ($r^2 = 96\%$).



3.2.2 Experiment IV: The effect of shade and growing environment temperature on growth and flowering

3.2.2.1 Flower initiation

Under fluctuating temperatures more flowers were initiated at a mean of 23°C (Greenhouse) compared with 17°C (outdoors) (Table 3.10, no. inflorescence buds in bulb). Shading did not affect rates of flower initiation (Table 3.10).

Table 3.10 Influence of environment on leaf and flower initiation and on inflorescence growth within the bulb. Means of 21 plants after 6 months growth (Feb - July 1989) under various conditions. Dissimilar letters within columns indicate significant differences ($P = 0.05$).

Treatment	No. leaves after 1° inflorescence bud	No. inflorescence buds in bulb	Size 3° inflorescence bud (cm) (initial mean size = 0.2 cm)
Greenhouse no shade	27.9a	5.4a	3.3a
Greenhouse shade (50%)	26.3a	5.1a	2.5b
Outdoor no shade	21.7b	4.3b	2.0c
Outdoor shade (50%)	22.7b	4.3b	1.9c

3.2.2.2 Flower development

Rate of growth of the unemerged inflorescence buds was greater in mean 23°C compared with mean 17°C (Table 3.10, size of 3° flower). Although the rate of inflorescence growth was slower in outdoor grown plants, inflorescences emerged in June when mean temperatures were approx. 13°C.

Shading resulted in a high rate of inflorescence bud abortion (Table 3.11). Bud abortion was greater at the higher temperature (i.e. mean 23°C compared with mean 17°C).

3.2.2.3 Flower quality

The effect of shading on flower quality was not determined as no flowers emerged in the shade treatments.

Table 3.11 The influence of environment on the growth and emergence, or abortion of inflorescences in *C. elatus*.

	Greenhouse		Outdoors	
	Shade	No shade	Shade	No shade
<u>No. inflorescences emerged</u>				
1st inflorescence bud	0	7	0	5
2nd inflorescence bud	0	9	0	4
Sub Total	0	16	0	9
<u>No. inflorescences aborted</u>				
1st inflorescence bud	19	13	17	13
2nd inflorescence bud	4	1	0	0
Sub Total	23	14	17	13
<u>No. inflorescences unemerged (viable)</u>				
1st inflorescence bud	2	1	4	3
2nd inflorescence bud	17	11	21	17
Sub Total	19	12	25	22
TOTAL	42	42	42	42

Shade = 50% shade cloth.

Refer Table 3.1 for temperature and light levels.

Scape and pedicel lengths (Figs 3.7b, 3.8b) and flower size (Fig. 3.9b) were greater in flowers emerging at a mean temperature of 21°C compared with those emerging outdoors (mean ≈ 13°C).

Floret longevity was greatly increased by the low outdoor temperature (Table 3.3).

Flowers emerging outdoors were a deeper, darker red in colour compared with those in the greenhouse (Table 3.12). Number of florets per inflorescence was not influenced by the difference in growing environments (Table 3.12).

Table 3.12 Influence of environment on floret number and colour. (Mean). Dissimilar letters within columns indicate significant differences (P = 0.05).

Treatment	Floret number	Colour	
		Lightness	a:b
Greenhouse no shade	4.9 a	50.1 a	1.1 a
Greenhouse shade	No flowers		
Outdoors no shade	4.0 a	46.8 b	1.3 b
Outdoors shade	No flowers		

3.2.2.4 Vegetative growth

The environment influenced rates of leaf initiation. The number of leaves initiated was greater at the higher greenhouse temperature. Shading, however, did not affect rates of leaf initiation (Table 3.10). The number of green leaves on plants after 6 months growth was greater in greenhouse grown plants, although numbers of leaves were not affected by shading (Table 3.13).

The environment affected shoot (including main bulb) and root dry weight (Table 3.13). Although growing environment temperature did not affect shoot dry weight, root dry weight was greater in the unshaded greenhouse plants compared with unshaded plants growing outdoors (Table 3.13). In shaded plants, however, temperature differences had no effect on root or shoot growth. At similar temperatures shading reduced dry weight of shoots and roots, the effect being greater at the higher greenhouse temperature.

Numbers of offsets and total offset dry weight were greater at mean 23° C compared with mean 17° C (Table 3.13). Shading did not affect offset numbers but it did reduce offset dry weight at the higher greenhouse temperature.

Bulb diameter increase was similar at mean 23° and mean 17° C but was greater in unshaded plants (Table 3.13).

Table 3.13 Influence of environment on vegetative growth in *C. elatus*. Mean of 21 plants after 6 months (Jan-July 1989) growth under various conditions. Dissimilar letters within columns indicate significant differences ($P = 0.05$).

Treatment	Bulb diameter	Shoot and main bulb dry wt (g)	Root dry wt (g)	Off-set dry wt (g)	No. off-sets	No. green leaves on main plant
Greenhouse no shade	5.9a	33.3a	6.3a	12.9a	5.9a	11.6a
Greenhouse 50% shade	5.0b	22.4b	3.4b	6.2b	5.3a	11.0a
Outdoors no shade	5.6a	27.8a	3.9b	4.6c	3.9b	8.2b
Outdoors 50% shade	5.3b	22.5b	4.0b	3.9c	3.4b	8.7b

About 5% of plants in the greenhouse had symptoms of viral attack (foliar chlorosis) similar to the plants kept at constant 17°C in experiment III.

3.2.3 Experiment V: The influence of a post-production environment on flower quality

The stage of inflorescence development at which plants were transferred to low light had some effect on flower quality but this was minimal. Scapes and pedicels were slightly longer in plants transferred at stage 6 compared with stage 10 (Figs 3.7c, 3.8c). Transfer at intermediate stages showed no difference.

Transfer to low light intensity at different stages did not affect size of florets (Fig. 3.9c) or number of florets/inflorescence (Table 3.14). Flower colour appeared similar to the naked eye but chromameter measurements showed that flowers transferred at later stages were darker in colour (Table 3.14).

Inflorescences developing from the macrobud stage in complete darkness developed a slightly paler, orangey, less-red colour compared with those developing to anthesis in a light intensity of $12.7 \pm 0.5 \text{ Wm}^{-2}$ (chromameter readings not shown).

Table 3.14 Influence of stage of development on transfer to a simulated home environment (mean temperature $20.3 \pm 0.4^{\circ}\text{C}$; light $12.7 \pm 0.5 \text{ Wm}^{-2}$; PAR $18.3 \pm 0.9 \mu\text{Mm}^{-2}\text{s}^{-1}$) on floret number and colour (mean). Dissimilar letters within columns indicate significant differences ($P = 0.05$).

Stage (refer Fig.)	Floret number	Colour	
		Lightness	a:b
6	6.5a	50.9a	1.2a
7	6.2a	50.2a	1.1a
8	6.0a	47.9b	1.3a
9	7.0a	47.1b	1.3a
10	7.5a	47.2b	1.3a

3.3 DISCUSSION

3.3.1 Flower initiation

Flowers of *C. elatus* were initiated over a wide range of temperatures. Rate of initiation of flowers, however, was temperature dependent but it was not influenced by reduced light intensity. Unlike many bulbous crops, vernalizing temperatures for either floral induction or initiation were not required in *C. elatus*.

Rates of flower initiation were temperature dependent (Fig. 3.4a,b). In the constant temperature treatments rates were slow at temperatures below 21°C but were optimum and similar from 21 - 29°C . A similar pattern was seen for rates of leaf initiation (Fig. 3.10a,b). Temperature treatment did not affect the number of leaves formed between inflorescences (Tables 3.7, 3.8) and hence, as the plastochron interval decreased with increased temperatures, the rate of flower initiation increased over time.

