THE EFFECT OF DAYLENGTH AND TEMPERATURE ON GROWTH AND 'ONSET OF BULBING' IN TROPICAL CULTIVARS OF ONION

SAMSON ZERAY TESFAY
B. Sc. Crop Science (Asmara)

Submitted in partial fulfilment of the requirements for the Degree of Master of Science in Agriculture

in the

School of Agricultural Sciences and Agribusiness
Faculty of Science and Agriculture
Discipline of Crop Science
University of KwaZulu-Natal
Pietermaritzburg
South Africa

December 2005

DECLARATION

I, **Samson Zeray Tesfay**, certify that the material reported in this thesis represent my original work except where acknowledged. I also declare that these results have not otherwise been submitted in any form for any degree or diploma to any university.

Signed __________
Samson Z. Tesfay

I, Peter Lorimer Greenfield supervised the above candidate in the conduct of his dissertation study.

Signed P. L. Greenfield

ACKNOWLEDGEMENT

All my special and sincere thanks go to the following:

Professor P. L. Greenfield, Head of Discipline of Crop Science, University of KwaZulu-Natal, for his supervision of the study from the onset to its completion. His support, friendly and interactive approach is never to be forgotten. Above all, his availability, whenever needed was key during the study.

Professor A. Cairns, now of the University of Stellenbosch, for accommodating me upon my arrival in Pietermaritzburg.

Dr Isa Bertling, Discipline of Horticultural Science, University of KwaZulu Natal, for her assistance and expert opinions on the subject in addition to her friendly and interactive approach is never to be forgotten.

Drs P Ndlovu and A. Girma, Department of Biometry and Statistics, University of KwaZulu Natal, for their expert opinion on the statistical analyses.

Lowie de Klerk, Senior Technician, Controlled Environment Research Unit (CERU), University of KwaZulu Natal, for his complete and relentless assistance during the experiment in the growth rooms.

My father, **Zeray Tesfay**, my mother, **Berzaf Gebre-ezghi**, my sisters (**Eleni, Eden, Meron, Feven**), my brothers (**Elias, Abraham**) and my girl friend (**Nonkululeko A. Zwane**), who have always supported me morally and financially.

Solomon G. Tesfamichael, PhD student, University of KwaZulu Natal, for his expert opinion on the structure of the thesis.

Postgraduate students of the disciplines of Crop Science and Horticultural Science (**Dr. Ochuodho, Molipa, Odindo, Tracy, Zelda, Alison, Dambuza, Mark, Mathlou, Mireille, Nathan, Rendani, Rorisang**), for their support and friendship.

My friends (**Mengesteab, Samuel, Michael, Esayas, Alemseged, Misgina, Yoseph, Fitsum, Demeke, Dr. Legesse**), for their respect and support.

Staff and members of the disciplines of Crop Science and Horticultural Science, University of KwaZulu Natal.

The Human Resources Department (HRD) of the University of Asmara, Eritrea, for sponsoring part of my work.

Above all, my creator, the Almighty God, for giving me life and energy and ability to conduct this study.

ABSTRACT

Onions are widely produced within the tropics, but little scientific research has been done specifically on the Eritrean cultivars, like Hagaz Red 1 and 2 (HR 1, and HR 2). Many onion cultivars are limited in their range of adaptation due to the combined effects of photoperiod and temperature. A priority for research on the crop was to elucidate the local crop's growth response to environmental conditions, particularly temperature and daylength.

The Eritrean cultivars HR 1 and 2 and an American (Louisiana) cultivar Red Creole (RC) grown in South Africa were grown in growth rooms under all combinations of three daylengths (11.5h, 12h, 12.5h) and three day/night temperatures (25/12°C, 30/15°C and 35/18°C). Growth responses were determined at 108 days and by using a growing degree day (GDD) base. A broken-stick regression model was used to determine the points of inflection, indicating the initiation of bulbing. Based on leaf area and plant height data, mathematical differentiation equations and coefficient of determination (R^2) were applied to determine the base temperature (6.4°C) for these particular cultivars.

All three cultivars needed at least 12 h daylength for bulb initiation when assessed by a bulbing ratio ≥ 2.0. A bulbing ratio ≥ 2.0 characterizes the onset of bulbing. Under a 11.5 h daylength, a temperature higher than 25/12°C decreased vegetative growth. Temperature in this region may be a supra-optimal condition for the growth of these cultivars at this daylength. However, the 25/12°C and 30/15°C temperatures were found to be ideal for onion bulb production under 12 h and 12.5 h daylengths. The three cultivars (HR 1, HR 2 and RC) showed very similar growth response to the daylength and temperature interactions.

The thermal presentation of plant growth indicated that there were relationships between bulb initiation and rate of leaf area growth under inductive conditions (12 h and 12.5 h). Under the 12 h daylength, cultivars needed 343, 482, and 597 GDD units before bulb initiation and 405, 432, and 431 GDD to increase the rate of leaf area development at 25/12°C, 30/15°C, and 35/18°C, respectively. Under a 12.5 h daylength, these cultivars needed 344, 423, and 432.2 GDDs to initiate bulbing and 140, 411, and 579 GDDs to increase leaf growth rates at 25/12°C, 30/15°C, and 35/18°C, respectively. In the 12 h daylength, bulbing was initiated and followed by an increased rate of growth of leaf area. However, the reverse happened for the 12.5 h daylength. Overall, where plant response to temperature can be expressed as the rate of progress towards a morphogenetic change, GDD values can be used to predict a plant developmental stage at a particular temperature. It must be concluded that temperatures induced significant variations in growth components (leaf number, plant height, leaf area), and affected bulbing response.

The findings in this study confirmed that the cultivars require only a certain fixed amount of thermal time for their development at a particular temperature, and that, if anything, the slow growth rate at the higher temperature must be due to supra-optimal temperatures. They also require a minimum 12 h photoperiod for bulb formation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

CHAPTER 1
GENERAL INTRODUCTION

1.1 GENERAL BACKGROUND

Edible alliums are of major economic and dietary importance in all parts of the world. The common onion (*Allium cepa*) and garlic (*A. sativum*) are grown, traded and consumed in most countries. Because of their economic importance, great efforts have been made in the selection and breeding of locally adapted cultivars, and in the development of cultural techniques (Brewster and Rabinowitch, 1990).

Alliums are valued for their distinctive pungent to mild flavours and form essential ingredients of the cuisine of many regions. Onions are naturally packaged vegetables consisting of fleshy, concentric scales, which are enclosed in paper-like dry wrapping leaves, connected at the base by a flattened stem disc. They are produced in large quantities in many countries, and are traded within and between countries on a significant scale (Table 1.1). However, there are specific problems that occur when onions are grown and stored in the tropics (Currah and Proctor, 1990a). One such problem is splits or doubles. This condition is caused by cultural and environmental factors as well as being influenced by genetics.

Table 1.1 The leading ten producer countries for dry bulb onions (FAO, 2005)

Producer country	Total production (Mt)	Area harvested (Ha)
China	19,047,000	900,830
India	5,500,000	530,000
Russia	1,640,000	125,000
Turkey	2,000,000	78,000
USA	3,669,540	67,440
Brazil	1,058,960	56,598
Iran	1,450,000	45,000
Poland	700,000	34,700
Japan	1,200,000	23,000
Spain	1,042,700	22,500

The principal environmental factor initiating the onset of bulbing in the onion is daylength (Brewster, 1990) and cultivars are selected in the first instance on their ability to produce bulbs under the daylength conditions prevailing in the region where they are to be grown.

Researchers (Magruder and Allard, 1937; Kato, 1964; Butt, 1968; Terabun, 1971a; Steer, 1980a and Wiles, 1989) have shown that tropical onion cultivars bulb earlier under long day conditions and Austin (1972) concluded, based on four cultivars, that although bulbing occurred earlier under longer days, the sequence in which they bulbed remained similar. However, other factors can interact with daylength to influence the time of bulbing and, for example, Wiles (1989), reported that some cultivars behaved differently in terms of their bulbing sequence under field conditions compared with controlled environment conditions.

The photoperiodic response is a high irradiance response mediated by phytochrome (Lercari, 1982, 1984) and as such is affected by the spectral quality and irradiance of incident light (Woodbury and Ridley, 1969; Austin, 1972; Mondal *et al.,* 1986b). The response to light is modified by temperature, and numerous reports indicate that bulbing is promoted by high temperature, and delayed or prevented by reductions in temperature (Thomson and Smith, 1938; Heath, 1943; Kato, 1964; Butt, 1968). The situation is, however, complicated by the occurrence of flower stalk initiation at low temperature, which may prevent bulb development from taking place (Thomson and Smith, 1938; Heath, 1943). Interactions between daylength and temperature occur which may result in failure of plants to initiate bulbs in certain daylength/temperature combinations (Steer, 1980a), even though they may be able to bulb at lower temperatures in the same daylength. Steer (1980b) also found that diurnal variation in temperature might affect the timing of bulb initiation.

The control of bulb development in onions has been the subject of numerous studies reviewed by Brewster (1977). Amongst the factors promoting bulbing, a long photoperiod is of prime importance (Garner and Allard, 1923; Heath and Holdsworth, 1948; Butt, 1968; Steer, 1980a). Cultivars adapted to different localities differ primarily in their response to photoperiod (Magruder and Allard, 1937). In addition, bulbing is promoted by high temperatures (Thomson and Smith, 1938; Heath and Holdsworth, 1948; Steer, 1980a), and seasonal differences in temperature rather than photoperiod control bulb development in some tropical areas (Abdalla, 1967).

Despite the work by Kedar *et al.* (1975) and Steer (1980a, b) in controlled environments, the factors controlling the timing of bulb initiation in short day onions in areas with little variation in daylength are not well understood. The timing of bulb initiation is important in determining yield, since yield is related to the amount of radiation intercepted by the leaf canopy of a crop during bulb growth (Brewster, 1982; Brewster *et al.,* 1986; Brewster, 1990). Since bulb initiation is accompanied by cessation of leaf emergence (Heath and Holdsworth, 1948), early initiation can severely restrict the plant's yield potential. On the other hand excessive delay in bulb initiation can result in quality defects such as double bulbs, thick-necked bulbs and bolters (Robinson, 1971; Brewster, 1990).

Generally, the development rate of onions, which strongly depends on the environment and growing conditions, determines the earliness of the crop. This, in turn, can influence the quality of the bulbs. The most important characteristic of development is bulbing, which occurs when the plants no longer form green leaf blades but bladeless bulb scales (Brewster, 1990). Among the different measurements used to determine the onset of bulbing in onions, it was observed that the time to attain a bulbing ratio of 2.0 was close to that of bladeless bulb scale initiation. Under a 12 h photoperiod, bulb scale initiation occurred a few days later than the time at which a bulbing ratio of 2.0 was reached. However, under a 16 h photoperiod bulb scale initiation occurred a few days earlier, probably as a consequence of a more rapid switch-over to scale initiation under longer photoperiods (Mettananda and Fordham, 1997). Bulbing is the outcome of the combination of many factors of which daylength, temperature and the red:far-red ratio of the light are the most important (Magruder and Allard, 1937; Butt, 1968; Mondal *et al.,* 1986b). Because faster development leads to earlier bulb formation and thus earlier cessation of green leaf formation (Brewster *et al.,* 1987), development rate can also influence dry-matter production. However, the extent to which production is affected in this way depends on the extent to which maximum light absorption of the crop coincides with the maximum amount of available light during the growing season. Moreover, the production of green leaf blades, and therefore the leaf area index, has an effect on the red: far-red ratio of the light beneath the canopy. This in turn influences development rate (Mondal *et al.,* 1986b).

The work described in this thesis is an attempt to investigate the effects of photoperiod, and temperature on the 'onset of bulbing' in three tropical onion cultivars. The two local Eritrean cultivars (HR 1, HR 2), are from the Hagaz location in Keren, Eritrea (Latitude 15° 46′ 40″ N and Longitude 38° 27′ 29″ E, and altitude 960 m above sea level) (Figure 1.2). The third cultivar, Red Creole (RC), is widely grown in South Africa. Also, the thermal presentation of plant development is used to determine the growing degree days required to compare bulbing and leaf growth of the cultivars to relate time of initiation of bulbing under different daylengths.

The study was conducted under controlled environment conditions which were selected according to the climate of the growing period where the local Eritrean cultivars were grown under field conditions. The background to the climate of the area from which the Eritrean cultivars originated is presented (Table 1.2, Figure 1.1).

Eritrean production environment

The onion is an important crop in Eritrea and is used in most culinary recipes. It is produced nationwide in both the warmer lowlands and, to a lesser extent, in the highland regions. Most seed is produced from local breeding populations and the landraces are considered to be longday pungent types. Onions are considered to have a wide adaptability in Eritrea but they need improvement, with breeding objectives focusing on, among others, bolting and splitting resistance, as well as resistance to pests and diseases common to onion, such as thrips and *Fusarium spp.* basal rots (Garforth, 2001). Onions are almost exclusively planted by Eritrean farmers in non-raised beds, surrounded by dikes which are flood irrigated. Many farmers depend on ground water to irrigate crops, except during the rainy season between June and August. Onions are generally hand harvested.

Eritrea's agro-climatic conditions make it suitable for the production of a broad range of fruits, vegetables as well as cut flowers. The range of altitude, temperature and soil variability of the country has created an enormous ecological diversity and a huge wealth of biological resources. Onions are considered to be a major vegetable crop, cultivated over a larger area of the region. However, little scientific research has been done on the specific local cultivars. The present study is initiated on the basis of the researcher's experience of onion growing conditions in Eritrea, and the immediate need for adapted cultivars for improvement. A priority for research on the crop is to elucidate the Eritrean crop's growth response to environmental conditions, particularly temperature and daylength. The seasonal variation in temperature and daylength of the growing area is typical of the arid tropics (Figure 1.1). The daylength trend of the local growing site over the year is calculated using the standard formula shown below:

$$D = (2/15)\ \mathrm{Arc\ COS}\ (-\mathrm{Tan}\ \theta\ \tan \delta) \ldots\ldots\ldots\ldots\ (1) \qquad \text{(Roderick, 1992)}$$

Where:

D – daylength

δ – Declination (in decimal degrees) = $23.45\ \mathrm{Sin}\ [360(284+n)/365]$

– Where n is the day of year

θ – is the latitude e

N.B. to change degree decimals into radians, simply multiply it by $2\pi/360$.

The onion production period in Eritrea normally ranges between December and May when mean annual temperatures can range from 29°C to 34.8°C during the production period.

Table 1.2 Mean monthly temperature (°C) and daylength (h) of Keren (Latitude 15° 46′ 40″ N and Longitude 38° 27′ 29″ E) over a year (M.O.A, Eritrea, 2001).

Months	Max.Temp. (°C)	Min.Temp. (°C)	Mean temp. (°C)	Daylength (h)
January	28.7	12.4	20.6	11.3-11.33
February	29.9	12.8	21.4	11.34-11.67
March	31.6	15.2	23.4	11.69-12.12
April	33.8	16.9	25.4	12.13-12.52
May	34.8	17.7	26.3	12.53-12.82
June	33.3	16.7	25.0	12.83-12.88
July	28.6	16.9	22.8	12.88-12.68
August	27.3	16.3	21.8	12.67-12.31
September	30.5	15.0	22.8	12.29-11.88
October	31.6	15.5	23.6	11.86-11.46
November	29.9	14.9	22.4	11.45-11.18
December	29.0	13.5	21.3	11.17-11.12

*-Max- Maximum; Min- Minimum.

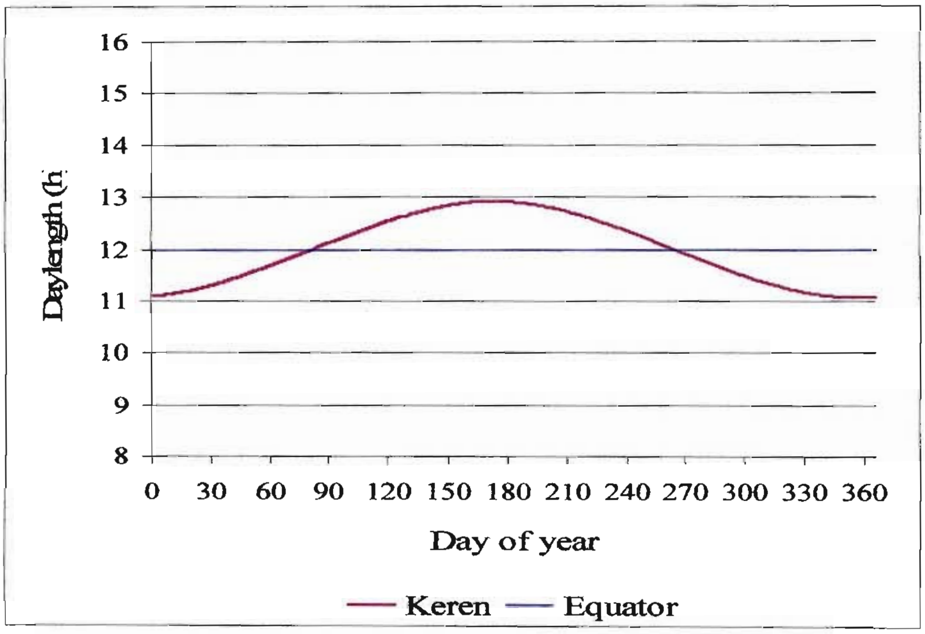


Figure 1.1 Annual fluctuation of daylength for Keren (Latitude 15° 46′ 40″ N and Longitude 38° 27′ 29″ E) over the year.

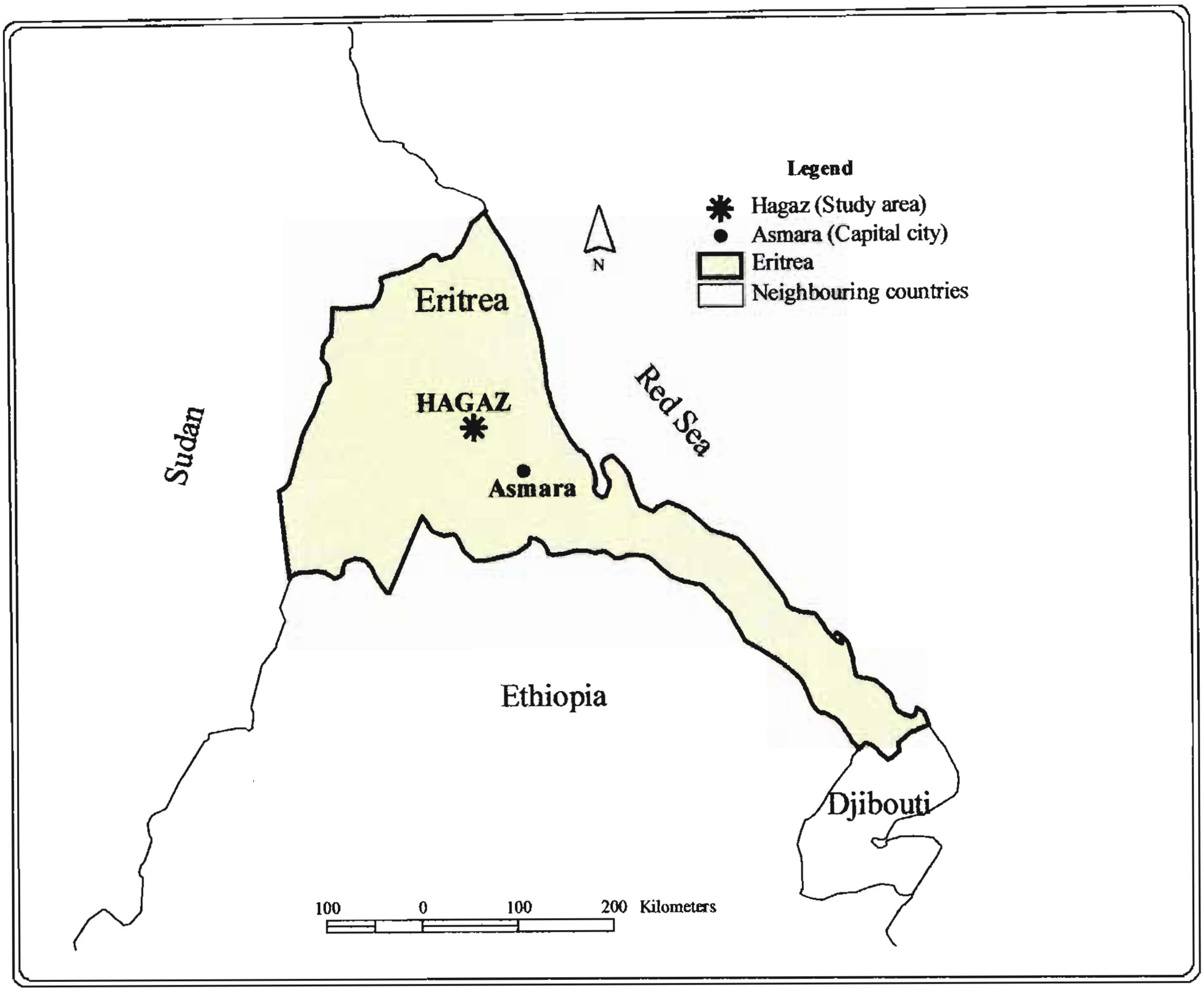


Figure 1.2 The geographical position of Hagaz (Latitude 15° 46′ 40″ N and Longitude 38° 27′ 29″ E) where the local varieties are grown.

1.2 ONIONS, THEIR GEOGRAPHICAL ORIGIN AND USES

1.2.1 The Geographical Origin of the Onion and Related Species

The onion (*A. cepa*) is no longer found as a wild species, though other closely related species still exist in the area which is regarded as the botanical centre or origin for the crop: this being the south western part of central Asia, largely covered by the countries of Iran, Afghanistan, Pakistan and the southern republic of the Russia (Jones and Mann, 1963, cited in Currah and Proctor, 1990a). Here wild *Allium spp.* such as *A. vavilovii*, *A. oschalinii* and *A.*

galatinum can still be found, which look very similar to the common onion and share common morphological features (Currah and Proctor, 1990a). During the long period of domestication, the onion has become adapted to a variety of climates and growing systems. There are vegetatively propagated variants of *A.cepa*, which are shallots and multiplier onions.

