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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 Schoenbrunn, 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 Burt, 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 Burt (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.

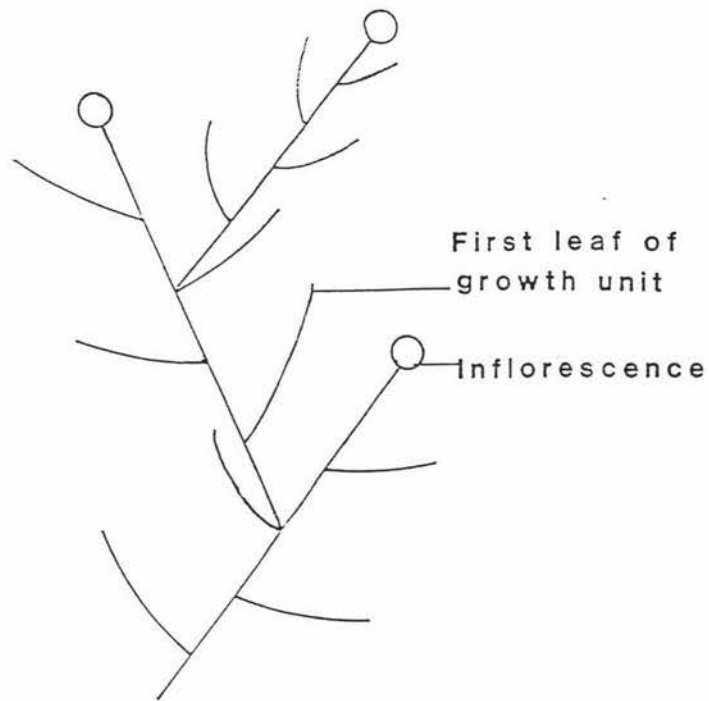


Fig. 1.1 Diagram to show sympodial branching system of *Hippeastrum*. Three growth units shown.

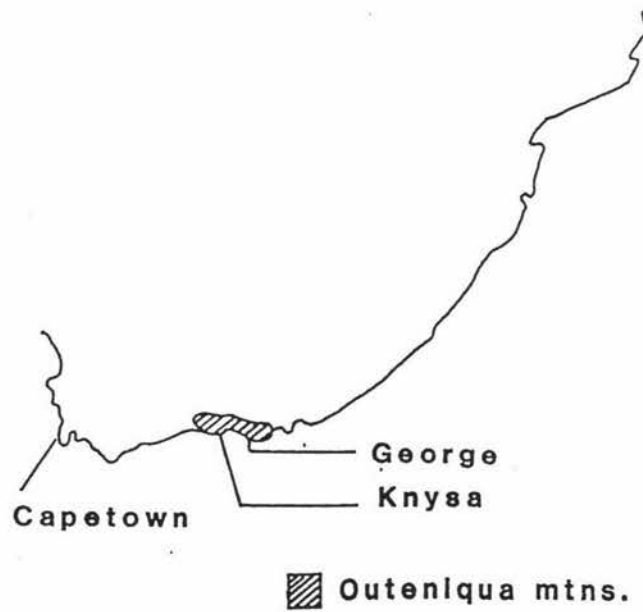


Fig. 1.2 Location of the Outeniqua mountains in the South-eastern Cape Province.

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 (Bergheof *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 (Dossier 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 *Brassia 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.