Leaf and flower initiation rates were similar when exposed to constant temperatures within the range 21 - 29°C . However, in plants grown under fluctuating temperature conditions, more flowers were initiated when mean temperatures were 23°C (i.e. Greenhouse, Table 3.10) compared with 17°C (i.e. outdoors, Table 3.10). Increases in the

rate of initiation of leaves and of inflorescence primordia at the bulb apex at 25°C compared with 21°C is seen in *N. bowdenii* (Berghoef and van Brenk, 1983). It is possible that some other factor in the controlled environment cabinets limited rates of flower (and leaf) initiation at temperatures above 21°C. For example, the difference in quality of light emitted by metal halide lamps compared with natural daylight. Another possibility is that diurnal differences in temperature may be important at higher temperatures.

As in *C. elatus*, flowers are initiated over a wide range of temperatures in *Hippeastrum* (Hyashi and Suzuki, 1970), in *N. bowdenii* (Berghoef and van Brenk, 1983) and in *N. sarniensis* (Warrington *et al.*, 1989). In contrast *Lilium longiflorum* (Langhans and Weiler, 1968) and bulbous iris (Rees, 1972) require low temperatures for floral initiation, while high temperatures are necessary for flower formation in *E. grandiflora* (van Bragt and Sprengels, 1983). (See 1.4.1.1).

The wide range of initiating temperatures in *C. elatus*, *Hippeastrum* and *Nerine* spp. result in flowers being initiated in a regular sequence after a certain number of juvenile leaves at any temperature which permits growth, with temperature optima for vegetative growth being similar to optima for flower initiation.

Shading did not affect rates of inflorescence initiation (Table 3.10). This is consistent with the lack of effect of light reduction on the initiation of leaves. Similarly, light intensity was found to be of little importance in growth and flowering in *N. flexuosa* 'alba' (Fortanier *et al.*, 1979).

The lack of effect of shading on flower and leaf initiation in both *C. elatus* and *N. flexuosa* 'alba' may relate to the fact that both species grow on south facing slopes in Southern Africa. Light levels are likely to be low during the early and latter parts of the day, particularly in early spring when flowers are initiated at the apex to emerge in the peak summer flowering period. Rising temperatures in early spring may well be the main stimulus for leaf and flower initiation.

Flowers of *C. elatus* emerged under a range of photoperiod. During this research flowers emerged in all months from January to July (i.e. during long day, short day and 12/12 day regimes). Similarly, photoperiod was observed to have no effect on flowering in *N. flexuosa* 'alba' (Fortanier *et al.*, 1979) and *Hippeastrum* (Rees, 1972). Flowers can form

in narcissus, tulip and iris at 'abnormal' times of the year (Rees, 1972), again indicating a general lack of photoperiodic requirements in many bulbous plants.

In contrast to this general rule, photoperiod affects flowering in some geophytic plants, including gladiolus (Schillo and Halevy, 1976), Easter lily (Bahadur and Blaney, 1968) and bulbous iris (Elphinstone *et al.*, 1986). In the latter, although initiation may not be affected, long days can result in bud abortion particularly if temperatures are high. (See 1.4.2.3). However, Hartsema's (1961) view, that flowering in most bulbous plants is unaffected by photoperiod, generally holds.

3.3.2 Environmental effects on inflorescences in their development from initiation to anthesis

Both temperature and light influenced the development of inflorescences to anthesis. Growth of the inflorescence bud within the bulb increased with temperature up to an optimum of 25°C (Figs 3.5, 3.6). Shading decreased inflorescence bud growth rate at the warmer greenhouse temperature (Table 3.10 - size 3° inflorescence bud).

In the constant temperature treatments, rates of inflorescence development after initiation increased with temperature up to 21°C. At 21°, 25° and 29°C rates were similar with a slight preference for 25°C. Similarly, in fluctuating temperature conditions, rate of growth was much greater in the greenhouse (mean $\approx$ 23°C) than outdoors (mean $\approx$ 17°C; Table 3.10).

Low outdoor temperatures (mean 13°C) did not inhibit inflorescence emergence, although rate of development within the bulb was much slower.

Low flowering levels in the outdoor/no shade treatment (43%) compared with the greenhouse/no shade treatment (76%) was probably due to a slower rate of development of inflorescences outdoors so that few inflorescences had time to emerge before termination of the experiment. Lower outdoor temperatures probably resulted in a reduced general growth rate.

Some species of *Nerine* require favourable temperatures for flower development to anthesis (see 1.4.1.1). Although cool temperatures favour flower initiation, warm

temperatures enhance subsequent flower development.

Responses of these plants to flowering relates to temperatures in the native habitat. Cool temperatures favour flower emergence in *N. flexuosa alba*, which grows on steep south facing cliffs, shaded from the radiant heat of the sun (Norris, 1973). *N. sarniensis* flowers naturally during March when temperatures are in the 18-22°C range. *N. bowdenii* also flowers during warm autumn temperatures. *C. elatus* flowers in the hottest part of the year when mean temperatures are approximately 25°C, although temperatures can reach 30°C on some days (Parsley, Personal communication 1989). Hence warm temperatures (25°C) may be expected to favour development of flowers to anthesis.

Some Mediterranean species require low temperatures after flower initiation in order to complete floral development prior to emergence (Kamerbeek *et al.*, 1972). Such plants, for example, tulip, narcissus and hyacinth, require similar low winter temperatures to those experienced during winter in their native habitat and warmer temperatures favour emergence of the inflorescence in spring. This contrasts with *C. elatus*, where inflorescence primordia are initiated at regular intervals, with more than one inflorescence bud developing within the bulb at any one time,. In the mature bulbs examined, moderate-warm temperatures generally stimulated two floral buds to reach anthesis within six months.

Light intensity reduction resulted in a slower rate of development of inflorescence primordia within the bulb. This effect was greater in warm (indoor) temperatures. Similarly, light interacted with temperature in affecting bud abortion rates. Vegetative growth also exhibited a similar response to temperature and shading levels (see section 3.3.4). Once again, flower growth rate paralleled vegetative growth and may be dependent on it. Similarly, adequate leaf growth is necessary for flower development in tulip (Ho and Rees, 1975, 1976) and in bulbous iris "Wedgewood" (Rees *et al.*, 1987). This probably relates to the need for adequate photosynthate levels for flower bud growth.

Inflorescence bud abortion

Reduction in light intensity was the most important factor examined and it resulted in a high rate of bud abortion (Table 3.11). A similar effect is seen in many other bulbous crops. Reduced irradiance increases flower bud abortion in Easter lily (Miller and Langhans, 1989; Einert and Box, 1967), and bulbous irises (Kamerbeek, 1969). Flower abortion in *Gladiolus* in winter in Israel is thought to be due to reduced PAR, as daily sum irradiance in winter is approximately 50% of that prevailing in summer (Schillo and Halevy, 1976).

In Easter lily, flower abortion occurs after emergence. However, in this plant flower buds develop on an above-ground stem. In *C. elatus* the flower bud developed to a later stage (see Fig. 2.6a) below ground level within the bulb. Abortion before emergence in *C. elatus* may be comparable to post-emergence abortion in many other plants where flowers develop above-ground.

In addition to a light intensity effect on inflorescence bud abortion, an interaction between light and temperature was found. A higher number of buds aborted in warm, low light intensity compared with cool, low light intensity (Table 3.11). This interaction is observed in other bulbous crops. For example, in Easter lily longer dark periods and higher temperatures increase the percentage of bud abortion (Mastalerz, 1965). Higher temperatures require higher minimum light intensities to ensure normal flower development of bulbous iris and Easter lily (Kamerbeek, 1969).

This interaction between light and temperature was probably related to carbohydrate availability for completion of bud development. At low temperatures the rate of bud development was slow and carbohydrate levels in a lower light intensity may be adequate to prevent death of immature bud tissue. Conversely, at high temperatures growth rates were fast, respiration levels high and more carbohydrate may be required to compensate. A developing flower bud is a relatively weak sink until anthesis (Mastalerz, 1965). When growth rate was high, starvation of the bud tissue may occur if carbohydrate levels were depleted or the plant may abort flowers and redirect remaining reserves to stronger sinks. In the tulip, inhibition of sucrose translocation to developing buds induces abortion (Moe, 1979), again indicating the importance of adequate carbohydrate supply. This is also supported by the observation that with a large reduction in irradiance small bulbs of Easter lily aborted flower buds, whereas in larger bulbs with more food reserves, only a few buds aborted (Miller and Langhans, 1989).