1.2.2 Domestication and Utilization

Many onion cultivars are limited in their range of adaptation due to the combined effects of photoperiod and temperature. Cultivars bred in temperate countries such as cv. Ailsa Craig will not form bulbs in the tropics as the daylength is too short (Purseglove, 1972). Although onions are long-day plants, short long-day cultivars have been developed, which initiate bulb formation under the relatively short daylengths of the tropics. Cultivars also vary in their susceptibility to floral induction (bolting), which is induced by low temperatures. Cultural adjustments such as altitude, date of planting, type of propagating material and spacing, may help in attaining successful production of cultivars. It is essential that cultivars should be carefully tested under local conditions to ascertain their adaptability to the environment.

Cultivars recommended for the tropics include Early Cape Yellow Flat, Excel, Granex, Red Bermuda, Red Creole, Texas Grano, White Creole and Yellow Bermuda. White Lisbon is widely grown in temperate countries for spring onions, but it is a long day cultivar; Crystal white and Long white, which are short long-day cultivars, are better suited to production in the tropics (Purseglove, 1972).

Since classification of plants according to photoperiodic response can be complicated, it is simplified to the following:

1. Short day plants (SDP)
    A. Qualitative – flowering only occurs in short days.
    B. Quantitative – flowering is accelerated by short days.
2. Long day plants (LDP)

A. Qualitative – flowering only occurs in long days

B. Quantitative – flowering is accelerated by long days

3. Day neutral plants (DNP) – flowering occurs at any daylength. Not affected by daylength. (Currah and Proctor, 1990a)

There are also other classifications, such as:

- Long short day plants – flower in short days of autumn, following the long days of summer.
- Short long day plants – flower in long days of summer following the short days of spring.
- Intermediate day plants – flower when the days are neither too short nor too long. Short day plants need not necessarily require short days to flower nor long days to flower. It depends on the critical photoperiod. (Currah and Proctor, 1990a)

In the tropics, however, well-adapted onion populations are found in regions where the daylength varies little throughout the year. Evidently, photoperiod must carry less importance as an environmental signal in tropical parts of the world; at the equator itself days oscillate narrowly around 12 hours long, and in regions within the tropics the variation over the year in daylength is within a narrow range (approximately 11 to 13 hours). The onions, which can be grown in the tropical regions, are often referred to as short long-day cultivars. This does not imply that these onions are physiologically short-day plants, but they have a long-day response at a short daylength (Currah and Proctor, 1990a).

1.3 ONION GROWTH

Vegetative growth of onion is divided into three stages (Brewster, 1990). First, a period of slow growth, followed by a second period of rapid leaf growth, where successive leaves grow larger, and the third phase when the bulb grows. Onion leaves must be exposed continuously to bulb-inductive photoperiods in order to start and complete bulbing. Numerous authors have shown that bulbing can be reversed and green leaves will resume growth if plants are transferred to short, non-inductive photoperiods following inductive photoperiods (Kedar *et* *al.*, 1975). This can occur even in plants that are at an advanced stage of bulb development. The bulbing process remains sensitive to a photoperiodically inductive phase virtually up to the senescence of all green leaves on the ripening bulb (Brewster, 1997).

There was some evidence that leaf senescence was more rapid in long than in short days (Austin, 1972). Using defoliation techniques, it was shown that bulbing in onions relies on the perception of a long day stimulus by young developing leaves. Bulbs always grew more rapidly in older plants, and young plants would not bulb until they had approximately four foliage leaves. By removing leaves from differently aged plants, it was shown that plant age, rather than leaf area, is a major factor determining the plant's response to long days (Sobeih and Wright, 1986).

The greater efficacy of younger leaves to cause bulbing may be because of a greater photosynthetic rate rather than to a greater photoperiodic sensitivity, and further investigation would be needed to clarify this point (Sobeih and Wright, 1986).

Seedling size in terms of leaf number, leaf area and total weight at transplanting has a marked effect on the time to 'onset of bulbing', bulb quality and yield. Bulbing can not take place prior to the achievement of specific age, irrespective of plant size. Old plants (4.5 months) were able to induce bulbing at the same time or faster than young plants (1 or 2 months) even when the latter had a much greater leaf area (Sobeih and Wright, 1986).

Some results indicated that the size of transplanting, in terms of leaf number, leaf area and total weight, continues to affect the size of the plant until maturity. Under low light conditions (maximum PAR levels of 800 μmol m^{-2} s^{-1}) and low night temperature (minimum 11°C) in the UK, transplant size negatively correlated with time to onset of bulbing and maturity, and positively correlated with bulb weight, and percentage contribution from scale leaves to total bulb weight positively correlated the higher PAR and the higher the temperature (Mettananda and Fordham, 1999).

Leaf primordia in onions may develop in to green leaves. Green leaves, produced in short days, have long cylindrical sheaths and long green blades. Scale leaves, produced in long days have only a rudimentary blade, and consist of leaf sheaths, which thicken into storage tissue instead of elongating. Leaves produced in lengthening days during bulbing may develop an area of thickened storage tissue at the base of a green leaf (Bertaud, 1990).

1.4 AIM AND OBJECTIVES

The aim of this study was to investigate the effects of photoperiod, and temperature on the 'onset of bulbing' in three tropical onion cultivars. They were grown in controlled growing conditions of varying daylengths and temperature levels simulating tropical field conditions required by local Eritrean cultivars for growth and development. The specific objectives of this study were:

1. To elucidate response of leaf area, leaf number, plant height and 'onset of bulbing' of three onion tropical cultivars to combined effects of daylength over the range experienced in Eritrea (11.5 h, 12 h, 12.5 h) and temperature (25/12°C, 30/15°C, 35/18°C).

2. To determine the growing degree days required to initiate bulbing and stage of plant development in terms leaf area, leaf number and plant height towards 'onset of bulbing' of the tropical cultivars.

3. To determine the growing degree days in terms of both 'onset of bulbing' and development of growth components of the tropical onion cultivars. This would be important in assisting growers in scheduling planting dates and harvesting time. Accurately predicting harvest date and the crop's developmental stage has widespread application for improving crop management.

CHAPTER 2

LITRATURE REVIEW

2.1 MORPHOLOGY AND PROPAGATION OF ONION

2.1.1 Distinguishing Characteristics of Onions

Onion plants develop a distinct bulb. According to the cultivar, these bulbs vary in size (small, medium, large), colour (white, yellow or red), shape (flattened, round, or globular), texture (fine, or coarse), and pungency. The plant is naturally biennial, with fleshy bulbs developing the first season and seed stalks developing during the following season. The leaves develop from a short flattened stem at the base of the bulb. They consist of two parts: the blade and sheath.

The sheaths are fleshy and surround the younger leaves within them. The blades are terrate green, pointed and hollow. The onion is a biennial herb usually grown as an annual. All parts produce a strong onion odour when crushed.

2.1.2 Morphology

Each leaf arises as a ring of tissue, which grows upwards as a tubular sheath. The leaf blade elongates from one side of the top of the sheath. As the stem grows upwards, it also broadens, as is shown by the divergent arrows in Figure 2.1. New roots continually arise in the younger (upper) part of the stem (Jones and Mann, 1963a).

The primary root and its derivatives are produced from the seedling axis (Figure 2.1). All additional roots are adventitious and arise from root initials above nodes on the compressed stem disc. Root diameter is 1 to 2 mm, with no subsequent increase in thickness; primary branches may be produced, but these seldom re-branch. New adventitious roots are initiated as the plant top enlarges and older roots may die as the plant ages (Halfacre and Barden, 1979).

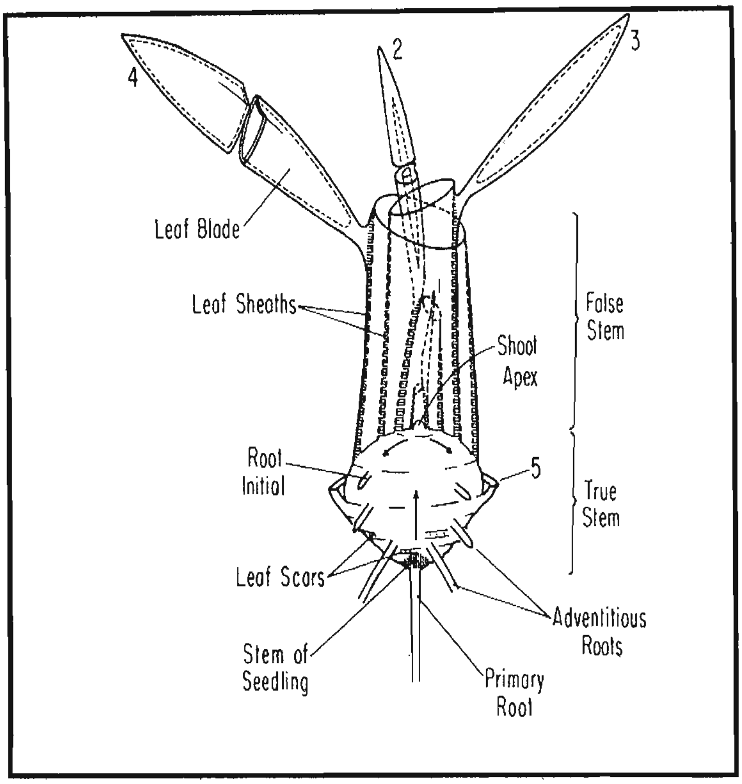


Figure 2.1 A diagrammatic sketch of the development of the stem, leaves, and roots, in a young plant of the common onion. Each new leaf arises at the stem or shoot apex, leaf 1 being the youngest and leaf 4 the oldest of the four leaves shown (Jones and Mann, 1963a).

A very short compressed stem is produced at the base of the leaves, which increases in diameter as growth continues, producing the shape of an inverted cone. The older part later decays. New leaves are produced by the apical meristem; the later eventually grows out to produce the inflorescence axis, which pushes up through the pseudostem formed by the sheathed leaf bases. Short-stemmed branches or buds may rise singly at the base of, and within, the leaf sheath.

Alternate distichous leaves are produced in succession from the apical meristem, each arising as a ring, which elongates to form the tubular leaf sheath and projects above ground. The cylindrical leaf blade, at first solid and later becoming hollow, emerges from the apex of the leaf sheath of the previous leaf (Figure 2.1).

Under favourable conditions of daylength and temperature, when the plant has reached a certain stage of growth, a bulb forms from the thickening of the leaf bases a short distance above the stem. The outer leaf sheath bases are thin, fibrous and dry, enclosing thickened leaf sheaths with aborted leaf blades; these in turn enclose entire leaves with thickened leaf sheaths. Later, as the bulb matures, the leaf sheaths weaken above the bulb and fall over (Jones and Mann, 1963a).

When the bulb reaches full maturity, the meristem ceases to produce new leaf primordia. After a dormant period, provided the temperature is favourable, an inflorescence is initiated from the apical meristem. The inflorescence is raised through elongation of the internodes on top of an enlarged scape that is at first solid, but later through differential growth, becomes hollow. The scaope, 0.3 to 1.0 m long, is swollen below the middle. The developing inflorescence is protected by a membranous spathe, which splits to give 2 to 3 persistent papery bracts enclosing the terminal umbel. The number of inflorescences per bulb varies from 1 to 12 or more, depending upon the number of lateral bulbs present. A terminal umbel of 50 to 2000 flowers is produced, which is an aggregate of cymes of 5 to 10 flowers each. The flowers in each cyme open in a definite sequence, but, as there are many cymes, the flowers of the umbel appear to open irregularly (Jones and Rosa, 1928, cited by Jones and Mann, 1963a). The development of the flower parts has been described in some detail by Jones and Emsweller (1936) (cited in Jones and Mann, 1963a).

Nectaries occur in the septa of the ovary opposite the enlarged base of the three inner stamens. The nectar collects between them and the ovary wall. The flowers are protandrous; the inner stamens shed their pollen first, followed by the outer stamens, the whole process taking two to three days, after which the style reaches its full length and becomes receptive. Insects, such as bees, blowflies and green bottles, feed on the nectar and transfer pollen within an umbel and between different plants.

After fertilization of the ovule, the developing seed is smooth and plump while maturing, but becomes black, wrinkled and irregular on drying to dimensions of about 6 × 4 mm. The embryo is crescent shaped or curved into a circle and is embedded in a thick-walled endosperm, containing reserves of carbohydrates, proteins and fat.

2.1.3 Propagation

The propagation of onion has been described in some detail by Jones and Mann (1963b). Farmers propagating their crops from seeds, dry sets or transplants produce large mature bulbs. In direct seeding, the seed is sown at a depth of about 10 mm. In row seeding they are planted about 0.30 m apart, with a seeding rate of 4 to 5 kg ha^{-1} and later thinned to about 75 mm apart within rows.

Onions for bulb production are best sown in nursery boxes or seedling trays and transplanted after six weeks when the stem diameter is about 4 to 5 mm. When transplants reach the proper size, they should be transplanted and not held in the nursery. To aid in pulling, plants can be undercut or given a light irrigation; but, often they can be pulled without preliminary treatment. To facilitate transplanting, the roots, if long, are trimmed with shears or a knife, and the excess tops are cut or twisted off, so that the pruned seedlings are about 125 or 150 mm. In most places transplanting is still done by hand. Seedlings are usually distributed just ahead of the planter. A short stick or dibble is used to make a hole for the seedling and to firm the soil after planting.

For the production of dry sets in tropical areas, the seed is sown thickly in beds at a seed rate of 67 to 90 kg ha^{-1} in order to produce seedlings with stunted growth and early maturing bulbs of small size, usually less than 25 mm in diameter. The small plants are pulled and the drying tops are removed. The young bulbs are cured for 4 to 8 weeks in trays, in which time they are spread to a depth of about 100 mm. Cured dry sets can then be stored for several months. Storage at above 27°C or below 0°C results in less bolting of the subsequent crop than storage at intermediate temperatures of 7°C to13°C. Smaller dry sets produce plants bolting less than large sets (Jones and Mann, 1963b).

Sexual propagation

Use of F_1 hybrid seed, produced on male sterile female parent, is on the increase in temperate countries. A simple method has been found for obtaining 100 % cross pollination on a large scale in plants that normally have both sexes within the same flower. The method utilizes biological emasculation of the plants, in which the pollen grain either fails to develop or is not viable. Such plants are referred to as being male-sterile. Male sterility of some form has been found in many crops, and breeders are always on the alert for such plants among their selections. Male-sterile plants appear unexpectedly even in long-established commercial cultivars (Jones and Davis, 1944).

Two types of male sterility have become economically significant, and are used by plant breeders: cytoplasmic male sterility and genetic male sterility (Duvick, 1967). In the former, sterility is carried in or influenced by the cytoplasm. In the latter, it is carried in or influenced by the germplasm of the nucleus, which contains the genes or hereditary characters.

In commercial production of onion seeds, 4 to 12 rows of plants are planted with a male-sterile type for each one to two rows of male-fertiles, and they must both flower at the same time. Bees transfer the pollen to the male-sterile heads, and the hybrid seed is produced on these heads. The male-fertile flowers may be destroyed or harvested separately after pollination is completed. The seed that is harvested, being hybrid, produces an onion superior both in yield and flavour.

Bulbing onions typically produce one large bulb. It is generally considered that warm conditions are essential for the production of mature onion bulbs. Onions are basically long-day plants, with a critical minimum daylength of about 12 hours. However, temperature is also a critical factor for bulbing and even more so for flowering and consequent seed production. For the latter a relatively low temperature (10-20°C) is required, regardless of daylength (Halfacre and Barden, 1979).

The number of apices developing into flower initials increased with decreasing plant temperature. When seedlings were grown at a temperature of 9°C, up to 90 % of the plants at harvest had flower initials (Dragland, 1972). Wiebe (1990) has shown that plants will not form flower initials unless they have been subjected to temperatures below 18°C and he suggests that they have a juvenile phase.

As reported by Cober and Curtis (2003), understanding the control of flowering time in photoperiod-sensitive plants has been furthered by grafting experiments. In soyabean (*Glycine max* (L.) Merr.), genes which control flowering time have been identified and their response to photoperiod, characterized. Grafting experiments allow the study of interactions between genotypes. It appears that both floral inhibitors and promoters are active in determining flowering time for soybean under non-inductive conditions. Under non-inductive conditions, early flowering in soyabean results from a combination of a lack of floral inhibitors plus the action of floral promoters. It was indicated that both floral inhibitors and promoters are produced in fully expanded leaves, developing leaves, or buds. Promoters and inhibitors mediate flowering time simultaneously and antagonistically.

Bolting (premature or untimely production of inflorescences) is induced by low temperature, provided that the bulbs have already grown to a sufficient size. Bolting is not influenced by photoperiod. Cultivars vary in their susceptibility to bolting, but this depends on the climatic conditions under which they are grown. The bulb is produced during the first season and seed stalks are produced during the second season. During the early part of the season the plants develop leaves and roots and during the latter part they develop their bulbs. Consequently, environmental conditions should permit extensive foliage and root growth before bulbing begins. Since foliage and root growth precede bulb formation, carbohydrate utilisation is dominant during the first part of the growing season, and carbohydrate accumulation is dominant during the latter part (Purseglove, 1972).

Although seed production is essential for the perpetuation of the onion as a crop, premature seed stalk production or bolting is undesirable and can be economically disastrous as bulbs produced by a bolted plant are unmarketable. Low temperatures induce bolting with the production of inflorescences, provided that the bulbs have already grown to a sufficient size. It is not influenced by the photoperiod. Cultivars vary in their susceptibility to bolting, but this does also depend upon the climatic conditions under which they are grown (Purseglove, 1972).

As reported by Sanders and Cure (1996), the efficacy of undercutting as a technique to control bolting of two short-day cultivars (Buffalo and Granex 33) was studied in controlled-environment chambers. They were grown to the third, fifth, and seventh visible leaf stages in a 10-hour photoperiod at 22/18°C (day/night) and then exposed to 30, 40, 50, 60, or 70 days of vernalizing temperatures (10/10°C). Half of the plants were undercut at the initiation of the vernalizing treatment. After vernalizing treatments, plants were returned to 14 hour photoperiods at 22/18°C. 'Buffalo', which is resistant to bolting, did not flower significantly under any of these conditions. The flowering response of cv. Granex 33 increased with both leaf number at vernalization and duration of vernalization. Undercutting cv. Granex 33 increased the days of vernalization required for flowering and reduced the proportion of flowering relative to controls. Overall, dry matter accumulation was unaffected by leaf number at vernalization or the duration of vernalization but was reduced approximately 30% by undercutting. In both cultivars, fresh mass per bulb decreased with increasing leaf stage of vernalization and number of vernalizing days. Undercutting also decreased fresh mass per bulb, but through its effect on bolting, undercutting increased marketable yield for plants vernalized and undercut at the fifth and seventh leaf stage.

2.2 GROWTH AND VEGETATIVE DEVELOPMENT OF ONIONS

2.2.1 The Life Cycle of Onion

The normal life cycle of onion has been described by many authors (for example, Hayward, 1938; and Jones and Mann, 1963, cited in Currah and Proctor, 1990b). The onion seed, which contains a small, coiled embryo and an endospermic food reserve, imbibes water when wetted and the cells re-hydrate. The embryo starts active growth, drawing on the nutrients in the endosperm, to which it is attached by a haustorium-like structure at the tip of the cotyledon. When the seed germinates the radicle emerges, then the cotyledon elongates forming a looped structure, which breaks the surface of the ground while the seed is still below the ground. The seed leaf (cotyledon) continues to elongate at the base until, eventually, the remains of the seed coat from which it has grown is carried up above the ground level, still attached to the tip of the cotyledon. The meristematic growing point of the seedling remains below the ground, within the area where the cotyledon joins the radicle. This zone is crucial to the organization of the onion plant throughout its life. From the apical meristem the seedling develops a succession of leaves, which grow from the flattened stem or base plate, which forms around the meristem. Each foliage leaf is made up of a hollow photosynthetic blade and a cylindrical sheath, which connects the blade to the base-plate shaped stem. Cell division takes place near the base of the leaf blade and the sheath, so that the oldest part of each leaf is the tip, and the youngest part is the base of the leaf sheath and leaf blade. Each new leaf is produced inside the encircling leaf sheaths of older ones and grows up through them, so that a neck or 'pseudostem' is formed from the concentric leaf sheaths. Each new leaf blade emerges through a small hole or pore at the junction of the blade and sheath of the previous leaf. The hollow tapering leaf blades are carried in rows arranged opposite to each other.

Adventitious roots are also produced from the base plate. New roots form in irregular rings above and around the older ones and emerge through the corky outer tissue. Each successive ring contains more roots than the previous one throughout the time that active vegetative growth continues.

The leafy plant eventually ceases to form leaf blades. Instead, the apex begins to initiate a number of bladeless, concentric, thickened leaf sheaths; these form the bulb scales. Together with the swollen lower leaf sheaths of the older leaves, they make up the fleshy part of the onion bulb. Studies on the movement of assimilates during bulbing have shown that most of the dry matter in the green leaves is transferred down to the bulb at this stage, contributing to both the swollen leaf sheaths and to the bladeless fleshy scales. The papery outer bulb scales are formed from the expanded dried out bases of the older leaf sheaths (Currah and Proctor, 1990b).

When no further leaf blades are produced to support the plant from the inside, the onion's neck becomes hollow, and the top of the plant falls down under the weight of the leafy blades. The green blades gradually senesce and die, but during this period nutrients from the leaf blades are still exported into the bulb, which continues to store them (Currah and Proctor, 1990b). When this process is complete, the onion ceases to grow and is ready for harvest. If it remains in the ground, the plant may root again and re-growth may start, particularly if the soil is wet.

2.2.2 Climate and Cultural Requirements

Onions can be grown under a range of climatic conditions, but they succeed best in a mild climate without excessive rainfall or extremes of heat or cold. They are not suited to regions with heavy rainfall in the lowland humid tropics. Cool conditions with an adequate soil water supply, are most suitable for early growth, followed by warm, drier conditions for maturation, harvesting and curing. They can be grown on a variety of soils, but the soil should have good total available moisture (TAM), be non-packing and friable; good fertile loam usually gives the best results. The optimum soil pH range is from 6.0 to 7.0. Onions thrive best on highly fertile, slightly acid, well-drained sandy loams and organic soils. These soils permit normal development of the bulb, and have adequate water-holding capacity (Currah and Proctor, 1990b).