Reduction in carbohydrate levels has also been suggested as a reason for flowerless shoots in roses (Halevy, 1972). Lower photosynthetic rates in winter result in thinner shoots with a greater tendency for flower abortion (Van den Berg, 1988), and conversely, increasing light intensity increases the proportion of flowering shoots (Cockshull, 1975; De Vries *et al.*, 1982).

Other stresses also resulted in flower bud abortion. Initial dissection of 20 bulbs at the commencement of the experiment revealed that 25% of the oldest flower buds had already

aborted. This was probably due to stresses endured by bulbs during lifting, transport and storage, from factors such as low light levels, high temperatures and low humidity.

In addition to effects on carbohydrate reserves, environmental factors also affect growth regulator levels which play an important part in nutrient mobilisation and the establishment of sinks (Weaver and Johnson, 1985). Gibberellins (GA), auxins and cytokinins affect sugar and amino acid distribution in *Gladiolus* (Tonecki, 1980). Response to environmental factors may be controlled by growth regulators affecting nutrient distribution. This is well established for higher plants generally and appears to hold for bulbous crops as well. For example, sink capacity of tulip flower buds is strengthened by GA_{4/7} treatment (Mae, 1979) and distribution of assimilate in the bulbous iris is altered by the application of cytokinins (Mae and Vonk, 1974).

The stage of inflorescence development at which the plant was exposed to a low light environment appeared to be important. Where floral bud abortion did occur in *C. elatus* it involved only the largest, outermost (i.e. oldest) or rarely the second oldest bud (Table 3.11). Younger, smaller buds were not affected by reduced light intensity. This would be advantageous to the plant if shading or other stress factors were temporary. In the short term, photosynthate would be conserved for a later time when the younger, currently less demanding, buds could develop. Alternatively, even if low light conditions persisted, the conserved photosynthate may be directed to leaf growth and hence an increased photosynthetic capacity from which younger buds may benefit.

The differing response to low light, of buds at different stages of development, was supported by the post-production experiment. No bud abortion occurred in any of the plants transferred from the greenhouse to the simulated home environment room. (All plants had emerged inflorescences). It may be, that provided light levels had been adequate prior to emergence, there would be sufficient reserves in the bulb to support further inflorescence development. The inflorescence of *C. elatus* was relatively well developed just prior to emergence (see Fig. 2.6a).

Exposure to low light conditions in the post-production experiment did not result in abscission of flowers or parts of flowers. This contrasts with several other floricultural crops, where problems occur, such as petal drop in geraniums (Armitage *et al.*, 1980), flower drop in Begonias (Hoyer, 1985), and bract abscission in Bougainvilleas (Hackett *et al.*, 1972).

In these crops, it is possible that such abscission results in a conservation of photosynthate reserves, otherwise used for seed and fruit production. This result may be achieved in *C. elatus* by bud abortion or by the delay in flower emergence.

3.3.3 Environmental effects on flower quality

The environment influenced several aspects of flower quality and quantity. In particular changes in both temperature and light intensity influenced scape and pedicel length, flower size, number, colour and the longevity of flowers. All of these aspects are important in determining the suitability of *C. elatus* as a cut flower or potted flowering plant.

3.3.3.1 Scape and pedicel lengths

Elongation of both scapes and pedicels was affected by both temperature and light. Elongation of scapes and pedicels was greatest at warm temperatures (21-25°C). This supports the work of van Nes and Vonk Noordegraaf (1977) who found that flowers of *C. elatus* emerging in spring have shorter scapes compared with those emerging in late summer. Similarly, warm temperatures result in longer scapes in *N. bowdenii* (Systema, 1975) and *N. sarniensis* (Warrington *et al.*, 1989). High temperature (29°C, Fig. 3.7a) reduced scape length in *C. elatus*, which is seen also in *N. sarniensis*, where scape length in plants grown at 30°C is shorter than at 22°C.

Flower emergence, after development from initiation at constant warm temperature (25°C), indicated that *C. elatus* does not have a low temperature requirement for scape elongation. This contrasts with some bulbous plants such as tulip, narcissus and hyacinth. Low temperatures in these crops (1-9°C for tulip and narcissus, 9-13°C for hyacinth) are required to promote scape elongation (De Hertogh, 1974). These species initiate flowers only once, at a specific time during the year and low winter temperatures are required prior to flower emergence in spring. *C. elatus*, however, initiated flowers at intervals throughout the year and flowers emerged during spring, summer, autumn and winter.

Scape length in some bulbous crops is influenced by thermoperiod where plant growth is enhanced in response to diurnal temperature differences compared to the response measured under constant temperature conditions with the same diurnal mean (Warrington *et al.*, 1977). This effect was not evident in *C. elatus* when comparing scape length at constant

21°C with a mean of 21.5°C where there were diurnal differences in temperature. This effect is not found in Narcissus, tulip or hyacinth (Royal Heins, personal communication 1990) or in soybean (Warrington *et al.*, 1977). In contrast, increased scape length in differing day and night temperatures has been reported for Easter lily, where at a constant mean, larger differences in diurnal temperatures result in greater stem lengths.

Scape length in *C. elatus* may be influenced by photosynthate availability. An increase in temperature increases the rate of photosynthesis provided other factors, for example light levels, are not limiting. Higher temperatures up to 25°C increased net photosynthetic rate (Table 3.1). Warm temperatures (21 and 25°C) resulted in similar elongation in CE cabinets and greenhouse (mean = 21.5°C) where light intensity levels were comparable (Table 3.1).

Reduced scape length at high temperature (29°C) may be the result of lower rates of net photosynthesis at 29°C (Table 3.1) and higher rates of respiration. Although increases in temperature normally stimulate photosynthetic rate up to the point where enzyme denaturation occurs, losses of CO₂ due to respiration, also increase. Photorespiration especially, is stimulated by high temperatures because a rise in temperature increases the ratio of O₂ to CO₂ within the leaf (Hall and Keys, 1983). In addition, rates of respiration during the 12 hour period of darkness in the CE cabinets are likely to be greater at 29°C compared with 21° and 25°C.

Root growth was poor at 29°C (Table 3.9). This may have resulted in a lowered photosynthetic rate. Restricted root growth of pot-bound tobacco plants results in reduced activity of ribulose-1, 5-biphosphate carboxylase (Herold and McNeil, 1979). Lowered availability of photosynthate at 29°C may have reduced tissue elongation rate of *C. elatus*.

Plant elongation is influenced by both light quality and quantity. Elongation involves cell division, and to generate an increase in volume, it must be accompanied by cell enlargement. All the main photosensory systems are involved in the control of cell growth by light. These are phytochrome in the low energy mode and the HIR, cryptochrome and photosynthesis (Gaba and Black, 1983). Phytochrome in the PFr form and cryptochrome inhibit excessive elongation (refer 1.4.2.3) as does low photosynthate availability.

Light levels varied under the different treatment conditions and these influenced scape and pedicel elongation. Lower light intensity increased scape and pedicel lengths.

Higher outdoor light intensity, compared with the greenhouse (Table 3.1), resulted in much shorter scapes and pedicels in outdoor-grown plants (Figs 3.7b, 3.8b). It is difficult to determine whether this is predominantly a temperature or a light effect. Scape and pedicel lengths are likely to be influenced by both factors.

Shading is used to increase stem length and hence value in a number of commercially grown bulbous plants such as Easter lily (Einert and Box, 1967), *N. sarniensis* (Warrington *et al.*, 1989), tulip (Rees, 1972) and *Gladiolus* (Monselise, 1957).

Low light intensity ($324.3 \mu\text{Mm}^{-2}\text{s}^{-1}$, Table 3.1) and warm greenhouse temperatures (21.5°C) resulted in insufficient scape elongation for inflorescence emergence. Even though some inflorescence initials had reached 30 mm in length and scapes started to elongate, 90% of these inflorescences in the outermost position aborted.

Flower abortion occurs in many bulbous plants when they are exposed to unfavourable conditions (Doss, 1986; Warrington *et al.*, 1989). These conditions are species dependent. So although shading is useful in many crops, it obviously had a detrimental effect on flower emergence in *C. elatus*.

Light quantity probably affected tissue growth via its effect on photosynthetic rates and hence on photosynthate availability. Scape lengths were similar in the greenhouse (no shade) treatments to lengths in the 21° and 25°C CE cabinets (Figs 3.7a,b). Although light levels were similar in 21° and 25°C cabinets (Table 3.1), photosynthetic rate was higher in the 25°C cabinet (Table 3.1), probably because photosynthetic rate increases with temperature until other factors become limiting (Flore and Lakso, 1989). Similar scape lengths at 21° and 25°C may be due to negation of the photosynthetic rate increases at 25°C by higher rates of respiration during the dark period. Light levels were similar in the 25°C and 29°C cabinets, but scape length was less at 29°C . Net photosynthetic rate was higher at 25°C (Table 3.1). This may be due to some inhibition of the photosynthetic apparatus at 29°C , in a plant not adapted to constant high temperatures (Berry and Björkman, 1980).

Scapes and pedicels were longer in the lower light intensity of the greenhouse compared with outdoors (Figs 3.7b, 3.8b). Photosynthetic rate, however, was higher under the outdoor light intensity compared with that in the lower light intensity of the greenhouse (Table 3.1). Plants grown under shade had considerably lower light intensity (Table 3.1) but

no flowers emerged for comparison. Measurements of photosynthetic rates were taken at midday on a warm sunny day in March. Flowers emerged from plants grown in the greenhouse in April/May and from outdoor plants in June/July. Changing seasons over this period also influenced light intensity with longer, brighter days with less cloud cover in April/May than in June/July. PAR available to greenhouse grown plants was probably greater than to outdoor plants at the time of flower emergence and scape elongation. Photosynthetic rates and hence the availability of photosynthates would similarly be higher in the greenhouse situation. The effect of lower outdoor temperatures on photosynthetic rate would also reduce amounts of available photosynthate.

Photosynthetic rate is likely to fall on transfer from a high light environment, e.g. greenhouse, to the low light of the simulated home environment room. Nevertheless, scapes and pedicels shared a tendency to be longer in plants transferred at an early stage (where total scape elongation occurred under low light) than in plants transferred at a late stage (Fig. 3.7c, 3.8c) where most of the scape elongation occurred in the greenhouse. Scape lengths in low light were probably a compromise between lower levels of photosynthate availability which would reduce growth rate, and the photomorphogenic etiolation effect which would increase stem length (Rees, 1972). Different species have different light intensity optima for greatest tissue elongation. For example, 37% full sunlight results in longest tulip stems (Rees, 1972) while 60% shade is optimum for stem length of *Caladium bicolor* (Conover and Poole, 1973).

Light intensity effects on tissue elongation are compounded by effects of light quality which influences photomorphogenesis. Plants grown in the greenhouse, home environment room and CE cabinets were exposed to light of different spectral distributions. Artificial lighting does not exactly reproduce the physical characteristics of daylight. Natural sunlight is rich in red light (i.e. a high R:FR ratio). However, the spectral distribution changes throughout the day with changes of cloud conditions and angle of the sun (Warrington *et al.*, 1978). Water vapour absorbs FR while there are lower R:FR ratios at sunset (Attridge, 1990).

Alterations in spectral distribution will affect phytochrome and hence elongation of scapes and pedicels. Irradiation from cool white lamps (used for lighting in the simulated home environment room) results in a higher ratio of PFr:Pr than does natural daylight, so scapes are shorter (Vince-Prue and Canham, 1983). However, both daylight and cool white

lamp emission are rich in blue and red light, both of which are important in the HIR. The much higher light intensity in the greenhouse compared with the simulated home environment room (Table 3.1) probably resulted in the longer scape length of inflorescences which emerged in the home environment room where temperatures were similar (Fig. 3.7b,c).

Scapes and pedicels of plants emerging under metal halide lamps in the CE cabinets were similar in length to those in the greenhouse at comparable temperature, light intensity and photoperiod (Figs 3.7a,b, 3.8a,b). Spectral output from these lamps is rich in blue and red light with some emission in the FR region. The effect on phytochrome photoequilibrium is very similar to that of daylight with a slightly greater proportion of PFr than is produced by daylight (Tibbitts *et al.*, 1983). Metal halide lamps also produce a very similar blue photon flux density to that of daylight. Hypocotyl length of lettuce, spinach and mustard show a strong negative correlation with blue photon flux density suggesting that a blue-absorbing photoreceptor is controlling hypocotyl extension in these species (Tibbitts *et al.*, 1983). The similarity of stem lengths of *C. elatus* in daylight and with metal halide lamps suggests that the blue absorbing photoreceptor cryptochrome, in addition to phytochrome, may be involved in scape extension.

No flowers emerged under either of the shade treatments. Mean light levels in the outdoor/shade treatment were not much lower than mean light levels in the greenhouse/no shade treatment, but this difference was obviously significant in terms of flower development (Table 3.1). There were two possible reasons for non-emergence. One was that low light levels induced abortion of the unemerged inflorescence bud, the other that viable buds remained within the bulb. A higher rate of unemerged floral bud abortion was found in the shade treatments (Table 3.11). However, even viable buds did not emerge. Very low light levels within the bulb (a little light may penetrate through the neck of the bulb) might be expected to induce elongation. However, this did not appear to happen. It is possible that unfavourable light conditions were perceived by the leaves and a hormonal message was transmitted to the bud, inhibiting elongation of the scape. The influence of low PAR levels on photosynthate availability may also be involved.

Photoperiod may affect the growth of the scape of *C. elatus*. Plants grown outdoors and in the greenhouse experienced a natural variation in photoperiod. This experiment ran from January to July. This period covered the range from 15 hr to 9 hr daylight including the

12 hr photoperiod of the CE cabinets and simulated home environment room. Flowers emerged outdoors during the short days (9 hr daylight) of winter, greenhouse grown flowers emerged mainly during April and May (11.4-9.4 hr daylight).

Scape lengths of tulip (Hanks and Rees, 1979; 1980) and Easter lily (Kohl and Nelson, 1964; De Hertog, 1974) are shorter when grown under short days. A greater effect occurs at 9 than at 18°C in tulip. The shorter stem length of outdoor grown *C. elatus* plants may therefore be partly due to short days, though this was compounded by other factors such as temperature and light intensity.

Photomorphogenic, photoperiod and light intensity effects may be mediated via endogenous hormones including GA (De Greef and Fredericq, 1983). Environmental factors may also operate via endogenous hormones in the control of stem elongation in *C. elatus*. IAA produced by the gynaeceum controls scape extension in tulip and narcissus (Hanks and Rees, 1977). Flowers of Easter lily influence elongation of upper internodes probably as a result of basipetal transport of hormones including GA₃ and IAA (Gianfagna *et al.*, 1986). The scape itself also produces IAA (Edelberth and Kaldewey, 1976). GA sprays increase floral stem elongation in Dutch iris (Halevy and Shoub, 1964). In contrast, ABA (Rees, 1985) and ethephon (ethylene) inhibit flower stem extension in several bulbous crops (Moe, 1980). *C. elatus* is more likely to be sensitive to endogenous hormones during the early part of scape extension when elongation rates are greatest.

In summary, photosynthetic rates are affected by both temperature and light intensity. Interaction occurs between these environmental factors in their affect on photosynthate availability and hence tissue growth. There is further interaction with photomorphogenic effects. Scape growth at cool temperatures and high light levels was reduced compared with warm temperatures and medium light intensity. Moderate to warm temperatures and low light intensity resulted in longest stem length.

Scape elongation in low light is important ecologically in that flowers are carried up to regions of higher light intensity, away from other vegetation. This results in increased chances of cross pollination, seed set and dispersal.