Onions grow optimally at temperatures ranging from 10°C to 25°C. Seeds can germinate at temperatures from 7°C to 30°C, but do best at about 18°C (Hartmann *et al.,* 1981). Onions require cool temperatures during the seedling stage and moderately high temperatures during bulbing. Moderately high temperatures, particularly when combined with a dry atmosphere and low relative humidity, facilitate harvesting and curing of bulbs (Edmond *et al.,* 1957).

Scully *et al.* (1945) have shown that when onion plants are subjected to photoperiods which are well above those that are critical for the cultivar, bulbing starts immediately; within the critical range, however, bulbing is somewhat slower, and the plant is more susceptible to the influence of other environmental factors. Thus, at photoperiods that were much above the critical stage, nitrogen nutrition did not influence the bulbing response, but when plants were grown near the critical photoperiod, a deficient nitrogen supply had the same effect as lengthening the photoperiod, and a high nitrogen supply had the same effect as shortening the photoperiod. At critical photoperiods, then, a deficiency of nitrogen hastens bulbing, and an excess of nitrogen slows the bulbing process. The 'critical' photoperiod, as used here, refers to that daylength which is just sufficiently long to induce bulbing. At this critical daylength, changes in such factors as nutrition and temperature have their most decisive effect on bulbing.

Induction of bulbing is controlled by the photoperiod, the stimulus being received through the leaves. Under very short daylengths, the plants form new leaves indefinitely, without bulbing. The critical daylength varies from 11 to 16 hours, depending on the cultivar. Long-day cultivars developed in temperate countries will not form bulbs in the shorter days of the tropics, for which short-day cultivars are required. Temperature also plays an important role. Bulbing takes place more quickly at warm than at cool temperatures, provided that the minimum photoperiod for the cultivars has been reached. Plant size also has some effect and good vegetative growth should be obtained before the bulbing stage is reached. Onions mature quickly when planted closely. Excessive nitrogen fertility slows down the bulbing process (Halfacre and Barden, 1979).

2.2.3 The Effect of Photoperiod, Temperature and Radiant Flux on Bulbing

2.2.3.1 Induction of bulbing and bulb development

Changes in onion plant growth and development are closely attuned to seasonal changes throughout the year. This is most noticeable in the timing of the onset of bulbing or flowering. Onion plants have dual photoperiodic requirements. Bulb formation is promoted by long days. Short-day conditions (non-inductive) are unfavourable for bulbing; further responses of plants to inductive temperature results in flower initiation, while after that, long day conditions usually accelerate flower stalk emergence. Genotypic variation in photoperiodic sensitivity appears to be determined by several factors such as critical day length, duration of juvenile phase, and responsiveness to the ratio of red:far-red light enhancement during the twilight period. For onion bulbing, it is impossible to determine the real length of inductive period, because bulbing is photoperiod dependent right until 'maturity' (Tarakanov, 2002).

Bulbing in onions is induced quantitatively by long days. This concept means that for a particular onion population, a certain length of day can be determined which must be attained before bulbing takes place. Regardless of the other environmental conditions within this concept, factors such as temperature, nutrition and spacing play important parts in accelerating or slowing down the bulbing process. Internal factors such as plant age or size also have a strong influence on the readiness of onion plants to respond to external stimuli (Jones and Mann, 1963b). Brewster (1994) illustrated the main factors that control onion bulbing and how they interrelate (Figure 2.2).

The onion plant is very responsive to both temperature and photoperiod. The critical minimum daylength for bulbing varies among cultivars but is normally between 12 and 15 hours. Even if the photoperiod is adequate, a minimum temperature must be met, or bulbing is further delayed. The ideal climate would be a cool weather early in the season with increasing temperature as maturity approaches (Williams *et al.,* 1991). The lengths of day to which particular onion cultivars respond by forming bulbs vary greatly. Onions adapted to high latitudes start to initiate bulbing when daylengths of 14 to 16 hours are reached, and often complete the bulbing process under declining day lengths in the autumn. The onion cultivars adapted to these regions are commonly referred to as long-day onions. They are sown or planted as sets (in the spring so that they can grow during warm summer).

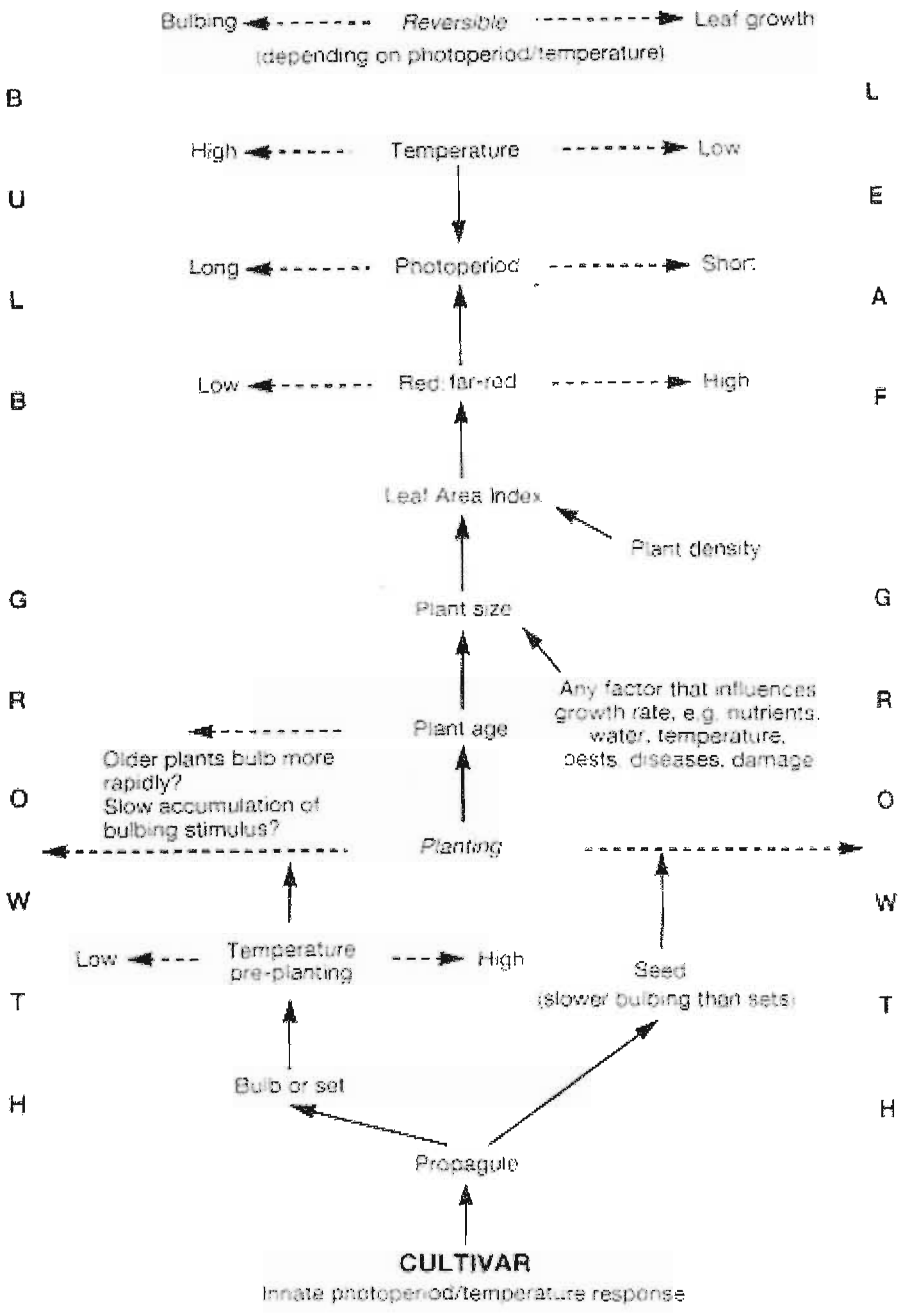


Figure 2.2 A schema showing the main factors that control bulbing in onions and how they interrelate (Brewster, 1994).

2.2.3.2 Photoperiod

Bulbing in onion is primarily controlled by photoperiod and is promoted by long day conditions. Cultivars differ in their sensitivity to increasing photoperiods, and cultivation of onion in tropical regions is dependent on identifying accessions capable of bulbing under the relatively short prevailing daylengths. The bulbing behaviour of 21 onion cultivars was studied under short (12 h) and long (16 h) photoperiods in controlled environments in the UK and under field conditions in Sri Lanka with the objective of developing simple and rapid screening techniques for identifying cultivars for tropical regions. There was a high correlation between the time taken for bulbing of individual cultivars under 16 and 12 hours photoperiods in both environments as indicated by a bulbing ratio of 2.0 (a bulbing ratio >2.0 characterizes the onset of bulb initiation (Clark and Heath, 1962)), bulb scale initiation, and bulb maturity. The sequence in which the cultivars bulbed was consistent under the two photoperiods but the time taken in the longer photoperiod (16 h) was reduced by between 50-70% (Mettananda and Fordham, 1997).

Five short-day cultivars of onions were induced to bulb by exposing them to long photoperiods and subsequently transferring them to a number of photoperiod and temperature treatments once bulbing had commenced. In an 8 h photoperiod, all cultivars resumed bladed leaf production. In cv. Bon Accord, bladed leaf production also resumed in an 11 h photoperiod. It is concluded that in photoperiods insufficient for bulb initiation, reversion to bladed leaf production will eventually occur. In the 8 h photoperiod, bulb scale formation continued for a while, particularly in the cultivar with the shortest photoperiod requirement for bulbing, before reversion to bladed leaf production. Considerable bulb swelling took place after plants were returned to short (8 h) photoperiods. Once bulb-scale formation had occurred, the swelling of these scales and the leaf bases of the bladed leaves surrounding them continued even in an 8 h photoperiod. Thus, photoperiod serves primarily to determine the fate of developing leaf initials. High temperature increased the rate of leaf senescence and hastened neck fall and maturity (Wiles, 1994).

Many photoperiodic flowering plants show a juvenile phase in which they are not responsive to induction (Roberts and Summerfield, 1987). Exposure of onion seedlings that had just emerged and at the 'loop' stage to 8 days at 24 h photoperiods or by 10 days at 8 h photoperiods, resulted in small bulbs in which bulb scales had formed. On these plants the cotyledon and the first true foliage leaf had developed. The latter is already initiated within the embryo and differentiates during germination (Hoffman, 1933), hence its development is unlikely to be affected by photoperiod. Terabun (1971b) also exposed single leaves of four-leaf stage plants to a 24 h photoperiod for 14 days, having removed the other leaves. Bulbing was similar whichever leaf remained for photoperiodic treatment. These experiments show no evidence for a juvenility response in onions and prove that even emerging seedlings can be induced to bulb by a strong long day stimulus. However, Sobeih and Wright (1986), observed that the rate of bulbing upon transfer from 8 to 16 h photoperiods increased as plants grew older. Also, in defoliation experiments, they found that 4.5 month old plants defoliated to the two youngest leaves bulbed more rapidly than younger plants of greater leaf area at the start of long day treatment. The experimental evidence for juvenility seems contradictory. There is no evidence for an absolute juvenile phase in which bulbing cannot occur given a strong photoperiodic induction (Brewster, 1997). On the other hand, the results of Sobeih and Wright (1986) indicate that the sensitivity to moderate long day treatments may increase with age.

Photoperiodic regulation of bulbing seems to differ in this respect from the classic photoperiodic regulation of flowering, which is truly inductive, as it requires a photoperiodic stimulus for its initiation only (Kedar *et al.*, 1975). For some species vernalisation has only a furthering effect on flower induction and differentiation. The cold requirement for those is facultative or quantitative. For effects like these, criteria such as date of flowering, number of leaves or flower stalk length on a key day must be used (Wiebe, 1990). Steer (1980a) found that two Australian cultivars adapted to production in the short day lengths of the Queensland winter (Bartholomew, 1986) were capable of bulbing in an 11 h photoperiod (8 h given as daylight) in a Canberra phytotron. However, bulbing response was also affected by temperature.

By using controlled environments, high temperature effects were minimized so that photoperiod, not temperature, was characterized as the critical mediator of plant growth rate in lettuce. In this case, extremes of temperature, as well as other stresses, appear to mediate the effect of daylength (Waycott, 1995).

As reported by Wright and Sobeih (1986), a high level of PAR combined with a long photoperiod accelerated both bulbing and final bulb size in onion (Figure 2.3). Plants grown under a short photoperiod with a low level of irradiance produced bulbs earlier when transferred to a long photoperiod with high radiance than did plants that received a short photoperiod with a high irradiance level and were then moved to long photoperiod with low irradiance. A long photoperiod with a high irradiance level showed a rapid decline in leaf numbers due to bulb formation. This was caused by the cessation of new leaf growth and the senescence of older leaves. An experiment was conducted in order to examine the relationship between photoperiod, photon flux density (in the region 400-700 nm) and bulb development. Each compartment had a different light environment as follows:

1. Long photoperiod (LD) with high irradiance (HI): 16 h light at 135 Em^{-2} s^{-1} of photosynthetically active radiation (PAR).
2. Long photoperiod (LD) with low irradiance (LI): 16 h light at 67.50 Em^{-2} s^{-1} PAR.
3. Short photoperiod (SD) with high irradiance (HI): 8 h light at 135 Em^{-2} s^{-1} PAR.
4. Short photoperiod (SD) with low irradiance (LI): 8 h light at 67.50 Em^{-2} s^{-1} PAR.

Using defoliation techniques, it was shown that bulbing in onions relies on the perception of the long day stimulus by young developing leaves. Bulbs always grow more rapidly in older plants, and young plants would not bulb until they had approximately four foliage leaves (Wright and Sobeih, 1986).

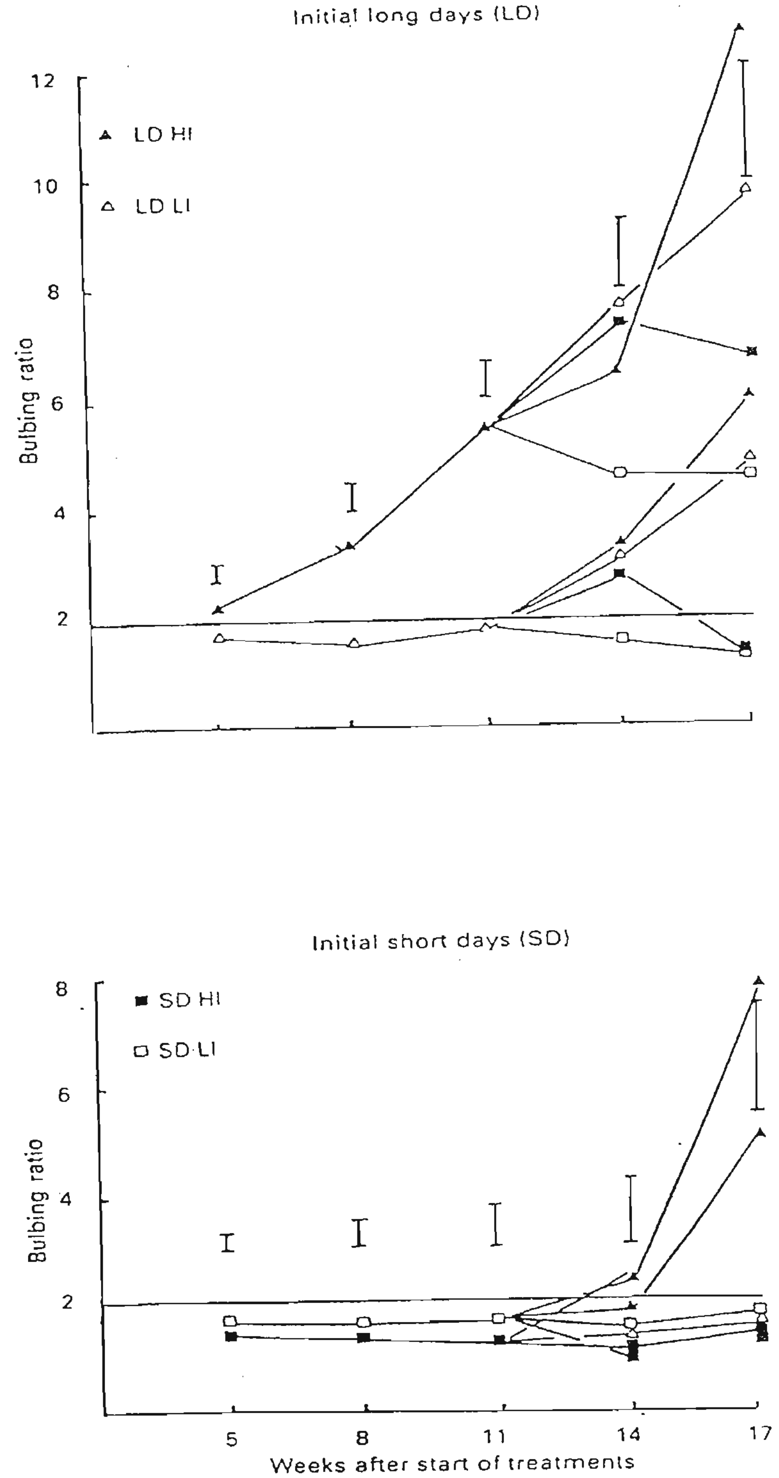


Figure 2.3 Effect of radiance level and daylength on bulbing ratio in onion cv. Rocket. Bars Represent LSD at P=0.05. LD (Long daylength); SD (Short Daylength); HI (High Irradiance); LI (Low Irradiance) (Wright and Sobeih, 1986).

The site of daylength response has been shown to be in the leaves in many long- and short-day plants (Vince-Prue, 1975; Summerfield and Roberts, 1987). Several researchers have also shown that the sensitivity to daylength changes with the age of the leaf (Evans, 1969; Vince-Prue, 1975). In the onion, Heath and Holdsworth (1948) have demonstrated the photoperiodic perception for bulbing by the leaves and it has been reported that the position of the leaf had an effect on the time of bulb formation (Terabun, 1971a). A decline in photoperiodic sensitivity of old leaves may result from the decline in metabolic activity due to changes in their mineral nutrition, protein and chlorophyll contents as they age (Moss and Peaslee, 1965). The expansion of young leaves could be important in controlling bulbing. Salisbury (1955) demonstrated that the most rapidly expanding leaf is the most sensitive to photoperiodic induction.

An interesting effect of soil temperature on bulb shape was found by Yamaguchi *et al.* (1975) in glasshouse conditions in California, using three white onion cultivars, two of which were grown for dehydration. Comparisons were made at soil temperatures of 13°C, 18°C, 24°C and 29°C and it was found that the higher the soil temperature, the more elongated was the resulting bulb. The height of bulb increased while the diameter remained the same, except at the highest soil temperature, 29°C, at which bulb diameter was slightly reduced. High soil temperatures may therefore contribute to the occurrence of bottle or cigar shaped onion.

The number of days from sowing to the start of bulbing decreased with increasing night temperature. The rate of bulbing increased with increasing night temperature. Photoperiod and temperature had a marked influence in the bulbing responses of all cultivars. There is no extensive published evidence on the role of night temperature on bulbing of onions, although Heath and Holdsworth (1948) stated that high night temperature was more effective in accelerating bulbing than high day temperature.

As reported by Steer (1980b), bulbing in onion may be divided in to two phases with respect to the influence of environmental factors: the time of initiation of bulbing and the rate of bulb development after initiation. The bulbing ratio of 2.0 was obtained by extrapolation of the bulbing ratio data, and the rates of bulbing were obtained from the period of most rapid bulbing in each treatment. There were three daylengths (13, 14, 15 h); three day temperatures (22°C, 26°C, 30°C) and a night temperature drop of 5°C or 15°C from each day temperature (Figure 2.4).

2.2.3.3 Reversibility of bulbing and sensitivity to photoperiod

Onions require a certain minimum length of day to continue bulbing and for the maturation process. The transfer of bulbing plants to non-inductive short-day conditions causes reversal of the bulbing process and renewal of vegetative growth (Heath and Holdsworth, 1948; Kato, 1964). The reversibility of bulbing can thus be used to test and evaluate the relative sensitivity of onion cultivars to photoperiod during the bulbing process (Figure 2.4).

Kedar *et al.* (1975) grew plants in a glasshouse with 18 h supplementary light until reaching a bulbing ratio of 3.5, and then transferred them to naturally decreasing daylength (Figure 2.5). The increase in bulbing ratio continued for some time after transfer to decreasing daylength conditions (Figure 2.5A and B). After the first date of sowing (Figure 2.5A), cv.Beta Alpha and the other two early cultivars managed to mature before natural daylength decreased below 11 h 42 min. The two late cultivars, whose bulbing ratio increased more slowly, were influenced by decreasing daylength; bulbing stopped and they reverted to vegetative growth, as indicted by the decreasing bulbing ratio. cv.Beta Alpha responded similarly to the other cultivars. Bulbing stopped when daylength decreased below 11 h 3 min. and bulbing ratio decreased gradually thereafter in all three cultivars. In the two cultivars, Riverside and Zittau Giant Yellow, the bulbing ratio decreased later and it seems that their response to changes in daylength was delayed in comparison with that of cv.Beta Alpha.