3.3.3.2 Flower size

Temperature influenced flower size with 21 °C being optimum for development of large flowers (Fig. 3.9a). Flowers were smaller at higher and lower (Fig. 3.9b) temperatures. Low availability of photosynthate may not be the only factor affecting flower size. Flowers have a high surface area/volume ratio and are particularly susceptible to dehydration. It is suggested that a reduced flower surface area may be advantageous at high temperatures where rates of water loss are increased.

Several other floriculture crops have optimum temperature for large flower size. These include *N. sarniensis* (Warrington *et al.*, 1989), tulip (Dosser and Larsen, 1981), chrysanthemum (Kohl and Mor, 1981), hydrangea (Bailey and Weiler, 1984) and rose (Salinger, 1987) (see 1.4.1.5). Optimum temperatures for flower size probably reflect conditions during flowering where these species originate. Tulips are endemic to cool mountainous regions and bloom in late spring when temperatures are moderate. Chrysanthemums flower in the cooler temperatures of autumn as does *N. sarniensis*. Although roses are summer flowering, they are endemic to cool temperate regions. Flowers of *C. elatus* would probably be exposed to 17-30 °C in their native habitat (see Chapter 1) and this approximates the optimum temperatures for flower size observed here.

Photosynthetic and respiration rates may influence available photosynthate and, in turn, affect flower size in a similar fashion to scape length. *C. elatus* flowers which emerged at low outdoor temperatures (13 °C, Fig. 3.9b) were smaller than flowers in any of the other treatments. This may be a result of low photosynthate availability owing to lower rates of photosynthesis. Flowers of *C. elatus* emerging in spring are smaller than those emerging in late summer (van Nes and Vonk Noordegraaf, 1977). A possible explanation is that in spring, carbohydrate reserves are reduced after low photosynthetic rates during winter. Summer temperatures give abundant leaf growth and high rates of photosynthate production from which developing flowers benefit. Flower size appears to depend strongly on photosynthate availability.

Plants used in this experiment had not previously flowered. Those bulbs producing flowers early, i.e. soon after being placed in the cabinet, produced inflorescences with fewer flowers/stem and smaller flowers than plants flowering later after a longer period of vegetative growth. This is supported by the observation that as the bulbs aged there was an increase in bulb size and in area of the emerged leaves (Tables 3.5, 3.6).

Light intensity influences available photosynthate and therefore would also affect flower size. This was not directly measured as no flowers emerged under either of the shade treatments. Flowers emerging outdoors were much smaller (Fig. 3.9b). However, this may be a temperature rather than a light effect.

Transfer of pot plants just after inflorescence emergence from the greenhouse to the home environment room, where mean temperature was similar but light levels were much lower, did not affect flower size (see Table 3.1 and Fig. 3.9b,c). This is similar to *N. sarniensis* where shading has no effect on flower fresh weight (Warrington *et al.*, 1989).

Flower size was not affected no matter at which stage of inflorescence development transfer took place (Fig. 3.9c). It is suggested that flower size was predetermined by this stage. Higher light levels increase inflorescence diameter in hydrangea (Hickleton, 1984) when they are exposed from an early stage of flower development. Provided flower initiation and early stages of development (Stage 1-5, Fig. 2.5) occurred under conditions of high light intensity and warm temperatures, transfer to low light after inflorescence emergence (Stage 6) did not reduce flower size in *C. elatus*.

3.3.3.3 Floret longevity

Many factors influence floret longevity. It is crucial that the influence of warm temperatures and low light intensity are determined for potted plants designed for indoor use, as these conditions prevail.

Increased temperature reduces the longevity of most flowers (Halevy and Mayak, 1979). In *C. elatus*, increasing the temperature from a winter mean of 13°C, to 29°C reduced floret life from 14.8 to 4.1 days (Table 3.3). Even an increase of 8°C, at warm temperatures (21-29°C) halved floret life. High temperatures also increase the rate of development of the flower (Time stage 6-10; Table 3.3) with a consequent reduction in the time needed for pollen and seed production. The reduction in floret longevity at high temperatures is due to a much greater respiration rate and an increase in the rate of processes leading to senescence such as increase in membrane permeability and leakage of ions (Halevy and Mayak, 1979).

High temperatures tend to stress plants and lead to an increase in the rate of endogenous ethylene production which is also associated with senescence. A wide range of

flowers is sensitive to ethylene resulting in a decrease in longevity (see 1.4.1.5). Sensitivity to exposure to exogenous ethylene also increases with temperature (Barden and Hanen, 1972).

Floret longevity was influenced by light levels. A 98% reduction in light intensity in the simulated home environment room compared with the 21 °C CE cabinet, resulted in a 36% loss of floret longevity (Table 3.3).

Reduced floret longevity at very low light intensity may be due to stimulation of endogenous ethylene production by light stress. Ethylene synthesis can increase to more than 50 times the basal level by severe stress including low light intensity or darkness (Tingey, 1980). Reduced irradiance results in loss of flower longevity in Easter lily (Miller and Langhans, 1989).

A reduction in photosynthate levels as a result of low light intensity may also reduce floret life. During flowering, tulip flowers are the strongest sinks for current photosynthate (Ho and Rees, 1975; 1976). Where this is limited, floret life is reduced. Sugar levels affect flower longevity in a variety of ways. Sucrose antagonises the effect of abscisic acid in promoting flower senescence of both carnation and roses (Mayak and Dilley, 1976). Sucrose enhances the effect of cytokinins in delaying flower senescence and reduces the effect of ethylene in promoting it. Sugars also act by inhibiting the activity of a membrane-bound form of ethylene forming enzyme (Mayak and Borochoy, 1984), thus reducing ethylene synthesis.

Sugar levels in the flower can be maintained by solutions containing sucrose. These solutions extend the vase life of many cut flowers such as iris, tulip, daffodils (Doss, 1986) and carnations (Nichols, 1973).

In *C. elatus* low light intensity may have reduced floret longevity by a drop in photosynthesis leading to a reduction in available photosynthate. This may have been mediated via ethylene or other plant hormones.

3.3.3.4 Florets/inflorescence

The number of florets/inflorescence was not influenced by temperature (Table 3.4) or light (Table 3.12). The environment may influence floret number during very early stages of

inflorescence development. However, in this research numbers were noted from inflorescences initiated prior to the start of the experiments.

Floret numbers were similar when bulb starting size was similar so no differences were observed among the various environmental treatments (Tables 3.4, 3.12). Neither did stage of development (stages 6-10) at transfer from greenhouse to low light levels affect the number of florets/inflorescence (Table 3.14).

Floret number was, however, different in bulbs of different age and size. Mean floret number was greater by 1.7 from large bulbs (4.5 cm) compared with small bulbs (3.2 cm; Table 3.5). Plants used in the simulated home environment trial had more florets than other plants. Plants used in this experiment had larger bulbs and this, rather than low light intensity was probably the causal factor.

Smaller numbers of florets/inflorescence from younger bulbs (Table 3.5) reflect a reduced leaf area as well as fewer food containing leaf bases than larger bulbs. Amount of photosynthate for inflorescence development would be limited. This is supported by the observation that *C. elatus* produces more florets/stem in flowers emerging in late summer compared with those emerging in spring (van Nes and Vonk Noordegraaf, 1977). This could be a temperature effect or it may be because plants in late summer have more leaf development and greater amounts of food stored in leaf bases.

In *C. elatus*, as is found in other species such as *N. sarniensis* (Warrington *et al.*, 1989), light and temperature did not influence the number of florets per inflorescence, a factor contributing to its suitability as a pot plant.

3.3.3.5 Flower colour

Temperature influenced the depth of colour of the perianth of *C. elatus* but light intensity had little effect. Warm temperatures (21-22°C, Tables 3.4, 3.12) produced bright orangey-red flowers. At 25°C, colour appeared similar, though a little less bright. While at 29°C flowers were a faded red with less orange colour. Flowers grown at low temperatures (13°C, Table 3.12) were a deeper red and darker in colour.

The red colour of tepals of *C. elatus* is probably due to the presence of anthocyanins, the orange colour to carotenoid pigments. Temperature influences the synthesis of both

pigments. Temperatures greater than 25°C inhibit the formation of a number of carotenoids, including lycopene (Tomes, 1965). Such pigments are frequently present in flowers and are probably present in the tepals of *C. elatus*. This may explain why flowers at 29°C were less orange in colour. High temperatures have similar effects on the colour of other flowers and plant parts. Orange coloured coronas of *Narcissus* (Rees, 1972) and 'Valencia' orange rind (Coggins *et al.*, 1981) develop more intense colour at lower temperatures.

High temperatures markedly reduce the stability of anthocyanins (Jurd, 1972). High temperatures decrease the anthocyanin content of rose flower buds (Biran *et al.*, 1972) and cause blueing of roses (Biran and Halevy, 1973). Anthocyanin production also depends on the supply of sugars. High temperatures result in a high respiration rate during hours of darkness, reducing sugar supply for anthocyanin synthesis (Blank, 1958). Another effect of heat was to increase the rate of flower development of *C. elatus* (see Table 3.3). Biran and Halevy (1973) suggest that this reduces the time period over which pigmentation can occur. Thus a reduction in anthocyanin synthesis and a decrease in its stability at 29°C would result in the observed decrease in red colouration of *C. elatus* flowers.

Cool temperature stability of anthocyanins could be partially responsible for the stronger red colour of flowers grown at low temperature (mean temperature = 13°C, Table 3.12). Higher anthocyanin content at low temperatures is found in *Zantedeschia* (Funnell *et al.*, 1987) and in Baccara roses (Zeislin and Halevy, 1969; Biran *et al.*, 1972).

Light intensity did not have a strong influence on colour development in flowers of *C. elatus*. Plants transferred to the low light level and similar temperatures of the home environment room prior to floret pigmentation, developed colour similar to plants left to flower in the greenhouse (Tables 3.14, 3.12). Inflorescences developing from the macrobud (Stage 6) to anthesis in complete darkness (Temp. mean $\approx$ 20°C) developed a slightly paler orange (less-red) colour compared with those transferred to the home environment room at this stage. The darker red colour of outdoor grown flowers may have been an effect of both lower temperatures and higher light intensity, with temperature possibly having a greater effect.

Light quality (frequency) and light intensity are involved in pigment synthesis. Light frequency can influence photomorphogenesis which in turn can regulate the control of specific biochemical pathways, in particular the photoregulation of anthocyanin and

carotenoid synthesis (see 1.4.2.3) (Rau, 1980). The enzyme phenylalanine ammonia lyase (PAL) which is involved in the metabolic pathway of anthocyanin synthesis shows striking changes in activity in response to light (Walker, 1975). It is possible that in *C. elatus* light is necessary for the production of enzymes involved in anthocyanin synthesis. Such enzymes may be present in the tissue prior to pigment development in the flowers, so that provided plants receive adequate light before inflorescence emergence, pigment synthesis will take place.

The development of bright orangey-red flowers at moderate temperatures and the maintenance of colour in a low light intensity make *C. elatus* suitable as a pot plant for the home environment. If a deeper red colour is more desirable for cut flower production, plants can be grown in cooler, outdoor temperatures.

3.3.4 Environmental effects on vegetative growth

The influence of the environment on vegetative growth was of secondary importance in this study. The main objective was to investigate flowering. However, bulb size and volume of foliage are important for pot plant quality and the development of offsets is also useful for increased leaf area and new bulb production.

Bulb size in *C. elatus* was affected by the number of fleshy leaf bases within the bulb, which was influenced by rates of both leaf initiation and senescence. Bulb size was also influenced by the size of offsets present in the axils of leaf bases. These develop in one plane only.

Number of emerged leaves and total leaf area were also dependent on rates of leaf initiation at the apex. Leaf area influenced photosynthate production and apparent growth rate.

3.3.4.1 Leaf growth

Between 13 and 25°C, increased temperature resulted in increased leaf growth. This was mainly due to greater rates of leaf initiation (Fig. 3.10a,b) and emergence (Fig. 3.11a,b) and increased leaf area (Table 3.6) at warm temperatures. Although leaves senesced earlier at temperatures above 13°C (Figs 3.12a,b), this factor was less important.

The greater rate of leaf initiation at temperatures above 13°C may be expected in a plant in which most vegetative growth occurs during summer (Parsley, 1989, personal comm.). Similar rates at 17°C and 21°C may reflect the fact that cool spring temperatures stimulate leaf initiation and emergence resulting in adequate leaf area to facilitate development of flowers emerging in early summer. However, under fluctuating temperatures leaf initiation rates were greater at mean 23°C compared with mean 17°C. Perhaps the more uniform temperature of the greenhouse compared with outside, especially warmer nights, stimulated leaf initiation rate. In addition, as winter approached, temperature differences between greenhouse and outdoors increased.

Rates of initiation were lower at 25°C in the constant temperature experiment. This may be due to high rates of leaf initiation in the first two weeks which was reflected in a smaller slope for the regression line than would otherwise have been expected. High, initial rates of leaf initiation at 25°C may be due to the high rates of abortion of the oldest inflorescence bud at 25°C in the plants dissected in the first two months. Abortion of the outermost bud may have increased sink strength at the apex, resulting in a shorter plastochron index.

Warm temperatures increase leaf production in a number of bulbous plants including *N. sarniensis* (Warrington and Seager, 1988), *N. bowdenii* (Berghoef and van Brenk, 1983), *N. flexuosa alba* (Fortanier *et al.*, 1979), *Hippeastrum* (Hyashi and Suzuki, 1970) and *Lilium longiflorum* (Wang and Roberts, 1983).

Rates of leaf emergence increased up to 21, and were similar at 21 and 25°C (Figs 3.11a,b). Similarly, tulip leaf emergence is stimulated as temperatures increase in spring (Rees, 1972). A slightly depressed rate at 29°C is probably due to lack of adaptation of *C. elatus* to prolonged constant high temperatures in its native habitat.

The rate at which older leaves senesced (defined as a loss of chlorophyll from the leaf blade) increased with temperatures up to 21°C (Fig. 3.12a) and higher temperatures produced similar senescence rates (Fig. 3.12b). Thus leaf life was shortened at temperatures above 21°C.

Leaf area was optimal at mean 25°C in fluctuating temperatures (Table 3.6) and at constant 25°C over the first three months. Thereafter leaf area declined at both constant

25°C and 29°C (Table 3.6). Leaf area was related to leaf initiation, emergence and expansion. Both leaf initiation rate and emergence were greater at 25°C. Although leaf emergence rate was similar at 17 and 21°C (Fig. 3.11a), leaf area was greater at 21°C after 12 months (Table 3.6). Leaves were smaller and chlorotic at constant 17°C, probably due to the effect of a virus.

Earlier work on *C. elatus* indicates that leaf production at 22° is higher than at 18° or 14° C (van Nes and Vonk Noordegraaf, 1977). Significant differences in leaf production between 17 and 21°C were not detected in the work described in this thesis, perhaps due to a lower replicate number or less uniform material.

Shading did not affect leaf initiation or emergence in *C. elatus*. Similarly leaf number of *N. sarniensis* was not affected by a reduction in light intensity (Warrington *et al.*, 1989). Shaded plants tended to have greater leaf area but the trend was not significant. Increase in leaf size with decreasing light intensity occurs in many plant species (Humphries and Wheeler, 1962). Shade adaptation can be physiological as well as morphological. Reduced irradiance may lower the light compensation point. It may also cause structural and functional changes in chloroplasts resulting in increased light harvesting capacities at lower light intensity (Berry, 1975; Kappel and Flore, 1983; Anderson *et al.*, 1988). However, none of these factors was examined.

3.3.4.2 Number of leaves per growth unit

The number of leaves between inflorescence primordia was not influenced by temperature (Tables 3.7, 3.8). This supports results reported by van Nes and Vonk Noordegraaf (1977) and is similar to *N. sarniensis* (Warrington and Seager, 1988).