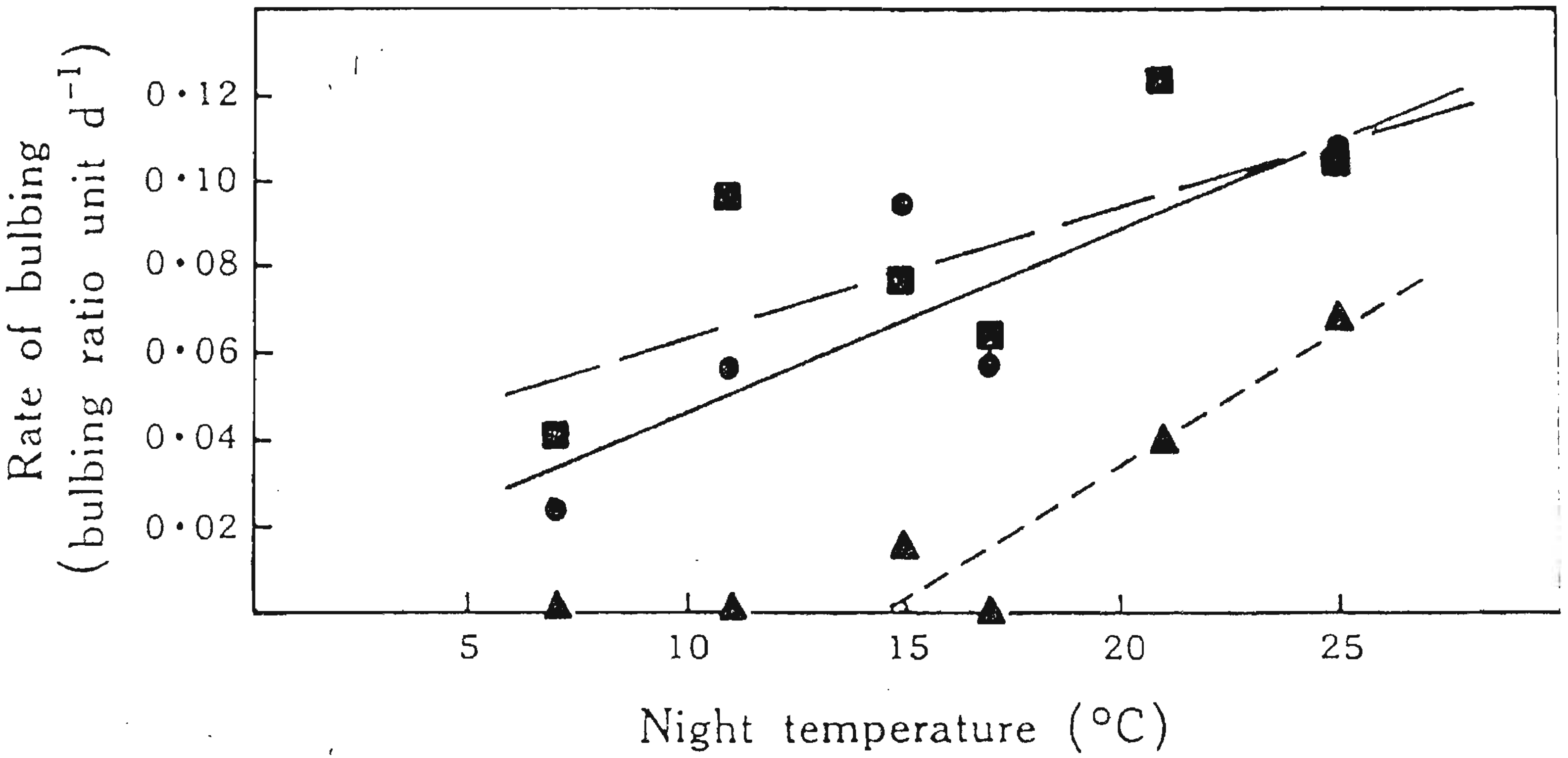


Figure 2.4 Effect of night temperature on the rate of bulbing (in bulbing ratio units per day) in cv. Creamgold. The fitted regression coefficient and r^2 are

$z = -0.09 + 0.00621x$, $r^2 = 0.85$, 13h daylength, ▲ ▲
$z = 0.00438 + 0.00433x$, $r^2 = 0.73$, 14h daylength, ●●
$z = 0.0273 + 0.00364x$, $r^2 = 0.58$, 15h daylength, ■ ■
Where x is the night temperature, and z bulbing ratio units per day (Steer, 1980b).

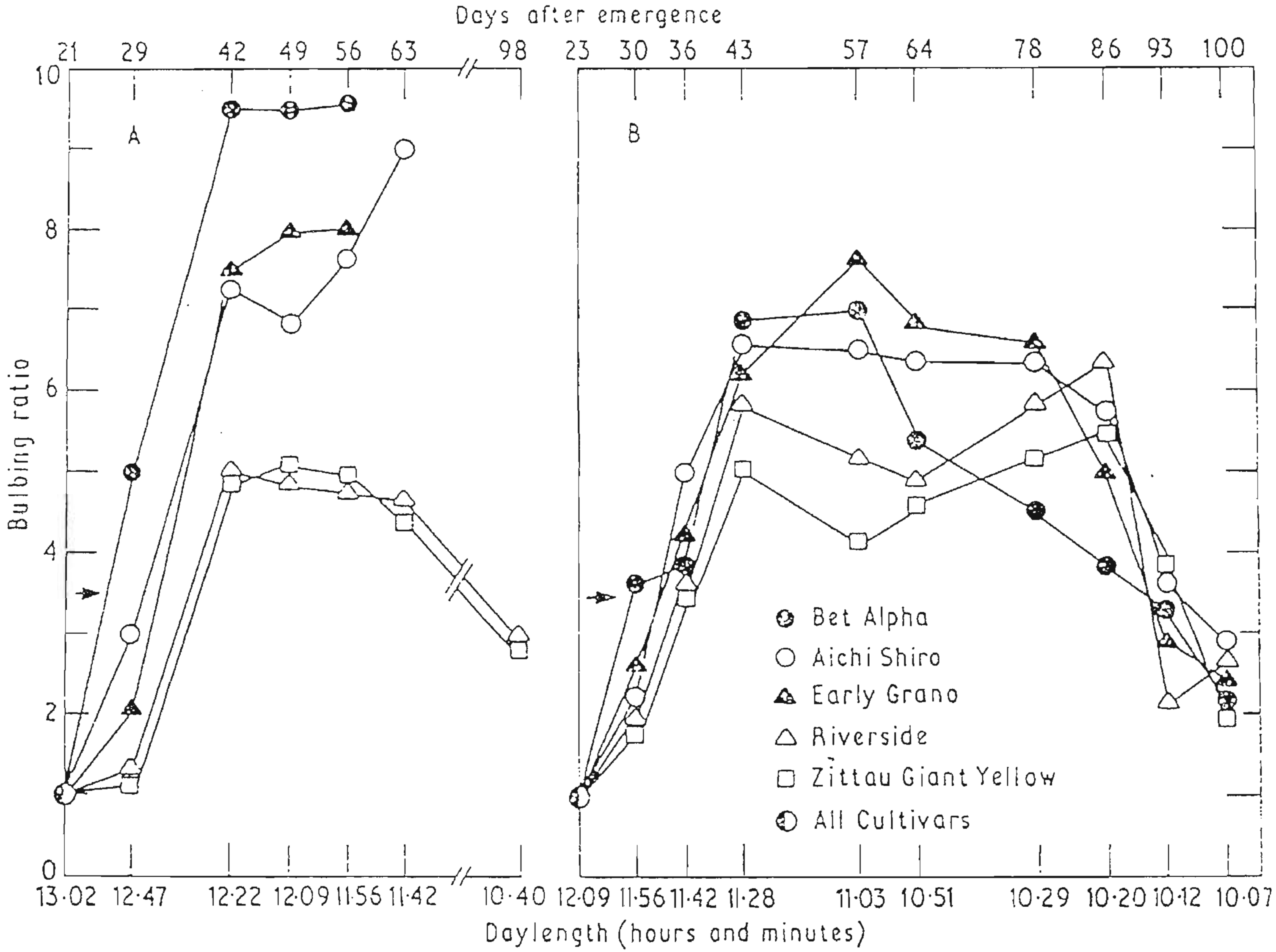


Figure 2.5 Reversibility and bulbing ratio of 5 onion cultivars grown under long-day conditions (18h supplementary light by 100W incandescent lamps, light intensity 18fc), and transferred to a glasshouse compartment with natural decreasing daylength after reaching a bulb ratio of 3.5 (indicated by arrows). Each point is the mean of 5 replications, in each replication there were 5 plants (Kedar *et al.*, 1975).

It is known that bulb maturation can be prevented and vegetative growth resumed when plants are returned to non-inductive short-day conditions even after the plant tops have fallen (Kedar *et al.*, 1975).

It could be argued, however, that once the bulbing process has reached an advanced stage, bulbing could be completed even under non-inductive photoperiods (Heath and Holdsworth, 1948).

2.2.3.4 Temperature

It is generally agreed that, for a given photoperiod, earlier bulbing takes place as temperature increases (Brewster, 1990). Roberts *et al.* (1988) argued that most temperature responses in plants showed an optimum temperature above which further temperature increases are stressful and delay the process in question (example germination, flowering, bulbing). They illustrated this with data on onion bulbing from Butt (1968) which must be regarded as somewhat unconvincing. However, Abdalla (1967) demonstrated a delay in bulbing as a result of extremely high temperatures obtained in a glasshouse in Sudan. Where temperatures reached 40–45°C in the glasshouse, bulbing was retarded in 10 out of 12 cultivars, though leaves were still produced at these temperatures. Steer (1980a, b) provided the best data available on the response of tropical onion cultivars to temperature in controlled conditions. Nevertheless, because of the infrequency with which bulbing ratio was measured, it is not possible to estimate accurately the time to 'onset of bulbing' in the different treatments. There is some evidence from bulbing ratio 49 days after sowing that the highest temperature he used, 34/26°C, was supra-optimal for bulbing. But more surprising was the of three cultivars to bulb in an 11h daylength at 22/14°C, while all three bulbed (within 91 days of sowing) in an 11 h daylength at 18/10°C. The possibility should therefore be born in mind that cultivars vary in their optimum temperature for bulbing and that rather low temperatures may be optimal, especially at marginal daylengths.

The way in which temperature affects bulbing in onions is not clear. Temperature has a marked effect on the rate of vegetative growth (Butt, 1968; Brewster, 1979) and on the rate of leaf initiation and emergence (de Ruiter, 1986). In so far as plant size or age modulate the response to photoperiod (Sobeih and Wright, 1986) it is probable that a measurement of plant age in terms of thermal time is more appropriate than chronological age in determining the plant's photoperiodic response. A model of this kind has been proposed for flower initiation by Roberts and Summerfield (1987), and its application to onion bulbing also suggested by Roberts *et al.* (1988).

Bulb size and maturity are key characteristics of an onion crop and the onset of bulbing is an important determinant of these (Lancaster *et al.,* 1996). Bulb diameter at bulbing was related to the thermal time accumulated prior to bulbing. Bulbing only occurred when dual thresholds of a minimum thermal time of 600 degree days and a photoperiod of 13.75 h were reached. Mathematical relationships were developed between leaf number, sowing date, bulbing rate and bulb growth and maturity. Final bulb size could be predicted from bulb size at bulbing and number of leaves produced after bulbing. Bulb maturity could be predicted by the number of leaves produced after bulbing (Lancaster *et al.,* 1996). The number of leaves produced before bulbing was related to accumulated thermal time. Bulbing terminates leaf production (Lancaster *et al.,* 1996).

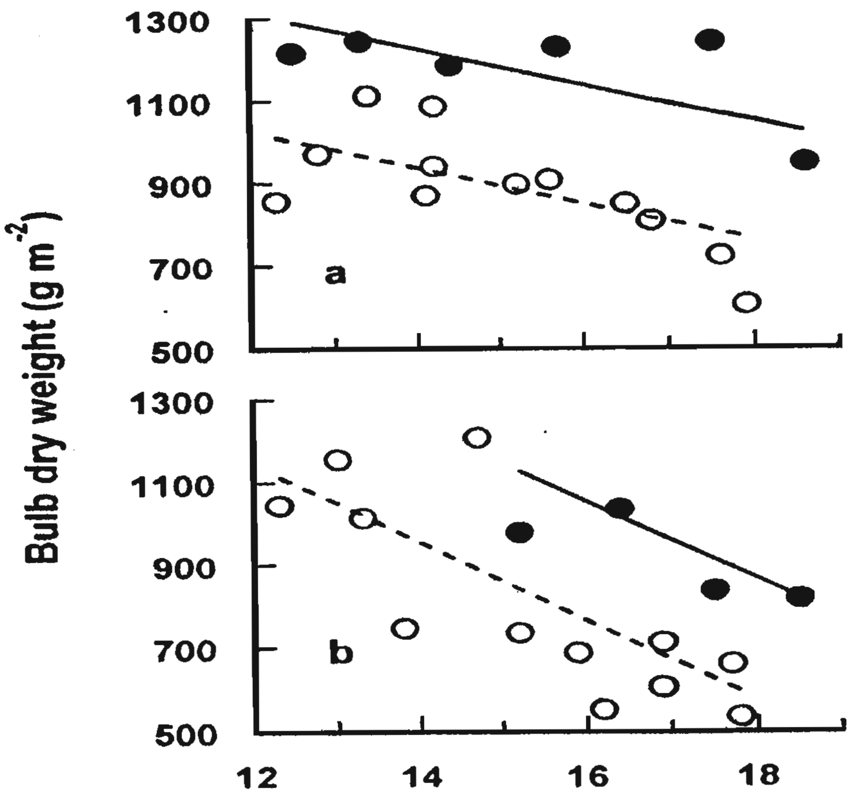
Other ways in which temperature can affect onion bulbing have been suggested. The partition of carbohydrate between different organs within a plant is affected by temperature (Johnson and Thornley, 1985) and this probably accounts for the effect of temperature on top:root ratio reported by Butt (1968) under non bulbing conditions. The effect of temperature on availability of carbohydrate to the developing leaf (bulb scale) initials could be important in determining the timing of bulb initiation. Brewster (1990) suggested that the effect of temperature on the dark reactions of phytochrome was another possible explanation for temperature effects on bulbing.

The productivity of onion crops is strongly influenced by the time of the onset of bulbing and the duration of bulb growth. Bulb formation in onion is a process consisting of both growth and apical development (Brewster, 1990). The rate of the progress towards the onset of bulbing (the reciprocal of the time from sowing to the onset of bulbing-D^{-1}) was more rapid at warmer temperatures (Brewster, 1990). The rate of progress from transplanting to the 'onset of bulbing' was also a positive linear function of mean temperature for each cultivar and at normal and elevated CO_2 (Daymond *et al.,* 1997).

There is some evidence that leaf rather than root temperature is more important in determining whether bulbing takes place (Terabun, 1981). When plants were given a range of controlled root temperatures, maturity was earliest at the highest root temperature (29°C), but the 'onset of bulbing' was more or less simultaneous with root temperatures ranging from 13°C to 29°C (Yamaguchi *et al.,* 1975). The number of days from sowing to the start of bulbing decreased with increasing night temperature. The rate of bulbing after initiation increased with increasing night temperature (Steer, 1980b).

2.2.4 Carbon Assimilation in the Development of Onion Bulb

The productivity of onion is strongly influenced by the time of onset of bulbing and the duration of bulb growth. Bulb formation is a process consisting of both bulb growth and apical development (Brewster and Rabinowitch, 1990). Yield increases of root crops grown at elevated atmospheric concentration of CO_2 are often greater than average, possibly because the harvested portion of the plant is a larger sink for photosynthetic assimilates (Clough *et al.,* 1981). However, whether or not CO_2 concentration affects the rate of onion bulb formation is not known. The rate of progress towards the onset of bulbing (the reciprocal of the time from sowing to the onset of bulbing) is more rapid at warmer temperatures (Brewster, 1990). Thus, the possible interaction between the effects of warmer temperatures and elevated CO_2 on the time to onset of bulbing in onion presents a potentially complex response (Figure 2.6). The existence of both long-day and short-day cultivars of onion further complicates assessments of the potential impacts of future climate scenarios on onion crop production.



Temperature (^{O}C)

Figure 2.6 Relationship between crop bulb dry weight at harvest maturity and mean temperature from transplanting to harvest maturity at elevated (•, —) and normal (o, ---) CO_2 in cv. Hysam (a) and cv. Sito (b) (Daymond *et al.*, 1997).

Variation of bulb size and time to maturity depend on the physiological processes regulating the development of bulbs. The production of leaves after bulbing is considered to be central to the process of bulb development since they are key suppliers of assimilates for bulb expansion.

The requirements of long days to induce bulbing in onion have been documented (Heath, 1945; Butt, 1968; Wright and Sobeih, 1986), but the mechanism by which the environment influences bulb initiation is not clear. One possible internal control mechanism may be through changes in assimilating translocation and accumulation. There is evidence for an increased rate of carbohydrate accumulation in leaf bases during the initiation of bulbing in response to photoperiods (Kato, 1965; Butt, 1968; Lercari, 1982). However, although photosynthetic products of plants grown in environments with high irradiance seem to be involved in controlling bulb growth, they are not the primary stimulus for the induction of bulbing (Wright and Sobeih, 1986). This may be because light affects bulbing significantly by directing available assimilates towards leaf bases rather than by a non-specific general effect on photosynthesis and on the availability of assimilates.

From the work reported by Daymond *et al.* (1997) for bulb yields at harvest maturity, the temperature rise needed to offset entirely the yield increases due to elevated CO_2 can be calculated for each cultivar. Thus, an increase in bulb yield due to a rise from 374 to 532μmol mol^{-1} CO_2 is offset by an 8.5 K-10.9 K temperature warming in cv. Hysan and by a 4.0 K–5.8 K increase in cv. Sito. A simple response to any future changes in climate is to change the cultivar of the crop grown (Parry and Carter, 1990). The yields of the short season cv. Sito are more sensitive to potential climate change than the yields of the long-season cv. Hysan. Using a common scenario of climate change (IPCC92a, Houghton *et al.,* 1992), Viner and Hulme (1993) estimated that a future CO_2 concentration of 560 μmol mol^{-1} would be associated with a 2.1 K rise in global mean temperatures.

The presence of high levels of endogenous hormones (for example cytokinins) (Kato, 1965; Lercari and Micheli, 1981) and carbohydrate accumulation in leaf bases during the induction of bulbing in onion suggests that they may be related, and bulbing may be regulated by hormone stimulated assimilate transport.

From the work reported by Sobeih (1988), a reduction in red:far-red spectral ratio without significantly modifying the PAR increased assimilate movement towards leaf bases during bulbing. However, with red:far-red ratio of 7.3 which is ineffective for bulbing, assimilate was preferentially transported to the leaf blades rather than to leaf bases, supporting the interpretation that the photoperiodic control of bulbing seems to involve changes in assimilate partitioning which acts *via* phytochrome. It seems possible that the long photoperiods and low red:far-red ratios which trigger the onset of bulbing also influenced the translocation of ^{14}C -photosynthate. This response was shown to be affected by plant growth substances, suggesting that phytochrome, through its involvement in the photoperiodic control of bulbing might change endogenous hormone levels, which in turn, might affect assimilate transport.

Previous reports indicated that hormone induced volume growth acts to set sink strength which in turn appears to be a strong determinant of assimilate partitioning (Cook and Evans, 1978; Patrick, 1982). Bulbing was delayed by Benzyl adenine (BA) application especially in conditions marginal for bulbing and was associated with a redirection of assimilate flow to leaf blades rather than to leaf bases. There are many reports that cytokinins can direct photosynthates to sites of their application (Boniolo and Romania, 1976; Mor *et al.*, 1981), which indicates that cytokinins may act more directly on transport. However, it could be argued that the initiation of rapid growth in onion by BA application at 100 ppm (Sobeih, 1988), is a result of the induction of the sink into which the assimilates are subsequently mobilized. Although GA_3 application decreased the total ^{14}C-assimilate export from fed leaves in the reported work, most of the assimilate was translocated downward to leaf bases. This result is consistent with another demonstration that gibberellins stimulate the movement of translocate to actively growing areas of plants (Ginzburg, 1974; Ben-Gad *et al.,* 1979).

2.2.5 Growth Substances in Stored Onions

Isenberg *et al.* (1987) reviewed studies on the growth substances of stored onions and their changes throughout dormancy. They explained the post harvest events of rest, dormancy and regrowth in terms of the hormonal changes occurring in the bulbs. Their conclusion, for a number of trials mostly on Japanese, North European and North American cultivars can be summarized as follows. Auxins decline in foliage leaves and bulb apices during the final stages or green leaf senescence and bulb expansion prior to harvest. When the leaf tops have fallen over, significant amounts of the growth inhibitor, abscisic acid (ABA), are found in the leaves. A high level of the inhibitor ABA appears to be transported to the bulb apex and simultaneously the levels of auxins, cytokinins and gibberellins decline, resulting in no visible sprouting. Further bioassays during the winter months showed a decline in ABA to a low level by February, while gibberellins increased to a maximum in December, followed by cytokinins, and then by auxins. In February–March a second gibberellin peak was found, accompanying sprout emergence. It was proposed that the first gibberellin peak took place at flower primordium induction after the first three months of cool storage, that the rise in cytokinins signalled the resumption of active cell division; and that the auxin peak was connected with shoot growth.

It is reported by Lipe (1975) that the bulbing process normally brought about by photoperiod and temperature is affected by ethephon (2-chloroethyl phosphonic acid). Very young onion seedlings treated with ethephon responded by enhanced swelling at the base. Ethephon reduced the number of leaf blades produced. As onions approached maturity, leaves near the centre of the bulb abort their blades leaving only the thickened leaf sheath, which does not protrude above the neck of the bulb. Lower leaf blade number at maturity may be an indication that the plant reached maturity at an earlier date. In contrast, application of GA_3 increased the total number of leaf blades per plant. This appears to have resulted from stimulation of regrowth of normally dormant leaf blades in the centre of the maturing bulb or through stimulation of adventitious buds on the shoot axis. Leaf primordia on both main axis and lateral buds normally begin regrowth after a period of rest. Furthermore Nojiri *et al.* (1992) reported that bulb development in onion plants (*A. cepa* L.) is considered to be regulated by bulbing and anti-bulbing hormones. Since bulbing involves the disruption of microtubules, both Jasmonic acid (JA) and methyl jasmonate (JAMe) are candidates for the bulbing hormone because of their microtubule-disrupting activities and wide distribution in higher plants.

CHAPTER 3

MATERIALS AND METHODS

3.1 DESCRIPTION OF CULTIVARS

The local Eritrean landrace which is referred to as 'Hagaz Red' is grown and harvested once per year during the period of December-May for bulb production. It is adapted to dry climates and fertile sandy-loam soils in an area where annual temperature and daylength ranges from 25 to 35°C and 11 to 12.5 h, respectively. In addition, 'Hagaz Red' has multiple skin with a good dark-red colour retention. The bulb has a large flattened globe shape. It has a strong pungency due to the high content of flavour-containing compounds. The propagation by farmers is from the seeds; they are selected from farmers' own plots. As a result, there are unequivocal genetical differences in response to environmental conditions within the landraces, because onions are open pollinated.

Three tropical onion cultivars, HR 1, HR 2 (which are separate selections from the landrace cv. Hagaz Red) and Red Creole were used in this study. The HR 1, HR 2 selections are well adapted to the Keren district in Eritrea (15° 46′ 40″N and 38° 27′ 29″E). The American cultivar Red Creole is grown locally in South Africa. Seeds of HR 1 and HR 2 were obtained from local Eritrean producers. Since they were produced on two different farms within one location, it is believed that they may have differences in response to given set of growth conditions.

'Red Creole' is a tropical short-day cultivar and it is adapted particularly to tropical and sub-tropical areas. The bulb matures in 100 to 160 days depending upon planting time, location and climate. The cultivar has a reddish-buff skin colour with small to medium size thick flat bulbs and pungent red-purple flesh. It has excellent storage characteristics for tropical climates if kept dry and ventilated.

3.2 DESCRIPTION OF GROWTH ROOMS

The experimental work of assessing the effect of daylength and temperature on 'onset of bulbing' of the onion cultivars and their morphological growth pattern towards bulbing was carried out in the Controlled Environment Research Unit (CERU) growth rooms, at the University of KwaZulu–Natal, Pietermaritzburg, South Africa (latitude 29.6°S longitude 30.4°E). The growth rooms are used for research requiring a greater level of environmental precision than a greenhouse can provide. The rooms provide uniform lighting so that daily or seasonal radiant flux change does not affect a long-term experiment (Plate 3.1). The operating-temperature range of the growth rooms is 12°C–37.7°C year-round. The growth rooms can be set to control temperatures to within ±1°C of set-point.

Three levels of each day/night photoperiods and temperatures in nine treatment combinations were used (Table 3.1) (each room 3 m × 2.3 m and 2.5 m high). The potted plants of nine week-old seedlings were placed inside the growth room until plants attained the bulb ratio $\geq$ 2.0 which marked the completion of the study. The potted plants were placed on moveable 0.81 m high tables. Plants were kept 1.47 m from the light source. The daylength was provided by lighting having 58 W/77 fluorescent tubes (118) in each chamber and 100 W-240 V incandescent lamps (12). The relative humidity (RH) was set at 70%. The mean photon flux density (PFD) of the rooms was 314 μmol m^{-2} sec^{-1} over the duration of the experiment.

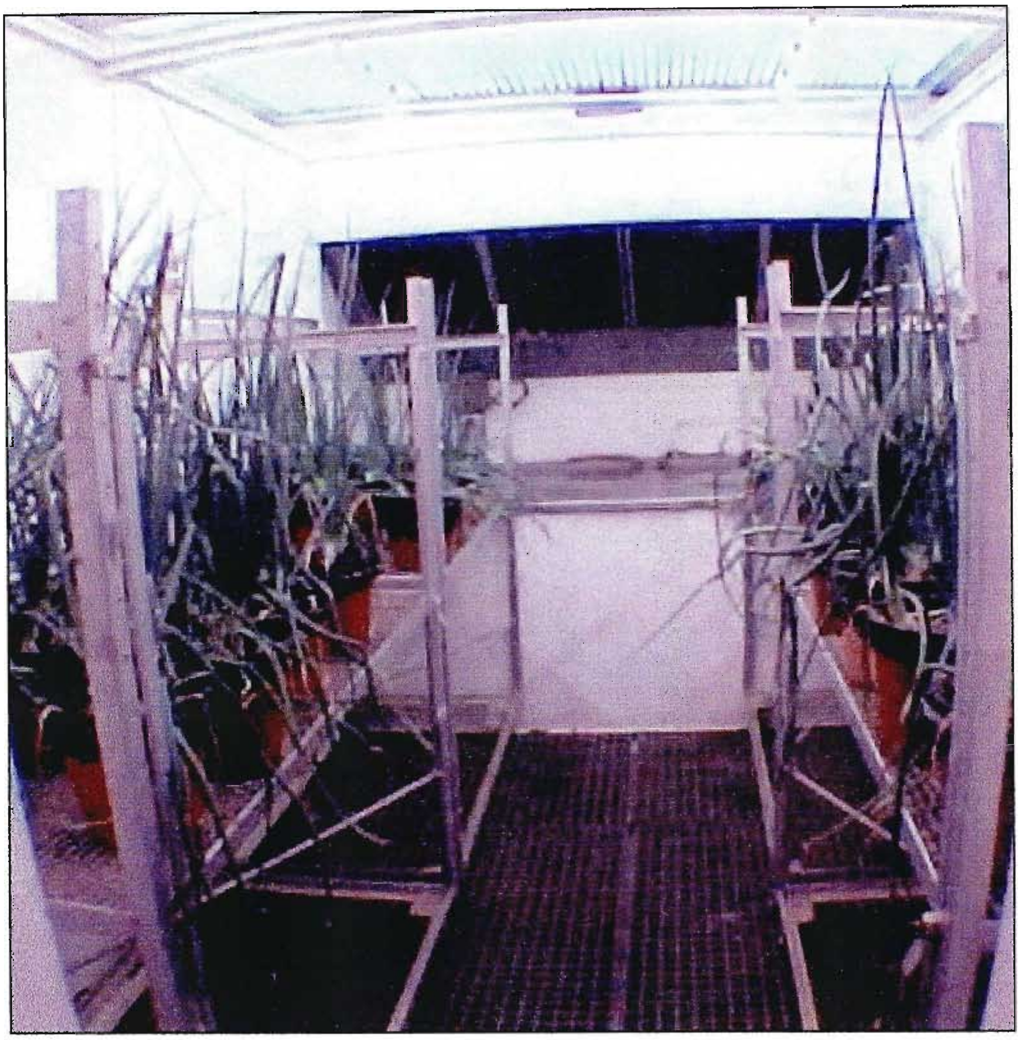


Plate 3.1 One of the growth rooms where the experiment was conducted.

3.3 PREPARATION OF GROWING MEDIA, PLANTING MATERIAL AND CONTAINERS

The local Eritrean onion cultivars (HR 1 and HR 2) are grown in the local Eritrean growth environment on a sandy-loam soil, where they are well adapted. Accordingly, a growing medium was prepared by mixing pine bark, peat moss and sand, to meet the soil physical requirements of the plants. The mixing was undertaken using an electrically operated drum mixer machine to ensure the required medium uniformity. The medium was then pasteurised for 24 hours by steam (Plate 3.2) prior to use to avoid soil-borne fungal diseases.

Onion seedlings were raised in 200-cell polystyrene seed trays containing the growing medium having a proportion: pine bark; peat moss; sand (1: 1: 2). This proportion was used throughout the experimental period. The standard pH of the growing medium was between 5.3 and 6.0.

Seeds were sown into polystyrene trays with 200-cells (each cell 28×28×36 mm). Three seeds per cell were sown and thinned to leave the strongest plant 2–3 weeks after sowing. Seedlings were grown under 8 h light and day/night temperature of 24/17°C in a growth room to prevent bulbing prior to application of the temperature/daylength treatments. After eight weeks of growth, three uniform seedlings were transferred to plastic pots of 200 mm diameter. The pots were lined with black plastic bags before filling them with the medium, to eliminate the danger of nutrient contamination in used pots and to make for easier cleaning of the pots on termination of the experiment (Anonymous, 1978). Before the imposition of treatments, the potted plants were conditioned for one week under the same environmental conditions of the seedlings to allow them to adjust from transplanting-shock. Plants were nine weeks old at the start of each of the nine treatment combinations and were at the 4-leaf stage of growth.

Plate 3.2 The chamber which was used for pasteurization of the growing media.

3.4 EXPERIMENTAL TREATMENTS AND DESIGNS

A split-plot design of main plot factors (growth rooms) that were a factorial treatment of three photoperiod and three temperature levels (3×3), in a single replication was used. The single replication in a design gives no estimate of error from the usual source, that is as a 'blocks × treatments' interaction. In this experiment, the single replication and series plantings were done because it is not feasible to do the experiment simultaneously, but it was assumed that conditions in the growth rooms were the same. The sub-plot factor of the three cultivars in four replications was accommodated within the main plot. The design within the growth rooms was a randomized complete block design (RCBD). The RCBD was recommended to avoid 'unwanted' source of variation within and between different experimental units due to possible gradients within growth rooms. A total of 48 pots of all cultivars per treatment were transferred to each growth room treatment following the week of transplant adjustment. One pot of each cultivar per fortnight was kept for destructive leaf area measurements for each replication. A total of 12 pots (3×4) from the 48 pots, were used for leaf area measurement over the duration of the experiment with three seedlings per pot, a total of 1296 seedlings in 432 pots were used throughout the experiment.

The factorial treatment arrangement of three levels of photoperiod and three levels of temperature resulted in nine treatment combinations. They all experienced a constant relative humidity of 70% over the experimental period. The treatment combinations and layout/growth rooms are shown in Tables 3.1 and 3.2.

The experiment was conducted under simulated tropical conditions with daylengths of 11.5 h, 12 h, and 12.5 h and day/night temperatures of 25/12°C, 30/15°C and 35/18°C which are suitable conditions for bulb initiation under field conditions. The choice of night temperature levels was backed by the findings of Steer (1980b). He reported that the number of days from sowing to the start of bulbing decreased with increasing night temperature, and the rate of bulbing after initiation increased with increasing night temperature.

Table 3.1 The factorial treatment arrangement with three levels of photoperiod and three levels of temperature.

Growth rooms	Main-plot factors		Sub-plot factors
	Photoperiod (Light/Dark)	Temperature (day/night)	Cultivars
1	11.5/12.5 h	25/12°C	HR 1, HR 2 and Red Creole
2	12/12 h	25/12°C	HR 1, HR 2 and Red Creole
3	12.5/11.5 h	25/12°C	HR 1, HR 2 and Red Creole
4	11.5/12.5 h	30/15°C	HR 1, HR 2 and Red Creole
5	12/12 h	30/15°C	HR 1, HR 2 and Red Creole
6	12.5/11.5 h	30/15°C	HR 1, HR 2 and Red Creole
7	11.5/12.5 h	35/18°C	HR 1, HR 2 and Red Creole
8	12/12 h	35/18°C	HR 1, HR 2 and Red Creole
9	12.5/11.5 h	35/18°C	HR 1, HR 2 and Red Creole

Table 3.2 Example of 'Layout' of the pots for each growth room.

Rep. 1				Rep. 3			
P_1HR 1	P_1HR 1	P_1HR 1	P_1HR 1	P_3HR 1	P3HR 1	P_3HR 1	P_3HR 1
P_1HR 2	P_1HR 2	P_1HR 2	P_1HR 2	P_3HR 2	P_3HR 2	P_3HR 2	P_3HR 2
P_1RC	P_1RC	P_1RC	P_1RC	P_3RC	P_3RC	P_3RC	P_3RC
Rep. 2				**Rep. 4**			
P_2HR 1	P_2HR 1	P_2HR 1	P_2HR 1	P_4HR 1	P_4HR 1	P_4HR 1	P_4HR 1
P_2HR 2	P_2HR 2	P_2HR 2	P_2HR 2	P_4HR 2	P_4HR 2	P_4HR 2	P_4HR 2
P_2RC	P_2RC	P_2RC	P_2RC	P_4RC	P_4RC	P_4RC	P_4RC

Cultivars: HR 1: Hagaz Red 1; HR 2: Hagaz Red 2; RC-Red Creole; Rep: replication.

$P_1 - P_4$ = numbering of pots according to replications

3.5 IRRIGATION AND FERTILIZATION

Pots were watered by hand daily or twice daily, depending on the wetness of the growing medium, using a 20 L of watering can. Nutrients were supplied once a week through irrigation with vita feed fertilizer. The vita feed fertilizer (GROMORE 3:1:3 (34) COMPLETE) is a hydroponics fertilizer formulated for use on plants and seedlings growing in a pre-enriched organic growing medium. Whilst it has complete (macro and micro elements), it does not contain adequate calcium or magnesium for sustained long term growth. The fertilizer was used at a dilution rate of 1 g L^{-1} of water (10 g/pot once per week). Limestone ammonium nitrate (LAN) was also supplied at later stage of plant development. The fertilizer was used at a dilution rate of 1.25 g L^{-1} of water (12.5 g/pot once per week).

3.6 MEASUREMENTS AND TERMINOLOGY

Growth measurements made on the onions were number of green leaves; leaf area (as split and spread blades); bulb diameter (taken at the widest part of the base of the pseudostem); neck diameter (minimum diameter of pseudostem above the swollen stem). Measurements of bulb and neck diameter, leaf number, leaf area and plant height were undertaken fortnightly until the onset of bulbing with an absolute digimatic digital caliper (CD-S6"C, Serial No. 0000749) (Plate 3.3).

3.6.1 Bulb Ratio

Bulb ratio, defined as the ratio of maximum bulb diameter to minimum pseudostem (neck) diameter (Clark and Heath, 1962), was used as a measure of bulbing. Bulbing ratios of two (2.0) characterize the onset of bulbing (Plate 3.4).

Plate 3.3 The digital caliper used to measure the bulb and neck diameter.

Plate 3.4 The 'onset of bulbing' at bulb ratio of ≥2.0.

3.6.2 Leaf Emergence

Leaf emergence was recorded by counting the number of leaves above the pseudostem. In onion, leaves are arranged alternately and emerge through the pore of the preceeding leaf (Hoffman, 1933). In determining the number of leaves produced before bulbing, only leaves present on the main shoot were considered. Records of leaf appearance were used to determine the time to 'cessation of appearance' (Mondal *et al.,* 1986a) and also to compare treatment differences in the rate of leaf appearance.

3.6.3 Plant Height and Leaf Area

The plant height was taken as the distance from the base of the pseudostem to the tip of the longest leaf. A 0.50 m graded ruler was used to take the measurements. Onion leaves develop from the upper surface of a broad, conical basal stem. Leaf blades are tubular and markedly flattened on the upper surface. For the destructive measurement of leaf area, leaves were split and opened. The spread leaf blade was measured using a portable area meter (LI-COR, LI-3000) (Plate 3.5).

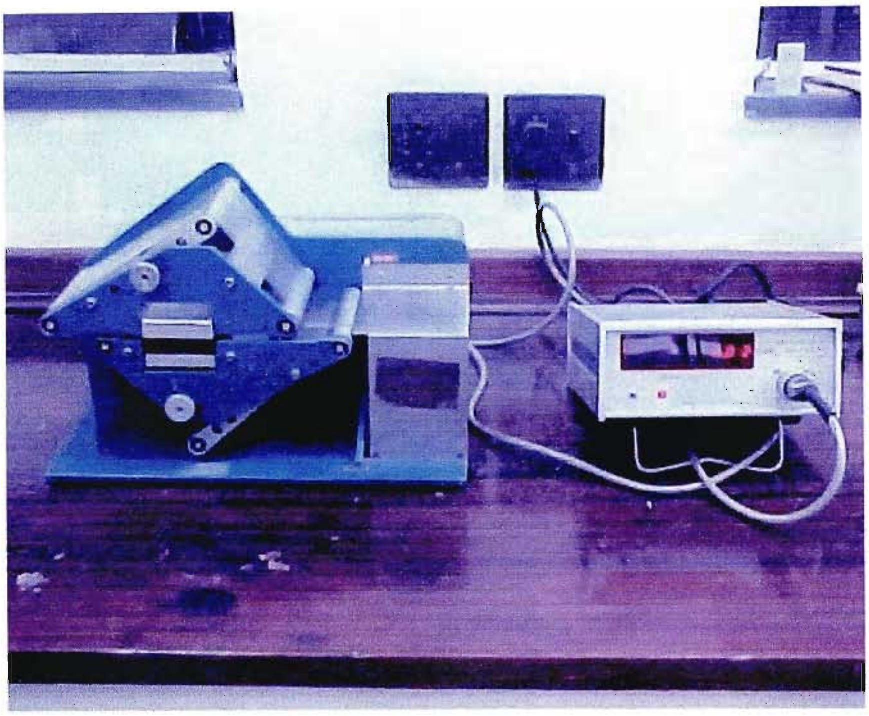


Plate 3.5 The Portable LI-COR, LI-3000 leaf area meter used to measure leaf area.

3.7 STATISTICAL ANALYSES

Statistical analyses of data were carried out using the GenStat package version 7.1 (Anonymous, 2003) and the PlotIT graphics programme (Anonymous, 1996) was used to plot data. The analysis of variance, for a split plot design, was done to test the individual effect of a single photoperiod and temperature combination on the cultivars. The cultivars responded differently in different growth conditions with time (Appendix 3.1). For demonstration purposes, data from a single plant age (108 days of plant age) presented. However, growing degree days (GDD) was considered to be more appropriate.

The cultivars which were grown under 11.5 h of photoperiod over the different levels of temperature, achieved the onset of bulbing 15 days later than the other treatments (123 days of plant age). All the data cannot be included in a valid analysis based on time, as only measurements which have the same phenological development as the rest of the treatments can be compared. This allows for keeping the orthogonality of the sample for the analysis of the data. However, the data was presented for the cultivars (123 days of plant age), grown under 11.5 h at the levels of temperature, using GDD.

Regression analysis was also done to investigate the degree of correlation for the growth components over GDD. Details of the statistical analyses of individual experiments are given in the appropriate sections.

Broken-stick regression model

The model was also used to find the point of inflection on the growth curve of the cultivars and this provided an appropriate point to evaluate bulb initiation and rate of plant growth (Appendices 3.2, 3.3). This regression model was used by Ochuodho (2005) to determine the point of inflection on the germination curve of *Cleome gyandra* seeds. Broken-stick regression is a modeling procedure of the GenStat statistical package that breaks a non-linear curve in to two linear components:

The Model.............. $E\ (Y) = \beta_o + \beta_1 Z_1 + \beta_2 Z_2 + \beta_3 Z_3$
The first line........... $E\ (Y) = \beta_o + \beta_1 Z_1$
Second line............ $E\ (Y) = (\beta_o + \beta 3) + \beta_2 Z_2$
And the point of intersection t is .... ${}^{\beta}{}_{1}{}^{t} = \beta_3 + \beta_2 t$

$$t = \beta_3 / (\beta_1 - \beta_2)$$

Where,

$E\ (Y)$ = estimated growth rate (induction)
β_o = is the intercept of the first trend line
β_1 = slope of the first trend line (linear curve)
β_2 = slope of the second trend line
β_3 = change in the intercept of the second line
Z = dummy variables
t = point of inflection of the two linear curves and represents rate of growth (induction), when the first line ends and the second line begins.

3.8 ESTIMATION OF BASE TEMPERATURE (T_b) AND GROWING DEGREE DAYS (GDD)

The heat unit system has found widespread use, particularly in the vegetable processing industry, for predicting the date of harvest and for the timing of successive plantings. Although the system as it is used is accurate enough to be a valuable tool, considerable error may be involved. This error manifests itself, in part, as a variation in the number of heat units required for a particular cultivar to complete a particular phase of development (Arnold, 1959).

The data from the comparative study derived from the nine treatment combinations (Table 3.1) was used in a method to determine the base temperature (T_b). The growing degree days (GDD) calculated for T_b ranging from 4 to 8°C and a set of GDD data was generated with respect to a given attainment of leaf area in order to get best fit relationships. Single bulbing-time data points were taken from each of the nine growth rooms at bulbing. The relationship between growth and T_b can be described using high order polynomials (mostly by 6 to 8 order polynomials). This method can be used to assess the pattern of relationships between growth and T_b. The six-order polynomial-fit approach results generate different R^2 values for all independent variables (GDD) over a dependent variable (L). In this case:

$\text{GDD} = \text{Days}\ [[(T_{day} \times \text{DL}/12\ \text{h}) + (T_{night} \times \text{NL}/12\ \text{h})]/2 - T_b]$ ----------(Equation 1)
(Holen and Dexter, 1996).

Where:

GDD – growing degree days; T_{day} – day temperature; T_{night} – night temperature;

DL – daylength; NL – night length; T_b – base temperature

The optimum T_b was determined by computing the optimal value of R^2 versus T_b. The optimum T_b occurs where T_b accounts for a large variation in the growth components (L) using a quadratic function. A mathematical approach of determining the point of inflection on the curve was used to determine the optimum T_b.

Suppose R^2 is a percentage variance accounted for and T_b is base temperature levels, then the polynomial curve that relates T_b to R^2 is:

$R^2 = a + b_1 T_b + b_2 T_b^2$ --------------- (Equation 2)

Where a, b_1 and b_2 are constants.

It is possible to fit this equation and find the optimum, if it exists, using standard mathematical notation and differentiation,

$\delta R^2 / \delta T_b = b_1 + 2b_2 T_b$ -------------- (Equation 3)

If f (x, y) is any continuous function, it cannot change sign except when (x, y) moves through a point where f (x, y) = 0. In other words, if (x, y) is positive in a certain region and negative in other, then it has to be 0 on the boundary between the two regions (Lady, 2002).

Since the boundary between the two regions would have to be more than a single point , we therefore conclude that if a function f (T_b, R^2) is zero at the origin but not zero anywhere else, then the function must be either always positive everywhere, except at the origin, or always negative, except at the origin. In the first case, f (T_b, R^2) takes its smallest possible value at (0, 0) so that f (T_b, R^2) has a maximum at (0, 0), and in the second case the function has a maximum at (0, 0).

Temperature is considered the primary factor determining the rate at which plants develop although other factors including daylength, moisture and light may modify the effects of temperature on the plant. Attempts to understand these relationships have spawned an enormous number of models and equations that quantify the amount of heat that is available for crop growth. The simplest of these methods is the growing degree day (GDD) concept, which uses the daily high and low temperatures to calculate an index of the useable heat produced each day. These daily values are summed for a cumulative value of heat available for development over a period of time and can be used to predict growth stages for individual fields or for entire regions (Holen and Dexter, 1996).

GDD equations have proven to be useful tools for researchers, crop managers and crop producers to predict plant development rate and growth stage. In certain crops, this information is used in scheduling harvests and as an aid in planning for crop management decisions such as the timing for planting, irrigation or pesticide applications. These equations are simple, use weather information that is readily available and allow a daily tracking of plant development. Sobeih and Wright (1986) reported that a measurement of plant age in terms of thermal time is more appropriate than chronological age in determining the plant's photoperiodic response. The data are presented according to the response of growth components over GDD. Thermal time was used as the base to investigate the photoperiodic response of the cultivars. Determination of T_b for the group of onion cultivars was part of the objective of the study. A regression method was used to determine T_b (Chapter 4.1).

CHAPTER 4

THE EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON ONION GROWTH AND DEVELOPMENT

4.1 INTRODUCTION

The environment and growing conditions govern the development rate of onions, which then influences the earliness of the crop. This, in turn, can influence the quality of the bulbs. The most important characteristic in the development of onions is bulbing, which occurs when the plants no longer form green leaf blades but bladeless bulb scales (Brewster, 1990). Therefore, it was vital to look at the growth components in response to daylengths (11.5 h, 12 h, and 12.5 h) and temperatures (25/12°C, 30/15°C, and 35/18°C) which, each as a separate factor and in combination, have an impact in determining onion growth and development.