A greater number of leaves/growth unit occurred in shaded plants at cooler temperatures (Table 3.8). Leaf, rather than flower production would be advantageous under conditions which result in reduced photosynthate availability.

Bulb size at the time of leaf initiation did affect the number of leaves formed between inflorescences. Bulbs showed a tendency to produce fewer leaves per growth unit as they aged. Older, larger bulbs had a larger apex and produced larger leaves (Table 3.6 cf GH with 25°C bulbs). Larger bulbs also have more reserves and would be less dependent on the number of photosynthesising leaves to support flower production, than would smaller,

younger bulbs. Temperatures which result in an increase in leaf initiation rate in *C. elatus* acted via a greater production of growth units rather than to a greater number of leaves per unit. Similar changes in leaf initiation of *N. sarniensis* are reflected in increased growth unit development (Warrington and Seager, 1988).

3.3.4.3 Offset growth

Bulb size in *C. elatus* is affected not only by numbers of leaf bases but also by the development of offsets in the axils of the leaf bases. Growth of offsets was influenced by the environment. Warm temperatures (25°C) and high light levels (full sunlight) were optimum for increases in offset dry weight. The increase in offset dry weight at 21°C in the second set of bulbs occurred at a greater rate than the first set (Fig. 3.13a,b). The second set of bulbs were initially larger (mean diameter = 3.2 cm, cf 2.8 cm) and also retained their leaves after being placed in the CE cabinets while the first set of bulbs lost their original leaves. Mother bulb reserves depleted for new leaf production in the first set of bulbs, would be available for offset production in the second set of bulbs.

Optimal offset growth at warm temperature (25°C) in *C. elatus* contrasts with *N. sarniensis* and *N. flexuosa alba*. Offset growth in *N. sarniensis* is similar at 14° and 22°C (Warrington *et al.*, 1989), while 17°C is most favourable for offset production in *N. flexuosa alba* (Fortanier *et al.*, 1979). Such differences may reflect different environmental conditions in the native habitat. Vegetative growth in *C. elatus* occurs mainly in summer while foliage of *N. sarniensis* emerges in winter when rainfall predominates. *N. flexuosa alba* grows on steep south facing cliffs in southern Africa where plants receive little heat from solar radiation (Norris, 1973).

High temperatures reduced dry weight of offsets in *C. elatus* (29°C), *N. sarniensis* (30°C) and *N. flexuosa alba* (25°C). These temperatures (if constant) are higher than those experienced by these plants in their native habitat.

Shading reduced offset dry weights under the higher greenhouse temperatures but outdoors shading had no effect (Table 3.13). The effect of reduced irradiance on photosynthate production may be greater at higher temperatures (see discussion on bulb girth differences, 3.3.4.4).

Weight of outdoor grown tulip daughter bulbs was reduced by shading. This suggests that offset weight is dependent on photosynthetic rate (Rees, 1972). Ho and Rees (1974) found that most tulip daughter bulb starch is derived from current photosynthesis.

3.3.4.4 Bulb size

Bulb diameter reflected environmental influences on leaf initiation, leaf senescence and offset growth. However, offsets develop in one plane only and measurements of the smaller bulb diameter only were recorded. The number of leaf bases was dependent on rates of leaf initiation and senescence. Diameter increase was optimum and similar at constant 21 and 25°C, rates were depressed at 29°C (Fig. 3.14a,b). The similarity of rates at 21 and 25°C is explained by the fact that although leaf initiation rates were greater at 25 compared with 21°C, senescence rates were greater at 25°C. Indoor grown bulbs were not different in size from those grown outside (Table 3.13). Although leaf initiation rates were greater indoors (Table 3.10), a higher percentage of indoor grown plants produced inflorescences resulting in a greater depletion of stored reserves in the leaf bases. Although shading did not affect leaf initiation rate, shaded bulbs were smaller. Possibly leaf bases of shaded plants contained less stored food material.

All bulbs in the 13°, 17° and 21°C constant temperature treatments showed some increase in diameter during the first month. This could be due to the fact that the leaves present on the bulbs when planted senesced within a short time and material from the leaves was translocated to the bulb. It may also be due to swelling of the leaf bases by water uptake. The subsequent reduction in bulb diameter 2-3 months after planting at 13, 17 and 21°C (Fig. 3.14a), was probably due to the use of stored photosynthate for leaf growth. It is suggested that continued reduction in bulb size at 13°C (Fig. 3.14a) was because the photosynthetic rate was too low to replace stored food material. Provided light was not limiting, decreased temperature lowered the carbon assimilation rate (Table 3.1). Leaf growth, though slow, continued at 13°C and food material in the leaf bases was presumably consumed. At 17°C and 21°C a higher rate of photosynthesis (Table 3.1) resulted in a greater rate of bulb growth (Fig. 3.14a). The initial reduction in diameter was comparable to the initial dry weight loss of *Narcissus* bulbs after planting (Rees, 1972). Subsequent increases occurred more rapidly at warmer temperatures in both *Narcissus* (Rees, 1972) and *C. elatus* (Figs 3.14a,b).

There was no initial reduction in diameter in the second set of bulbs. Leaves did not senesce after planting. Plants continued to photosynthesise so that material from the mother

bulb was not depleted in order to produce leaves. In the first set of bulbs, the tops of the leaves and the ends of the roots had been trimmed to 5 cm prior to transport. Root growth restriction leads to lowered photosynthetic rate and premature leaf senescence in tobacco (Herold and McNeil, 1979). Root removal in *C. elatus* may have resulted in stress leading to leaf senescence.

Increase in the diameter of the bulbs was very slow at 13°C. This was due presumably to a low rate of photosynthesis (Table 3.1). Reduced leaf initiation at 13°C is a reflection of the increased plastochron at the apex which is at least in part, dependent on carbohydrate availability. The plant may have a system to adapt to unfavourable weather (i.e. cool temperatures) and conserve reserves in order to survive winter. This was supported by the observation that although fewer leaf bases were present in bulbs grown at 13°C, the individual leaf bases were thicker. This is comparable to temperature induced dormancy in periodic bulbs.

Bulb diameter increase was greatest at 25°C (Fig. 3.14a,b). This was therefore the optimum temperature. At temperatures higher than 25°C, reduced photosynthate accumulation due to higher respiration rates, increased leaf senescence and reduced leaf initiation rate probably resulted in decreased bulb growth rate.

Temperature affects bulb size in other bulbous plants. Bulbs of *N. sarniensis* (Warrington *et al.*, 1989) and *N. flexuosa* 'alba' (Fortanier *et al.*, 1979) are smaller after growth at superoptimal temperatures (see 1.4.1.4). The different optimal temperatures for increase in bulb size may reflect differences in temperature regimes found in the native habitats of these species. Optimal temperatures give greater leaf emergence and photosynthetic rate resulting in an increase in the rate of leaf initiation and of offset growth, both of which lead to bulb diameter increases.

Shading reduced bulb girth (Table 3.13). Similarly, reduced light intensity also results in smaller bulb sizes in *N. sarniensis* (Warrington *et al.*, 1989). The effect in *C. elatus* was greater at the higher greenhouse temperature (Daily mean $\approx$ 23°C) compared with outdoors (Daily mean = 17°C). Higher temperatures increase respiration rate and, in turn, light compensation points (LCP) (Berry and Bjorkman, 1980). Possibly higher LCPs at the higher greenhouse temperature resulted in a greater depression in photosynthetic rate in shaded plants compared with plants growing in shade at lower outdoor temperatures. In

shade-adapted plants such a depression is less, compared with shade-intolerant species (Grime, 1965; Berry, 1975; Pass and Hartley, 1979). Shade adaptation in *C. elatus* may, therefore, be limited. In addition to higher temperature effects on LCPs, cool mornings and evenings may have resulted in lower photosynthetic rates in outdoor grown plants compared with those grown in the greenhouse, irrespective of light intensity. In outdoor grown plants photosynthetic rate may be similar at cool temperatures in both shaded and non-shaded plants.