The receptor site to daylength response has been shown to be in the leaves in many long- and short-day plants (Vince-Prue, 1975; Summerfield and Roberts, 1987). Several researchers have also shown that the sensitivity to daylength changes with the age of the leaf (Evans, 1969; Vince-Prue, 1975). In the onion, Heath and Holdsworth (1948) have demonstrated that the leaves are the photoperiodic perception site for bulbing and it has been reported that the position of the leaf has an effect on the time of bulb formation (Terabun, 1971a). A decline in photoperiodic sensitivity of old leaves may result from the decline in metabolic activity due to changes in their mineral nutrition, protein and chlorophyll contents as they age (Moss and Peaslee, 1965). The expansion of young leaves could be important in controlling bulbing. Salisbury (1955) demonstrated that the most rapidly expanding leaf is the most sensitive to photoperiodic induction.

Physiologically, according to the bulbing in onions is induced quantitatively by long days. This means that plants must be exposed to a number of days with daylength longer than a critical minimum for a particular onion population before bulbing takes place. Regardless of the other environmental conditions within this concept, factors such as temperature, nutrition and spacing play important parts in accelerating or slowing down the bulbing process. Internal factors such as plant age or size also have a strong influence on the readiness of onion plants to respond to external stimuli (Jones and Mann, 1963b). With these environmental influences in mind the current study on tropical onion cultivars investigated the bulbing response to the interacting influence of daylength and temperature.

As the cultivars which were grown under 11.5 h daylengths at all temperature treatments, started 'onset of bulbing' (bulb ratio ≥ 2.0) at 123 days (which was 15 days later than in the longer daylengths) (Table 4.14), comparisons of developmental events on a time basis are confounded. As an academic exercise, conventional statistical analyses were therefore only done on the data collected at one period of growth (108 days of plant age) to represent the same age of plants. In this analysis, the mean values in the combined analysis of variance table, which share the same letter had no significant differences ($P \leq 0.05$) in responses to the given growth factors; otherwise, the data not having common letters showed significant differences. As phenological development under different conditions of daylengths and temperature are not consistent, an elucidation of the effects of daylength at different temperatures compared over time is difficult, if not impossible. In an attempt to overcome these problems, growth was expressed in terms of growing degree days (GDD), so that the inductive effects of daylength on bulbing at different temperatures could be understood more clearly at a physiological level. The latter approach was used predominantly for interpretative purposes, but the linear time analysis at 108 days is presented for interest.

Determination of T_b

When the base temperature increases the heat unit summation required for the cultivars to attain a given growth stage decreases proportionally. There is an assumption that there is a linear relationship between growth and temperature, which holds above a certain base temperature (T_b), below which no growth occurs. In order to determine the T_b for the tropical onion cultivars, growing degree days (GDD) were calculated for base temperature between 4°C and 8°C for the period from transplanting (4-leaf stage) to bulb initiation at particular temperatures (25/12°C, 30/15°C and 35/18°C) and daylength (11.5 h, 12 h and 12.5 h) combinations (Table 4.1), using the methodology described in Chapter 3.8, using equation 3.1. The R^2s for GDD on leaf area were calculated for each T_b. Maximal value of R^2 indicates the T_b that best fits a linear relationship between leaf area and growth temperature, and this defines the T_b for onions. To determine this, a regression equation was plotted for the relationship of the R^2 against T_b (Figure 4.1).

Table 4.1 The GDD values calculated for different levels of base temperature (T_b) required to achieve the leaf area (L) of onion plants at the termination of growth recorded in 9 growth rooms set at three combinations of daylength and temperature.

Growth conditions	Days	GDD at 4°C T_b	GDD at 5°C T_b	GDD at 6°C T_b	GDD at 7°C T_b	GDD at 8°C T_b	Leaf Area (cm^2)
11.5 h×25/12°C	60	882.0	822.0	762.0	702.0	642.0	**256.4**
11.5 h×30/15°C	60	870.0	810.0	750.0	690.0	630.0	**397.4**
11.5 h×35/18°C	60	846.9	786.9	726.9	666.9	606.9	**1096.0**
12 h×25/12°C	45	842.6	797.6	752.6	707.6	662.6	**336.0**
12 h×30/15°C	45	832.5	787.5	742.5	697.5	652.5	**731.0**
12 h×35/18°C	45	812.3	767.3	722.3	677.3	632.3	**587.7**
12.5 h×25/12°C	45	1023.8	978.8	933.8	888.8	843.8	**359.2**
12.5 h×30/15°C	45	1012.5	967.5	922.5	877.5	832.5	**613.0**
12.5 h×35/18°C	45	989.3	944.3	899.3	854.3	809.3	**296.8**

R^2 of T_b on L 0.49 0.79 0.98 0.82 0.77

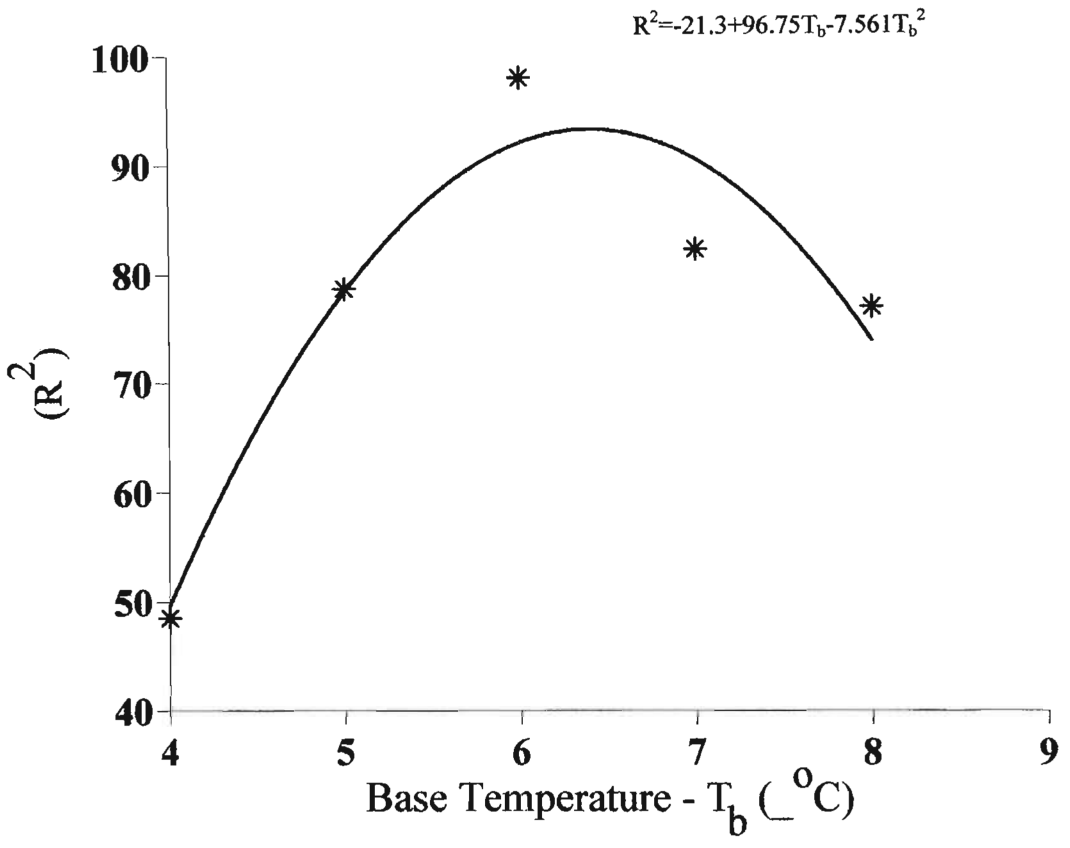


Figure 4.1 Percentage of variance (%) accounting for leaf area at various base temperatures.

The optimum base temperature (T_b) that leads to maximum leaf area can be obtained by setting $\delta R^2/ \delta T_b$ of the regression equation to zero and solving for T_b:

$-216.3 + 96.75\ T_b - 7.561\ T_b^2 (LA) = 0$

$96.75 - 2(7.561)\ T_b = 0$

$T_b = 96.75/15.122$

$T_b = 6.4$

Similarly T_b was calculated for plant height which showed similar values of curves with less distinct points of inflection (Figure 4.2) (Appendix 4.1). It was found that the T_b that best fitted the model at all temperature and daylength conditions in the study was 6.4°C. The T_b of

6.4°C was therefore used for all the growth components. Other values used would not significantly affect the conclusions to be drawn from this analysis. Wiles (1989) suggested the use of a T_b of 6°C on a tropical onion. A T_b of 5°C was used by de Ruiter (1986) and a T_b of 6°C was used on a temperate onion by Morris and Tucker (1985).

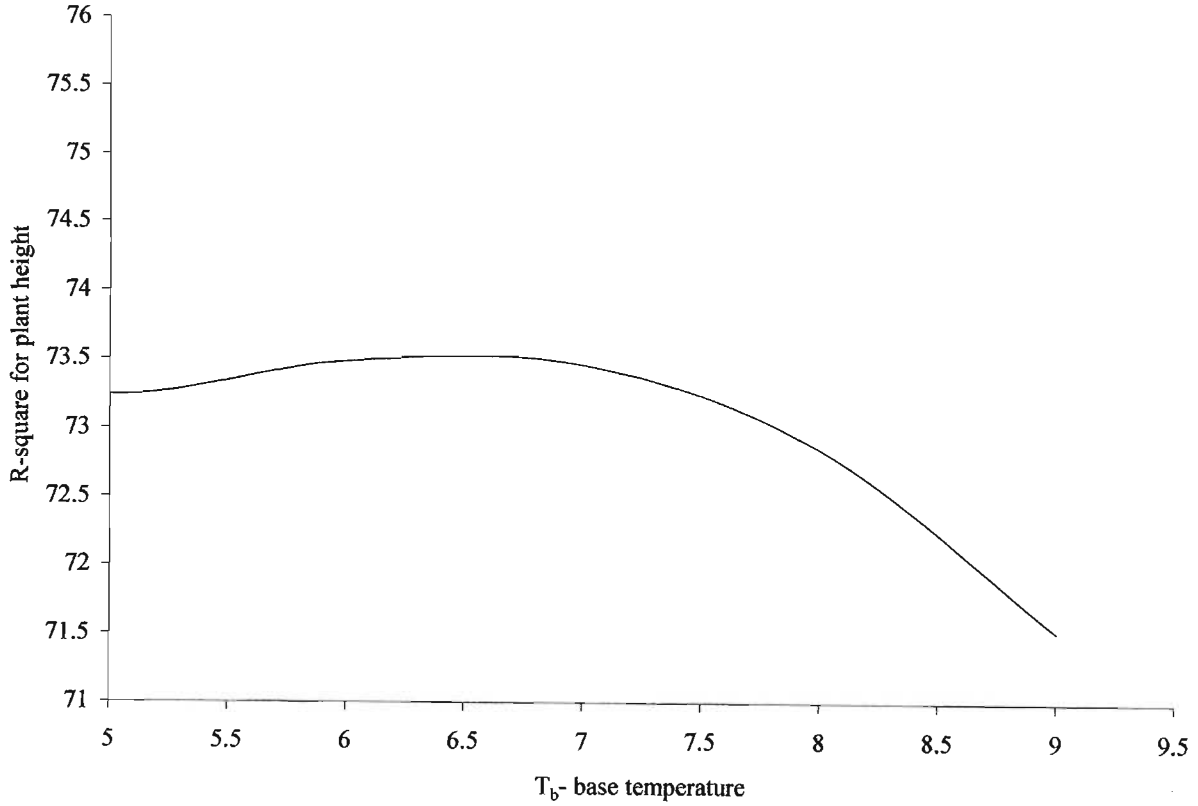


Figure 4.2 The percentage of variance accounting for (%) plant height at various base temperatures.

4.2 GROWTH RESPONSES AT 108 DAYS AFTER TRANSPLANTING

4.2.1 Leaf Number

There were significant responses to daylength and temperature, and to the interactions between daylength and temperature, daylength and cultivar (Table 4.2). There was also a higher order significant interaction.

Table 4.2 Analysis of variance table for measurements of leaf number at 108 days for three onion cultivars grown at three temperature regimes and daylengths.

Source of Variation	F Prob. (5%)	LSD $_{(5\%)}$
daylength	0.002**	0.2
temperature	<0.001**	0.2
cultivar	0.233	NS
daylength×temperature	<0.001**	0.4
daylength×cultivar	0.005**	0.4
temperature×cultivar	0.057	NS
daylength×temperature×cultivar	0.012**	0.7

**- highly significant ; NS-not significant.

Main effects

The data showed that the daylength had a significant effect on the leaf number (Table 4.3). There was no significant difference, in terms of number of leaves produced, between the 12.5h and 12 h daylengths. However, significantly fewer leaves were produced with a 11.5 h daylength.

The number of leaves emerging before 'onset of bulbing' was also significantly affected by temperature (Table 4.3). The most leaves were produced at 30/15°C (8.6), followed by 35/18°C (7.7) and the fewest at 25/12°C (7.0).

Table 4.3 The combined interaction effects of daylength and temperature on leaf number of 'Hagaz Red 1', 'Hagaz Red 2' and 'Red Creole' at 108 days when grown at different temperatures and daylengths.

Growth Rooms					
Daylength	**Temperature**	**Hagaz Red 1**	**Hagaz Red 2**	**Red Creole**	**Mean**
11.50 h	25/12°C	7.6	7.8	8.0	7.8
	30/15°C	8.5	6.9	8.0	7.8
	35/18°C	7.0	6.7	7.0	6.9
11.50 h Mean		7.8	7.1	7.7	7.5^{B}
12.00 h	25/12°C	6.3	6.9	6.6	6.6
	30/15°C	8.5	8.8	7.9	8.4
	35/18°C	9.0	8.8	8.3	8.7
12.00 h Mean		7.9	8.1	7.6	7.9^{A}
12.50 h	25/12°C	6.6	7	6.2	6.6
	30/15°C	10.0	10.1	9.3	9.8
	35/18°C	7.4	7.1	7.7	7.4
12.50 h Mean		8.0	8.1	7.7	8.0^{A}
Temp. Mean	25/12°C Mean	6.9	7.2	6.9	7.0^{C}
	30/15°C Mean	8.9	8.5	8.4	8.6^{A}
	35/18°C Mean	7.8	7.6	7.7	7.7^{B}
Cultivar Mean		7.9^{A}	7.8^{A}	7.7^{A}	

L.S.D. (0.05) marginal means= 0.2

L.S.D. (0.05) two-way interaction means= 0.4

L.S.D. (0.05) three-way interaction means= 0.7

Interaction effects

There was a significant interaction between daylength and temperature (Table 4.2) (Figure 4.3). At a 11.5 h daylength, an increase in day and night temperature from 25/12°C to

30/15°C did not significantly decrease the leaf number. However, when the temperatures were increased to 35/18°C, there was a significant decrease in leaf production. At the beginning, the plant seemed to adapt to the changing temperatures (25/12 to 30/15°C) by slowing down its normal leaf development (and rapidly declined due to increasing temperature). One might expect from a mean temperature increase from 18.2°C to 22.2°C in a temperate crop such as onions, that the rate of growth and hence leaf production would increase. As the data show a marginal decrease in the rate of leaf production at 30/15°C and a significant further reduction at 35/18°C, it would indicate that day temperatures in excess of 30/15°C at a daylength of 11.5 h are supra-optimal, inducing stress on the plant. Alternatively, the 11.5 h daylength induced physiological changes to the developmental processes in onions at the higher temperature. Under 12 and 12.5 h daylengths, the initial increase in temperature from 25/12°C to 30/15°C induced an expected significant increase in the rate of leaf production. However, further increase in temperature to 35/18°C provided no further significant increase in leaf number at the 12.5 h photoperiod. A rather large drop of leaf number across cultivars. In both these cases, it appears that as happened in the 11.5 h photoperiod, the day temperature of 35/18°C was supra-optimal (stress related), or that daylength-induced developmental processes were affected.

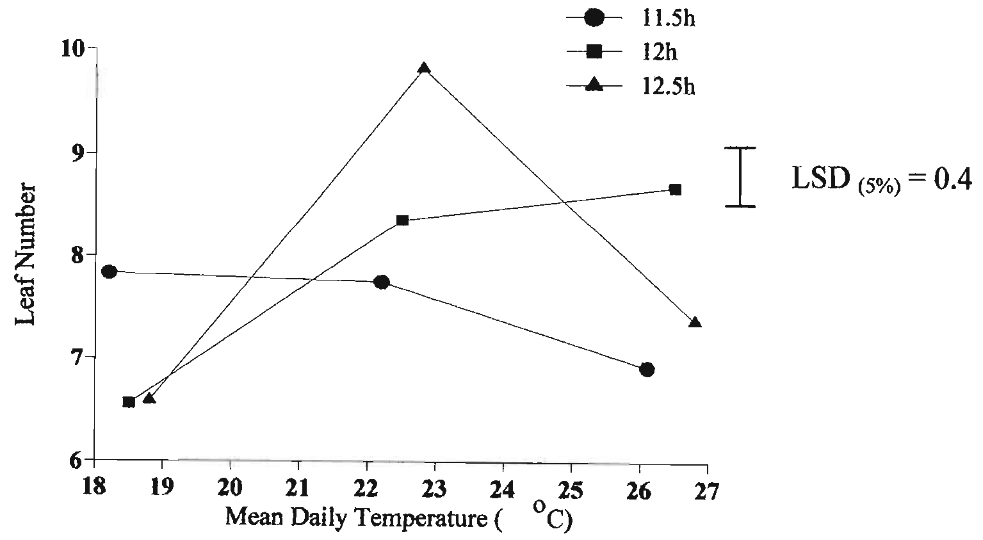


Figure 4.3 The effects of different daylengths (11.5 h, 12 h, 12.5 h) and temperatures (25/12°C, 30/15°C, 35/18°C) on leaf number of the onion plants. Each data point represents a mean leaf number per plant at 108 days.

The significant cultivar and daylength interaction (Table 4.3, Figure 4.4) was generated by HR 2, producing significantly fewer leaves under 11.5 h daylength than at 12 h and 12.5 h daylengths, whereas the other two cultivars produced similar numbers of leaves at each daylength treatment. However, HR 2 in the 11.5 h was affected in the growth room by a disease during the experimentation and therefore the apparent reduction in leaf number at 11.5 h daylength in the cultivar may be due to this factor. Clearly then, the apparent interaction is an artefact of the experimental process rather than treatment effects.

One might expect the Eritrean cultivars (HR 1 and HR 2), being fairly closely genetically related, to respond in a similar manner to environmental conditions. It is interesting that the RC responded similarly to the Eritrean cultivars. One could postulate that the three cultivars may be genetically related. This assertion may only be verified by comparing genetic material of Eritrean cultivars compared with those of RC. Alternatively, under inductive conditions, the cultivars might have to develop a certain number of leaves before they are induced into another stage of physiological development (Brewster, 1997).

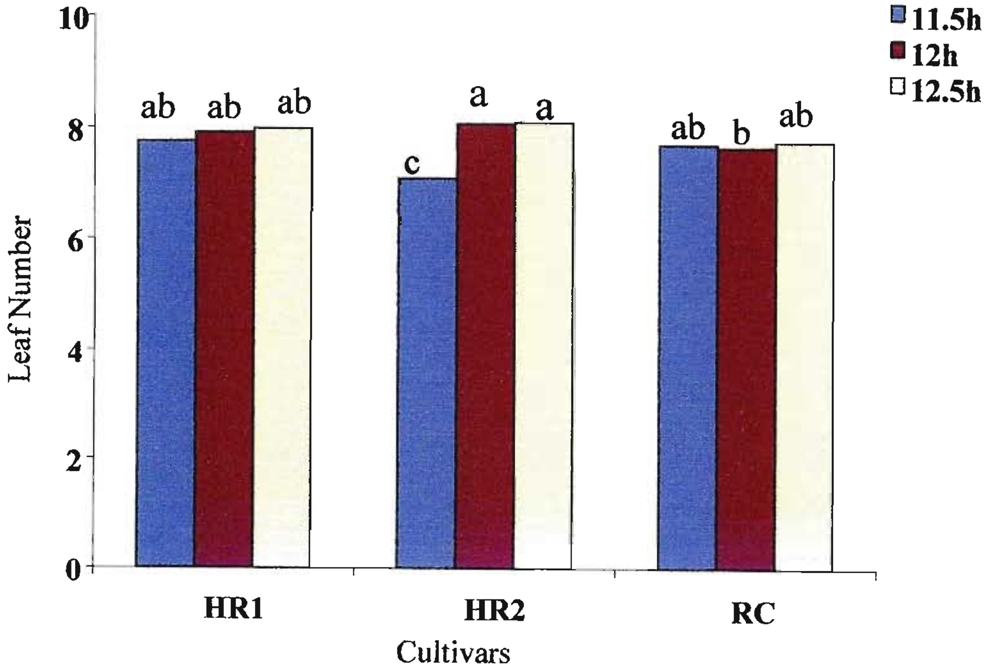


Figure 4.4 The number of leaves of three cultivars (Red Creole, Hagaz Red 1(HR 1) and Hagaz Red 2 (HR 2)) grown under three daylengths. (LSD $_{(0.05)}$ =0.4).

4.2.2 Height to Uppermost Leaf Tip

There were significant responses to daylength, temperature and cultivars, and to the interaction between daylength and temperature (Table 4.4), A significant interaction between daylength and temperature suggested that the growth in terms of plant height may show a significant response to the growth factors over the course of the experiment.

Main effects

Plant height significantly increased with each increment in daylength (512.0, 547.0 and 594.0 mm at 11.5, 12 and 12.5 h daylength, respectively) (Table 4.5).

Table 4.4 Analysis of variance table for measurements of plant height at 108 days of three onion cultivars grown at three temperatures and daylengths.

Source of Variation	**F.Prob. (5%)**	**LSD $_{(5\%)}$**
daylength	<0.001**	18
temperature	<0.001**	18
cultivar	0.002**	18
daylength×temperature	<0.001**	31
daylength×cultivar	0.066	NS
temperature×cultivar	0.355	NS
daylength×temperature×cultivar	0.257	NS

**- highly significant; NS- not significant

The significantly highest plant height was recorded at temperature treatments of 30/15°C (571.0 mm) and 25/12°C (560.0 mm) and shortest at 35/18°C (522.0 mm). While the shift from 25/12°C to 30/15°C had a positive influence on plant height, a further increase to 35/18°C led to a reduction in plant height. The Eritrean cultivars, HR 1 (561.0 mm) and HR 2 (560.0 mm), were also found significantly taller than Red Creole (532.0 mm). However, no significant differences were observed between the two Eritrean cultivars (HR1 and HR 2). As there was an interaction effect between daylength and temperature, it will be discussed in detail.

Table 4.5 The combined interaction effects of daylength and temperature on plant height (mm) of 'Hagaz Red 1', 'Hagaz Red 2' and 'Red Creole' at 108 days when grown at different temperatures and daylengths.

Growth Rooms					
Daylength	**Temperature**	**Hagaz Red 1**	**Hagaz Red 2**	**Red Creole**	**Mean**
11.50 h	25/12°C	675.0	657.0	633.0	655.0
	30/15°C	543.0	475.0	449.0	489.0
	35/18°C	409.0	398.0	366.0	391.0
11.50 h Mean		542.0	510.0	483.0	512.0^{C}
12.00 h	25/12°C	459.0	493.0	499.0	484.0
	30/15°C	595.0	627.0	532.0	583.0
	35/18°C	582.0	588.0	548.0	573.0
12.00 h Mean		545.0	569.0	526.0	547.0^{B}
12.50 h	25/12°C	537.0	560.0	524.0	540.0
	30/15°C	638.0	643.0	640.0	640.0
	35/18°C	613.0	601.0	595.0	603.0
12.50 h Mean		596.0	601.0	586.0	594.0^{A}
Temp. Mean	25/12°C Mean	557.0	570.0	552.0	560.0^{A}
	30/15°C Mean	592.0	582.0	540.0	571.0^{A}
	35/18°C Mean	534.0	529.0	503.0	522.0^{B}
Cultivar Mean		561.0^{A}	560.0^{A}	532.0^{B}	

L.S.D. (0.05) marginal means = 18.0

L.S.D. (0.05) two-way interaction means =31.0

L.S.D. (0.05) three-way interaction means = 54.0

Interaction effects

There was a significant interaction between daylength and temperature (Table 4.4 and Figure 4.5). At a 11.5 h daylength, an increase in temperature from 25/12°C to 35/18°C significantly and incrementally decreased the plant height. A significant decrease in the plant height indicated that day temperatures in excess of 25°C are supra-optimal, inducing stress on the plant. Alternatively, the 11.5 h daylength may also have induced physiological changes to the plant developmental processes at the higher temperatures. Under 12 and 12.5 h daylengths, the initial increase in temperature from 25/12°C to 30/15°C induced an expected significant increase in plant height. However, further increase in temperature to 35/18°C provided no further significant change in plant height in the 12 h photoperiodic treatment, but it decreased plant height significantly at the 12.5 h photoperiod. In both these cases, the day temperature in excess of 30°C appears to be supra-optimal (stress related), or alternatively, daylength-induced developmental processes were affected.

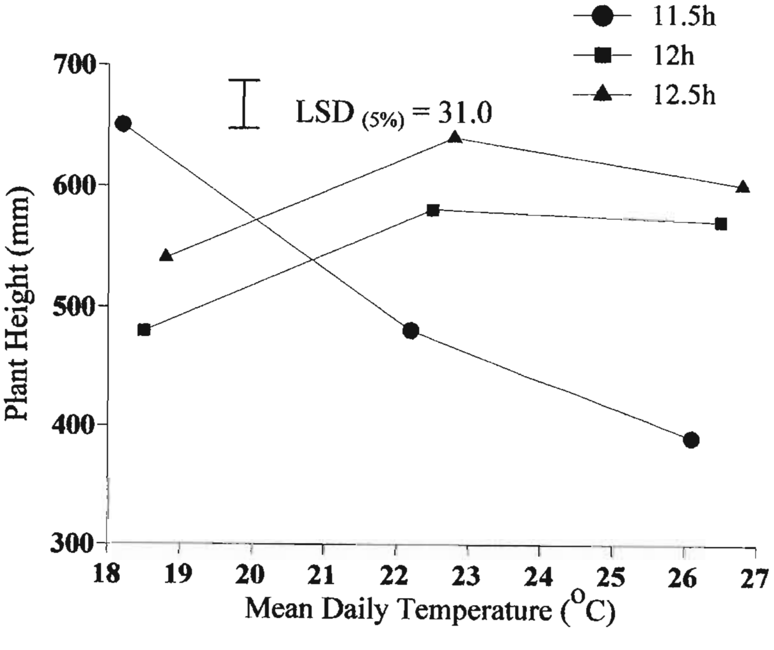


Figure 4.5 The effects of different daylengths (11.5 h, 12 h, 12.5 h) and temperatures (25/12°C, 30/15°C, 35/18°C) on height of the onion plants. Each data point represents a mean plant height (mm) per plant at 108 days.

4.2.3 Leaf Area

There were significant responses to daylength and temperature, and to the interaction between daylength and temperature (Table 4.6). A significant interaction between daylength and temperature suggested that the leaf area was affected by the combinations of environmental components over the course of the experiment.

Main effects

Leaf area significantly increased with each increment in daylength (266.0, 374.0 and 596.0 cm^2 at 11.5, 12 and 12.5 h daylength, respectively).

Table 4.6 Analysis of variance table for measurements of leaf area at 108 days of three onion cultivars grown at three temperature regimes and daylengths.

Source of Variation	F Prob. (5%)	LSD $_{(5\%)}$
daylength	<0.001**	63.3
temperature	0.005**	63.3
cultivar	0.111	NS
daylength×temperature	0.001**	109.7
daylength×cultivar	0.418	NS
temperature×cultivar	0.406	NS
daylength×temperature×cultivar	0.275	NS

** - highly significant; NS- not significant

Temperature had a significant effect on leaf area. The highest leaf area was recorded at a temperature treatment of 30/15°C (474.0 cm^2) and a smaller leaf areas were recorded at 25/12°C (384.0 cm^2) and 35/18°C (378.0 cm^2) (Table 4.7). There was a significant interaction between daylength and temperature (Tables 4.6, 4.7).

Table 4.7 The combined interaction effects of daylength and temperature on leaf area (cm^2)of 'Hagaz Red 1', 'Hagaz Red 2' and 'Red Creole' at 108 days when grown at different temperatures and daylengths.

Growth Rooms		Hagaz Red 1	Hagaz Red 2	Red Creole	Mean
Daylength	Temperature				
11.50 h	25/12°C	585.0	485.0	412.0	494.0
	30/15°C	282.0	116.0	179.0	192.3
	35/18°C	136.0	118.0	85.0	113.0
11.50 h Mean		334.0	240.0	225.0	266.4^{C}
12.00 h	25/12°C	207.0	235.0	256.0	233.0
	30/15°C	471.0	465.0	336.0	424.0
	35/18°C	515.0	525.0	359.0	466.0
12.00 h Mean		398.0	408.0	317.0	374.0^{B}
12.50 h	25/12°C	341.0	541.0	397.0	426.0
	30/15°C	904.0	786.0	731.0	807.0
	35/18°C	515.0	532.0	613.0	553.0
12.50 h Mean		587.0	620.0	580.3	596.0^{A}
Temp. Mean	25/12°C Mean	378.0	420.0	355.0	384.0^{B}
	30/15°C Mean	552.3	456.0	415.0	474.0^{A}
	35/18°C Mean	389.0	392.0	352.0	377.5^{B}
Cultivar Mean		440.0^{A}	423.0^{AB}	374.0^{B}	

L.S.D. (0.05) marginal means= 63.3

L.S.D. (0.05) two-way interaction means= 109.7

L.S.D. (0.05) three-way interaction means= 190.0

Interaction effects

The interaction between daylength and temperature for leaf area was similar in nature to that of leaf number Tables (4.2, 4.3) and Figures (4.3, 4.4). At a 11.5h daylength, an increase in temperature from 25/12°C to 30/15°C significantly decreased the leaf area. However, when the temperature was increased to 35/18°C, there was no significant further decrease in leaf area (Table 4.7, Figure 4.6). At the beginning, the plant was seemed to adapt to the changing temperatures (25/12 to 30/15°C) by slowing down its normal leaf development and leaf area declined due to increasing temperature. One might expect from a mean temperature of 18.2°C in a temperate crop such as onions, that the rate of growth and hence leaf production would increase. As the data show a significant decrease in the rate of leaf production at 30/15°C and a marginal further reduction at 35/18°C, it would indicate that day temperatures in excess of 25/12°C at a daylength of 11.5 h are supra-optimal, inducing stress on the plant. Alternatively, the 11.5 h daylength induced physiological changes to the developmental processes in onions at the increasing temperature. Under 12 and 12.5 h daylengths, the initial increase in temperature from 25/12°C to 30/15°C induced an expected significant increase in leaf area. However, further increase in temperature to 35/18°C provided no further significant increase in leaf area at the 12.5 h photoperiod. In both these cases, it appears that as happened in the 11.5 h photoperiod, the day temperature of 35/18°C was supra-optimal (stress related), or that daylength-induced developmental processes were affected. The leaf area data mirror the plant height data indicating that the changes in leaf area were more a consequence of leaf elongation responses to the treatments than of leaf number.

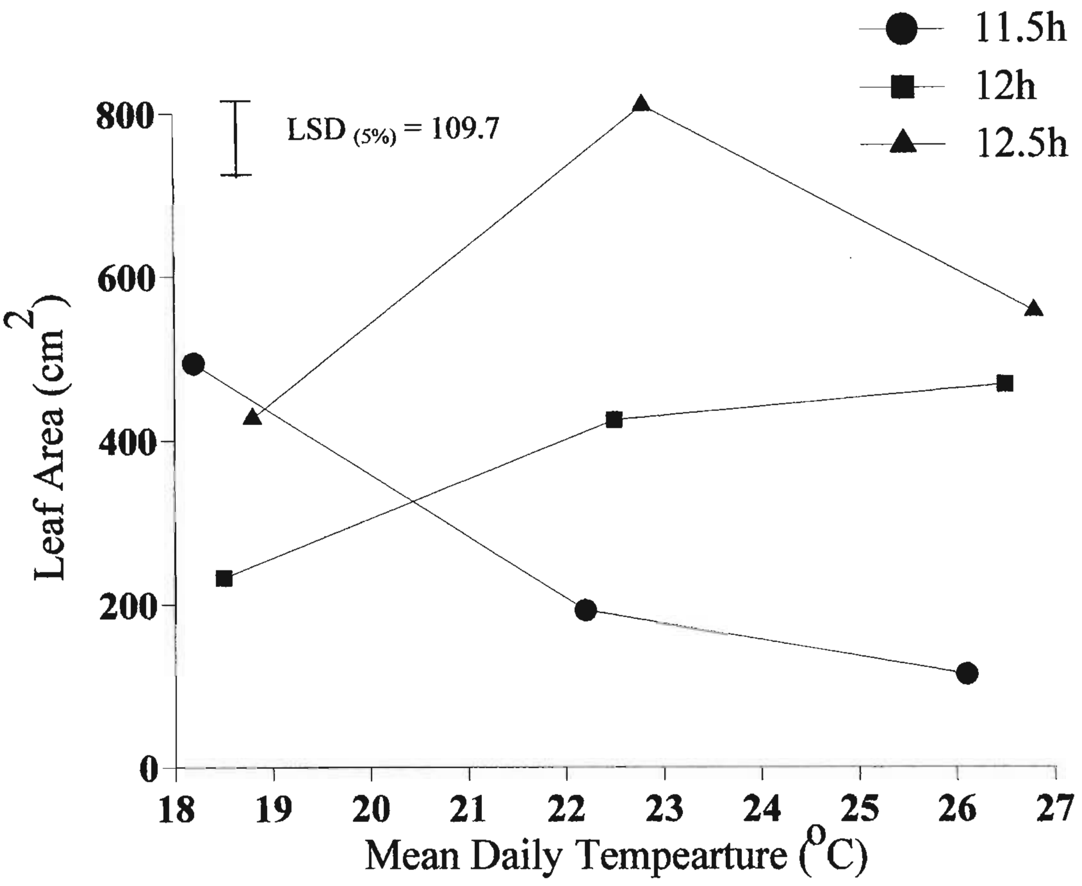


Figure 4.6 The effects of different daylengths (11.5h, 12h, 12.5h) and temperatures (25/12°C, 30/15°C, 35/18°C) on leaf area of the onion plants. Each data points represents a mean leaf area (cm^2) per plant at 108 days.

*** Mean Daily temperature, calculated as:**

$$\frac{\text{(Daylength} \times \text{Day temperature)} + \text{(Night length} \times \text{Night temperature)}}{24\ \text{h}}$$

4.2.4 Bulbing Ratio

There were significant responses to daylength, temperature, cultivars and all the interactions between daylength, temperature, and cultivar (Table 4.8).

Main effects

In terms of length of photoperiod, all treatment means differed significantly from each other. The highest bulb ratio was recorded at 12 h (2.5), followed by 12.5 h (2.2) and then the lowest at 11.5 h (1.6). The data showed that the 12 h daylength induced bulbing earlier than the 11.5 and 12.5 h daylengths (Table 4.9).

Table 4.8 Analysis of variance table for measurements of bulb ratio at 108 days for three onion cultivars grown at three temperatures and daylengths.

Source Of Variation	F Prob. (5%)	LSD $_{(5\%)}$
daylength	<0.001**	0.1
temperature	<0.001**	0.1
cultivar	0.005**	0.1
daylength×temperature	<0.001**	0.2
daylength×cultivar	<0.001**	0.2
temperature×cultivar	0.011**	0.2
daylength×temperature×cultivar	0.040**	0.3

**- highly significant

In terms of temperature treatments, all treatment means differed significantly from each other. The highest bulb ratio recorded at 35/18°C (2.2), followed by 25/12°C (2.1) and then at 30/15°C (2.0) (Table 4.9). In terms of cultivar response, there was no significant difference between HR 1 and HR 2, but they bulbed significantly earlier than Red Creole (Table 4.9). There was a highly significant interaction among all the treatments, which will be discussed in detail.

Table 4.9 The combined interaction effects of daylength and temperature on bulb ratio of 'Hagaz Red 1', 'Hagaz Red 2' and 'Red Creole' at 108 days when grown at different temperatures and daylengths.

Growth Rooms		Hagaz Red 1	Hagaz Red 2	Red Creole	Mean
Daylength	**Temperature**				
11.50 h	25/12°C	1.7	1.5	1.6	1.6
	30/15°C	1.5	1.7	1.6	1.6
	35/18°C	1.7	1.5	1.6	1.6
11.50 h Mean		1.6	1.6	1.6	1.6^{C}
12.00 h	25/12°C	3.0	3.0	2.2	2.7
	30/15°C	2.2	2.2	2.2	2.2
	35/18°C	2.8	2.7	2.3	2.6
12.00 h Mean		2.7	2.6	2.2	2.5^{A}
12.50 h	25/12°C	2.1	1.9	1.9	2.0
	30/15°C	2.2	2.3	2.3	2.3
	35/18°C	2.3	2.3	2.5	2.4
12.50 h Mean		2.2	2.2	2.2	2.2^{B}
Temp. Mean	25/12°C Mean	2.3	2.1	1.9	2.1^{B}
	30/15°C Mean	1.9	2.1	1.9	2.0^{C}
	35/18°C Mean	2.3	2.2	2.1	2.2^{A}
Cultivar Mean		2.2^{A}	2.1^{A}	1.9^{B}	

L.S.D. (0.05) marginal means = 0.1

L.S.D. (0.05) two-way interaction means = 0.2

L.S.D. (0.05) three-way interaction means= 0.3

Interaction effects

At a 11.5 h daylength, an increase in temperature from 25/12°C to 35/18°C did not affect the growth of bulb ratio (Figure 4.7). While temperature does not seem to have any effect on bulb development under 11.5 h daylength, it might increase the vegetative growth of the plant.

Under an inductive daylength, Steer (1990) found that temperature accelerated the rate of bulbing. However, in the current study, under a 12 h daylength, an increase in temperature from 25/12°C to 30/15°C significantly decreased the bulb ratio, but when the temperature increased to 35/18°C, there was a significant further increase in bulb ratio. At a 12 h photoperiod, increasing the temperature from 25/12°C to 30/15°C seems to have prolonged vegetative development. As daylength lengthened to 12.5 h, an increase of temperature from 25/12°C to 30/15°C significantly increased bulb ratio and a further increase of temperature to 35/18°C did not significantly increase bulb ratio.

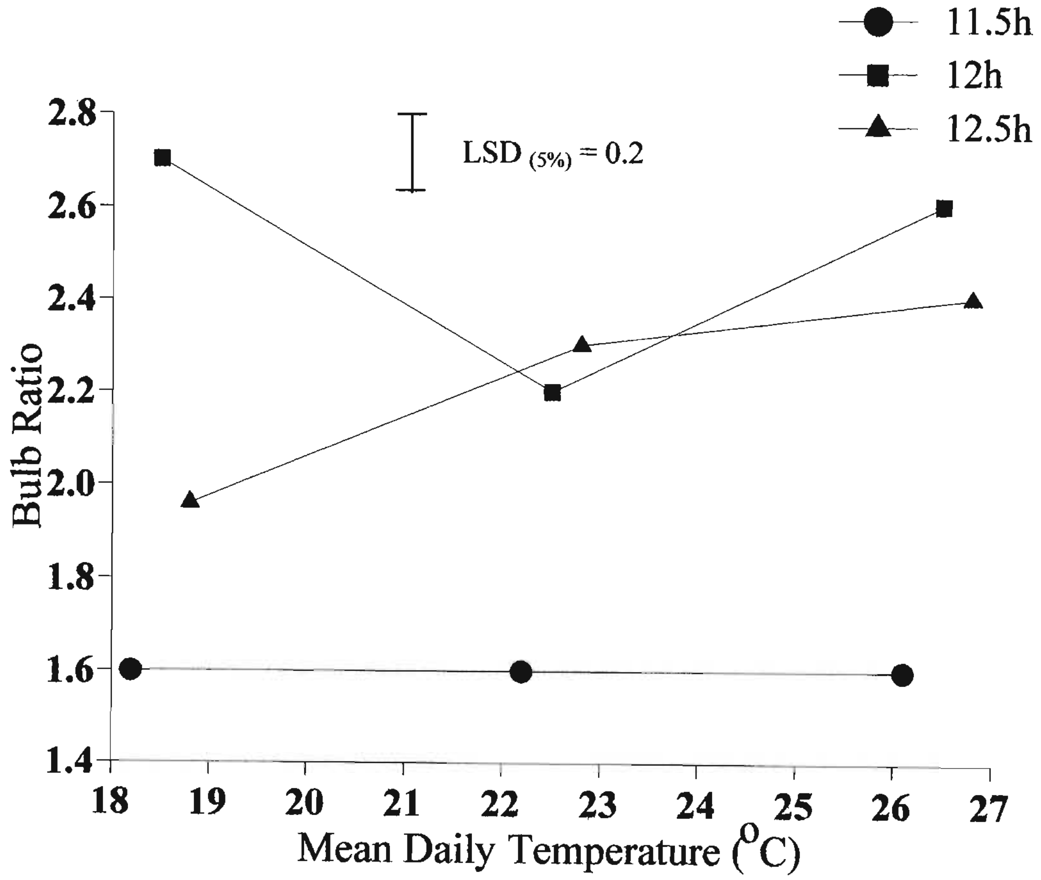


Figure 4.7 The effects of different daylengths (11.5h, 12h, 12.5h) and temperatures (25/12°C, 30/15°C, 35/18°C) on bulb ratio of the onion plants. Each data point represents a mean bulb ratio per plant at 108 days.

The significant interaction of cultivar and daylength was explained by the different response of RC to daylength in comparison with the Eritrean cultivars. Red Creole did not display the inductive response to the 12 h photoperiod, shown by the Eritrean cultivars (Figure 4.8).

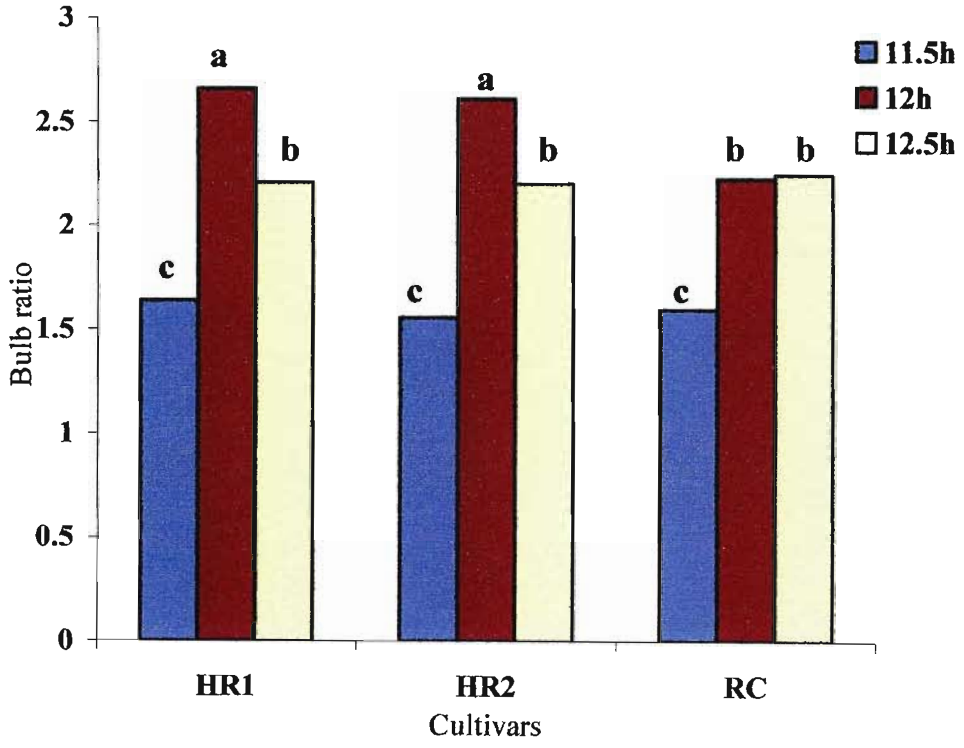


Figure 4.8 The bulb ratio of three cultivars (Red Creole, Hagaz Red 1(HR1) and Hagaz Red 2 (HR 2)) grown under three daylengths. (LSD $_{(0.05)}$=0.2)

The temperature and cultivar interaction was generated by RC having a low bulb ratio at 25/12°C, and the Eritrean cultivars had bulbing suppressed at 30/15°C (Figure 4.9).