Whole plant source-sink relationships may be affected by reduced irradiance (Gifford and Evans, 1981). Low irradiance results in reduced amounts of photosynthate in the leaves and, in turn, this may induce remobilisation of food reserves from bulb leaf bases to the leaf blades (Miller and Langhans, 1989) which would decrease bulb size.

3.3.4.5 Root and shoot dry weight

Leaf and flower initiation, growth and emergence, rates of leaf senescence, offset growth and increase in bulb diameters were all reflected in total plant dry weights. Although 21°C was the optimal temperature for total plant dry matter accumulation (Fig. 3.15a,b), growth at supra optimal temperatures, as measured by total dry weight, was initially similar but deteriorated with time. This was expressed in the chlorosis of leaves and a hastening of leaf senescence.

Root growth was greatest under constant 25°C and decreased with increasing or decreasing temperature (Table 3.9). This was consistent with greater root growth in unshaded greenhouse-grown plants compared with outdoor grown plants at cooler temperatures (Table 3.13). Although shoot growth at constant 25°C deteriorated with time, root growth was not so affected (Table 3.9). At 29°C root growth was poor. Similarly, Warrington *et al.*, 1989, reported less root growth of *N. sarniensis* at high temperatures.

Temperature affects total plant dry matter accumulation in *N. sarniensis*. High temperatures (30°C) inhibited growth compared with lower temperatures (14, 22°C) which could be expected from a plant with a summer dormant habit. This contrasts with *C. elatus* where total plant growth was much greater at 25 and 29°C than at low temperatures (13°C) (Fig. 3.15a,b). *N. sarniensis* flowers in autumn, leaves emerging later during winter as it is adapted to growth at low temperatures while *C. elatus* makes little growth in winter, leaves and flowers emerging during the warmer temperatures of summer.

Shading reduced root and shoot dry weights, which was exacerbated by high (Daily mean = 23°C) greenhouse temperature. This was consistent with a similar effect of shading at higher temperatures on bulb girth and offset growth. Although shading did not affect leaf initiation rate, leaf emergence, leaf area or numbers of offsets produced, bulb girth and root and shoot dry weights were greater in full sun-grown plants. This suggests that leaves, leaf bases and offset buds were heavier and thicker in non-shaded plants. Shading reduces dry matter accumulation in many other bulbous plants including *N. sarniensis* (Warrington *et al.*, 1989), *N. bowdenii* (Systema, 1971), tulip (Rees, 1972) and *Gladiolus* (Monseliese, 1957) (see 1.4.2.4).

In summary, vegetative growth of *C. elatus* was optimum at warm temperatures (21-25°C) and in full sunlight. At constant high temperatures (29°C) high photorespiration and dark respiration rates resulted in depressed photosynthate accumulation. Although temperatures may reach 30°C during summer in the native habitat (Paisley, personal communication), cool night temperatures (17°C) would result in a lower mean daily temperature (i.e. 23°C approximately). *C. elatus* experiences shading for part of the day on the southern slopes of the Outeniqua Mountains. Data suggested that it is adaptable to changing light levels at low rather than at high temperatures. On south-facing slopes plants would be shaded more during winter as the sun's angle deepens.

CHAPTER 4

CONCLUSIONS

4.1 MORPHOLOGY

Flower and bulb morphology was similar to *Hippeastrum* and *Nerine* spp. Inflorescences were produced in a sequence after a certain number of leaves. The main bulb persisted and produced offsets in outer leaf bases. Such features contrast with those of narcissus and tulip.

Inflorescence development was similar to *Eucharis grandiflora* and *Hippeastrum*, floret parts being initiated in like sequence.

4.2 INFLORESCENCE INITIATION

Vernalising temperatures were not required for inflorescence induction; flowers were initiated over a wide range of temperatures. Plants did not respond to photoperiod and were regarded as day neutral. The rate of inflorescence formation was determined by growth rate and this was optimal at warm temperatures (25°C). Bulbs must reach maturity, usually by the initiation of 12 or 13 leaves, before the initiation of the first inflorescence bud could occur. Five to seven leaves were formed between inflorescence buds, the smaller number being found in large, mature bulbs.

Light intensity reduction did not affect the ability of plants to initiate flowers but had other detrimental consequences for flower emergence.

The occurrence of inflorescence initiation over a wide temperature range, and irrespective of photoperiod, indicates year-round production is possible but this also results in greater difficulty in scheduling crops.

4.3 INFLORESCENCE EMERGENCE

More flowers emerged under high light intensity (704-785 $\mu\text{m}^{-2}\text{s}^{-1}$ (Growth cabinet-Greenhouse)) and moderate to high temperatures (21°-29°C). Under these conditions photosynthetic rate was high and growth rate was optimum. Flowers emerged at a slower rate from plants growing under low winter temperatures (13°C), where photosynthetic rate

and total growth rate were reduced. Light intensity reduction (50%) and consequent lower photosynthetic rate, inhibited flower emergence and resulted in inflorescence abortion, particularly at higher temperatures (21°C cf 13°C), where higher respiration rate is likely to result in greater reserve depletion.

4.4 FLOWER QUALITY

Floret number was unaffected by temperature or light intensity but was influenced by bulb size, being greater in larger, more mature bulbs. Florets open in sequence and hence an increase in floret number extended inflorescence longevity.

Moderate temperatures (21°C) were optimum for floret quality, resulting in larger flowers with a bright orangey-red colour. Cool temperatures (13°C) yielded small, dull, blood-red flowers. High temperatures (29°C) resulted in smaller, pale, watery-red flowers. This reduction in pigmentation is possibly a result of a higher temperature effect on the synthesis of carotenoids and anthocyanins.

Scape length was greatest under moderate-warm temperatures (21-25°C) and low light intensity. Although long stems are desirable in cut flowers, for pot plants a balance between pot size and plant height is more important. Outdoor, winter grown plants yielded the shortest stems.

4.5 VEGETATIVE GROWTH

Fluctuating warm temperatures (17-26°C) and high light intensity $785.3 \pm 100.6 \mu\text{Mm}^{-2}\text{s}^{-1}$) resulting in a high photosynthetic rate ($15.8 \mu\text{MCO}_2 \text{ m}^{-2}\text{s}^{-1}$) gave optimal root, shoot and offset growth. However, constant warm temperature (25°C) after a period of four months, resulted in stress which caused premature foliage senescence and reduced leaf and flower initiation rate. Constant warm temperatures are not experienced by *C. elatus* in its natural habitat, where day-time summer temperatures may rise to 30°C but fall to around 17°C at night.

Pest control was achieved to some extent. Bulbs treated with 0.2% Ridomil prior to planting did not develop bulb rot. However, in spite of this treatment, those bulbs in the CE

cabinets at a constant 13°C did start to rot when over-watered. Bulbs should be lifted or kept relatively dry outdoors during winter. Ravages of the Narcissus fly (*Merodon equestris*) were avoided by treatment of bulbs with Dasanit (a systemic insecticide) in early October. Plants kept at constant 17°C developed symptoms of a viral attack (acute foliar chlorosis). Symptoms were not detected in plants kept at constant 13, 21, 25 or 29°C. However, a few plants (approx. 5%) growing in the greenhouse, where temperatures dropped to 17°C at night, also developed similar symptoms. The maintenance of growth at 17°C (for any length of time) should be avoided.

High quality plants of *C. elatus* can be produced year-round under warm conditions (17-26°C) and high light intensity. Mature bulbs have the potential to produce 2 inflorescences/year independent of photoperiod. Shading is not recommended during production as inflorescence emergence is suppressed.

C. elatus was suitable as a pot plot plant for home or patio use. Inflorescence quality was maintained under a warm, low-light intensity environment, provided inflorescences were past the macrobud stage prior to transference to such conditions. Inflorescences at the macrobud stage reached anthesis in total darkness with little loss of colour. To avoid mechanical damage to the inflorescence, shipping at the macrobud stage is recommended.

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