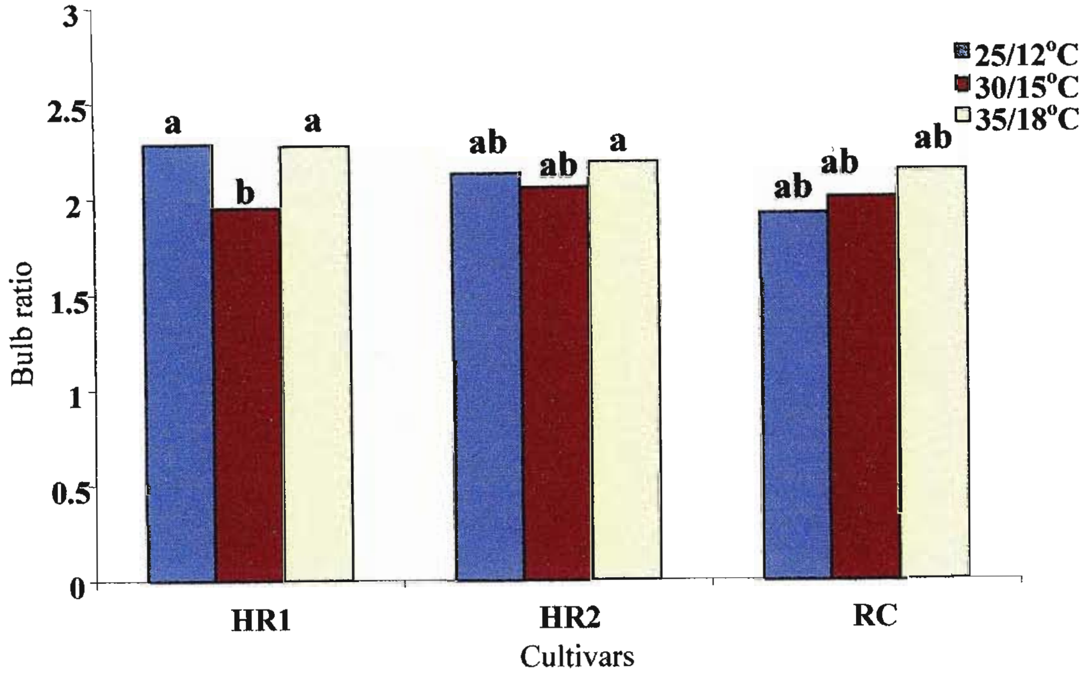


Figure 4.9 The bulb ratio of three cultivars (Red Creole, Hagaz Red 1(HR1) and Hagaz Red 2 (HR 2)) grown under three temperature regimes. (LSD $_{(0.05)}$=0.2)

High order interaction effect

In the higher order interaction (P=0.05), the two Eritrean cultivars (HR 1 and HR 2) responded differently from RC to the combination of daylength and temperature (Table 4.9). Bulbing was not induced in any of the cultivars at any of the temperature treatments under the 11.5 h photoperiod (bulb ratio range of 1.5 to 1.7). At the 12.5 h photoperiod all the cultivars also responded similarly with bulbing being induced significantly later at 25/12°C (bulb ratio range of 1.9 to 2.1) than at 30/15°C (bulb ratio range of 2.2 to 2.3) and at 35/18°C (bulb ratio range of 2.3 to 2.5). However, 12 h photoperiod, generated a 3-way interaction response, temperature significantly affected the bulbing response of the cultivars. Red Creole was induced to bulb at a 12 h photoperiod, but was insensitive to temperature at this photoperiod (bulb ratio range of 2.2 to 2.3). However, at this daylength, temperature significantly affected the bulbing growth of the Eritrean cultivars (HR 1 and HR 2). At the 25/12°C (bulb ratio of 3.0) and 35/18°C (bulb ratio of 2.7 to 2.8) temperatures, HR 1 and HR 2 were induced into bulbing earlier as compared to RC (bulb ratio of 2.2). At 30/15°C, the Eritrean cultivars HR 1 and HR 2 showed significantly delayed bulbing (bulb ratio of 2.2) in comparison with the higher and lower temperatures. Also, there were no significant differences in terms of bulb ratio (bulb ratio of 2.2) between all the cultivars at 30/15°C.

4.2.5 Discussion

As bulbing is an important physiological and economic response of onions, the discussion will focus on how leaf number, height and leaf area affected this response. Also, it was in the bulbing ratio that there was a cultivar x temperature x daylength interaction response, which needs interpretation (Table 4.8).

The 11.5 h photoperiod was a non-inductive environment for bulbing in all cultivars as the bulbing ratio (1.5 to 1.7) was well below the accepted value of 2.0 (Kedar *et al.*, 1975) (Table 4.9). This infers that growth responses were not interfered with by inductive physiological processes, so that photoperiodic and temperature responses can be interpreted as affecting vegetative growth only. At this daylength, the temperature increment from 25/12°C to 30/15°C did not significantly reduce the leaf production, but leaf production at 35/18°C was reduced, indicating that plants were stressed at the high day temperature. However, there was a marked effect of each incremental temperature significantly reducing plant height and leaf area. It seems that the 11.5h daylength only facilitates more vegetative growth than bulbing at 25/12°C (Kedar *et al.* 1975). However, the further increase in temperature in excess of 25/12°C decreases vegetative growth under the short daylength without development of bulbing (Roberts *et al.* 1988). The effect of temperature on growth components clearly indicated that the decrease in leaf number at 35/18°C was likely a temperature stress factor. The leaf height and area data show that the stress to leaf development already occurred at 30/15°C, probably associated with the day temperature.

At the 12 h photoperiod, an inductive environment for bulbing in all treatments, it was observed that growth responses were to some extent interfered with by interactive effects. The 12 h daylength at the temperature 25/12°C, which induced bulbing more strongly than any other increment, significantly reduced leaf number, height, and area in all cultivars in comparison to plants grown at the same temperature in the non-inductive environment of 11.5 h. The latter effects indicate that there was a marked effect of source-sink relationship which resulted in the cultivars producing the highest bulb ratio (3.0). The temperature increment from

25/12°C to 35/18°C increased leaf number at a 12 h daylength, similarly to plants grown at a 11.5 h daylength, and also increased plant height and leaf area of the cultivars, particularly at 35/18°C. In the case of RC, a temperature increment did not affect the bulbing response at the 12 h daylength, but the leaf number, plant height and leaf area increased with increased temperature. At the 12 h inductive daylength, the cultivars HR 1 and HR 2 showed a marked reduction in bulb initiation as the temperature increased from 25/12°C to 30/15°C. As expected, with the change in source-sink ratio, this was accompanied by an increase in leaf number, height and area. However, in contrast to this postulate of source-sink ratio effect, a further increase in temperature to 35/18°C in these cultivars led to a significantly increased rate of bulbing, but this was also accompanied by an increase in leaf number, height and area. The higher temperatures in this inductive environment which promoted leaf growth may also have played a part in temperature stress-related induction of bulbing. The plant size has also an effect on the time of onset of bulbing and further development of bulbing (Mettananda and Fordham, 1999). At 12 h daylength, the Eritrean cultivars (HR 1 and HR 2) responded in a similar way to RC under increasing temperature. The high number of leaves and leaf area produced by plants at 30/15°C would have had a higher potential source and hence growth compared with plants grown at 25/12°C. As the temperature further increased to 35/18°C, it only negated production of the growth components, but the bulb ratio remained the same. The small growth of bulbs at 35/18°C was probably temperature-stress related.

The 12.5 h daylength was inductive for bulbing in all treatments but temperature affected the rate of response. At 25/12°C, where bulbing had just started to be induced (bulb ratio of 1.9 to 2.1), there was also a lower leaf number, plant height and leaf area of all the cultivars in comparison to plants grown at the same temperature in the non-inductive environment of 11.5h. Plants, however, had higher plant height and leaf area as compared to those grown at the same temperature at a 12 h daylength. The 11.5 h non-inductive, the lower temperature environment increased the vegetative growth of the cultivars and under this growth condition, the active plant growth might be related to the readiness of a plant to receive bulbing stimuli as a result of an inductive growth environment trigger (12.5 h) for bulb initiation and growth. The increased leaf area and plant height under 12.5 h daylength, as compared to 12 h daylength at 25/12°C, might be related to increased availability of photoassimilates supplied to the apical meristem of a plant for bulb initiation and growth. The temperature increment from 25/12°C to 30/15°C increased leaf number, plant height and leaf area at 12.5 h to that similar to plants grown at a 12 h daylength. However, raising the temperature to 35/18°C decreased leaf number, plant height and leaf area at the 11.5 h and 12.5 h daylengths. This might be associated with temperature stress regulation of plant growth. Temperature increment affected the bulbing response of RC at a 12.5 h daylength, and leaf number, plant height and leaf area increased with a temperature increment from 25/12°C to 30/15°C, but decreased at 35/18°C. However, at a 12.5 h daylength, the 30/15°C temperature was expected to produce the highest onion production as these plants had a larger leaf area. Such plants are able to produce greater leaf carbohydrate to be assimilated in a longer period of time from the plant canopy into a growing bulb and hence delay foliage collapse (Daymond *et al.*, 1997). The 35/15°C temperature appears to have induced bulbing due to temperature stress-related growth conditions. At a 12.5 h inductive daylength, the cultivars HR 1 and HR 2 showed no marked differences in bulb initiation as the temperatures increased from 25/12°C to 35/18°C, but this was accompanied by an increased leaf number, plant height and leaf area at temperatures from 25/12°C to 30/15°C. However, a further increase in the temperature to 35/18°C in these cultivars did not increase the bulbing response and this was also accompanied by a decrease in leaf number, plant height and leaf area as compared to the 30/15°C temperature.

At the 12 h and 12.5 h daylengths, the cultivars which were grown at 30/15°C and 35/18°C, produced larger leaf areas. The larger leaf areas would be associated with the cultivars potential to have a higher assimilation rate and the supply of carbohydrate to the apical meristem would be more available. Carbohydrate photoassimilates in combination with a bulbing stimulus derived from other environmental triggers would be responsible for bulb scale initiation and growth (Mettananda and Fordham, 1999).

4.3 GROWTH RESPONSES TO DAYLENGTH BASED ON GROWING DEGREE DAYS (GDD)

4.3.1 Introduction

The way in which temperature affects bulbing in onions is not clear as it is inevitably confounded by daylength. Temperature has a marked effect on the rate of vegetative growth (Butt, 1968; Brewster, 1979) and on the rate of leaf initiation and emergence (de Ruiter, 1986). In so far as plant size or age modulate the response to photoperiod (Sobeih and Wright, 1986) it is probable that a measurement of plant age in terms of thermal time, commonly expressed as growing degree days (GDD), is more appropriate than chronological age in determining the plant's photoperiodic response. A model of this kind has been proposed for flower initiation by Roberts and Summerfield (1987), and its application to onion bulbing was also suggested by Roberts *et al.* (1988).

In the current study, the relation between growth components and GDD was also examined in order to investigate plant growth response to daylength over the growing period in this study. The GDD values were calculated and given over the corresponding plant growth measurements of the growing period (Appendix 4.2). The broken-stick regression model was used to find the point of inflection on the growth of the cultivars and this provided an appropriate point to evaluate bulb initiation and rate of leaf area growth. A close examination of the data suggests that all the cultivars responded remarkably similar manner to the daylength and temperature combinations. To this effect, at the end of this chapter, the responses to all components were meaned over all cultivars to assess an overall response to the interactions.

4.3.2 Leaf Number

At the 11.5 h and 12.5 h daylengths, temperature induced more variation in leaf production in response to GDD in all three cultivars than at a 12 h photoperiod (Figure 4.10). The 35/18°C temperatures decreased the rate of production at the 11.5 h and 12.5 h daylengths. One might expect that a supra-optimal 35°C day temperature would induce stress-related physiological disorders and cause a decreased rate of leaf production. This was observed on all plants grown at the supra-optimal temperature which would have increased respiration rates and utilization of carbohydrate reserves in order to cope with this particular growth condition. The high variability of leaf production under 11.5 h indicated that temperature treatments had a dominant effect in leaf production over daylength. However, under 12 h daylength, temperature treatments did not influence the thermal time response. It is expected that the daylength response of the cultivars will change with temperature increment as the leaves age (Salisbury, 1955). Hence, once the photoperiod induced bulbing, leaf production an onion plant would be terminated slowly after some time of plant growth. Under the 12.5 h daylength, the 35/18°C temperature decreased the rate of leaf production over GDD as they did under the short daylength (11.5 h). This might occur when the plants, induced by stress conditions to develop bulbing, hasten the growth cycle and start to accumulate stored carbohydrate for bulb development. The temperature treatments affected leaf production more dominantly at the 12.5 h daylength.

The cultivars produced fairly similar numbers of leaves (Figure 4.10). Differences in the growth trend of the cultivars were considered more likely to be due to temperature treatments. It seems that temperature controls the production of leaves (Wiles, 1989). Under the 11.5 and 12.5 h daylengths, there were significant variations in leaf production due to the temperature effects as compared to the 12 h daylength where there were none.

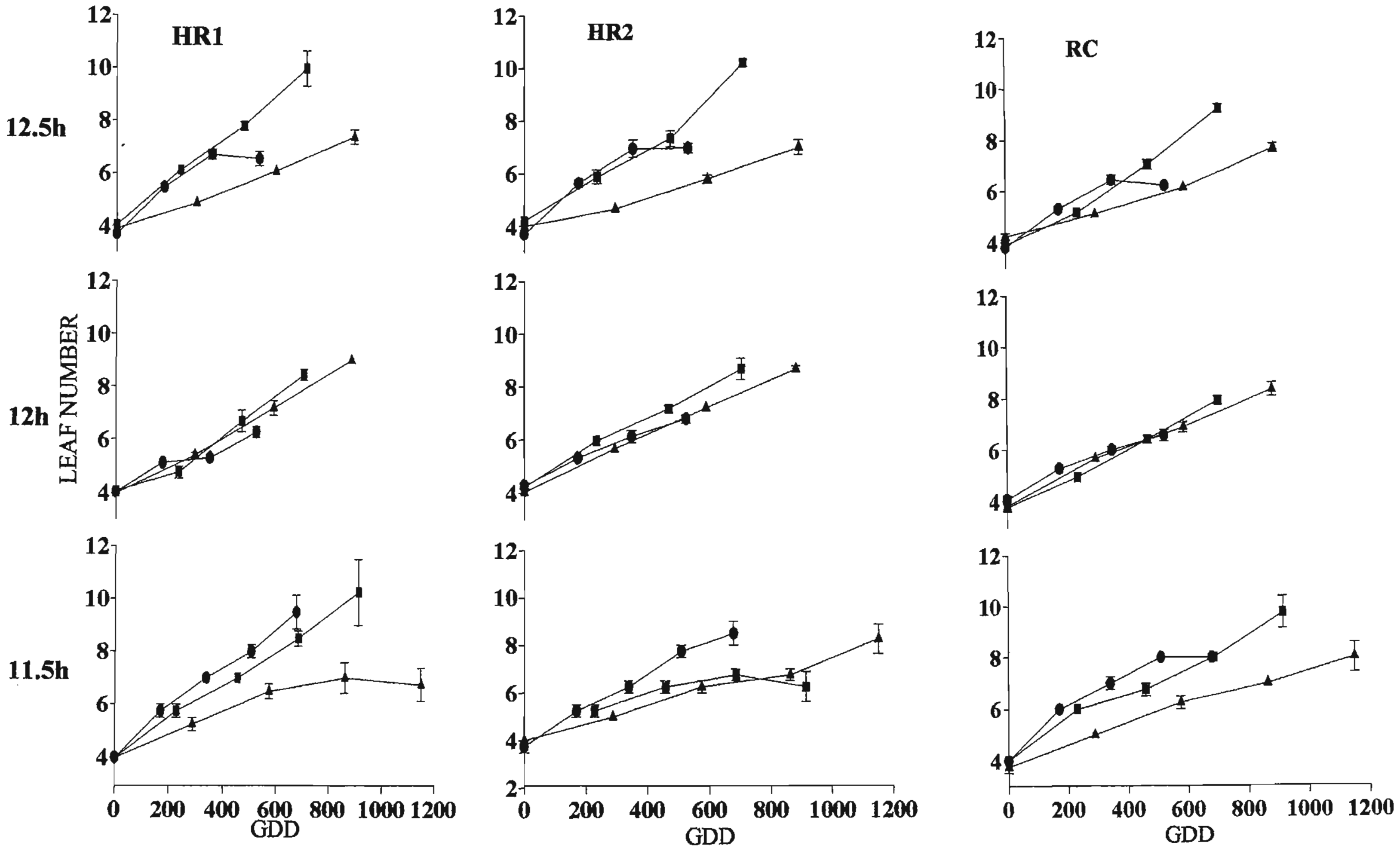


Figure 4.10 The growth response in terms of leaf number of the onion cultivars Hagaz Red 1, Hagaz Red 2, and Red Creole, grown under three regimes of daylength (11.5 h, 12 h, 12.5 h) and three levels of temperature (25/12°C–●; 30/15°C–■; 35/18°C–▲) over growing degree days (GDD). Bars represent SED.

The regression analysis of leaf number over GDD showed that the coefficient of determination (R^2) was 74.6% (Figure 4.11) (Appendix 4.3). As the amount of thermal heat had an effect on leaf production, it is possible to determine the number of GDD required to produce an estimated leaf number for a particular cultivar. Brewster *et al.* (1977) reported that plants needed to have initiated a certain number of leaves to be able to bulb when the daylength appropriate to that cultivar was reached. Bulbing is not initiated until plants are subjected to the minimum daylength for bulb induction and accumulate thermal time from emergence of approximately 600 degree days. There is evidence that leaf number is affected by temperature treatments and GDD can be used to estimate the rate of leaf production (Lancaster *et al.*, 1996).

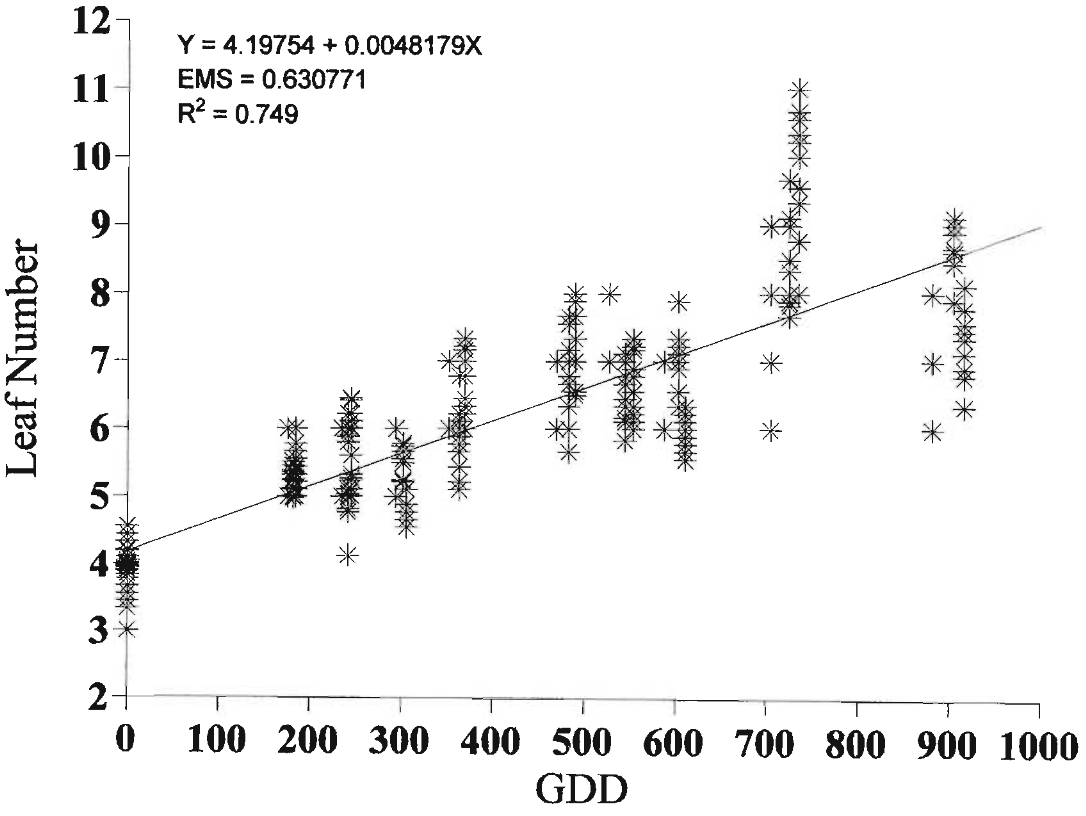


Figure 4.11 The regression line of leaf number and GDD for three cultivars of onions grown at nine combinations of temperature and daylength. (n=433).

4.3.3 Leaf Area

At the 11.5 h and 12.5 h daylengths, the temperature treatments induced more variation in leaf area of all three cultivars than at the 12 h photoperiod (Figure 4.12). The 25/12°C temperature induced increased rate of leaf area production of the cultivars earlier in comparison to 30/15°C and 35/18°C. This seemed to particularly occur under the 11.5 h daylength. The cultivars produced a higher leaf area when they were grown under the lower temperature at the 11.5 h daylength than the warmer temperatures. The 25/12°C temperature seemed to be the most suitable one for vegetative growth under short daylength (11.5 h). Under this temperature, plants required fewer GDD for leaf development than at the other two temperatures. The decrement of leaf area as temperature increased (30/15°C to 35/18°C) was most likely due to stress-related supra-optimal temperature conditions. High leaf area production might be associated with rapid induction of bulbing under the lower temperature (25/12°C). Plant size, in terms of leaf area, strongly affects response to bulbing stimulus in onion (Mettananda and Fordham, 1999). Plant size (Jones and Mann, 1963b) or plant age (Butt, 1968) have also been implicated in regulating the timing of bulb initiation. The broken-stick regression model was applied to find the point of inflection on the growth rate in terms of leaf area, with a view to detecting the induction of bulbing (Table 4.10). Since there were no significant differences between cultivars, the analysis was done only for one cultivar.

Table 4.10 Broken-stick analysis for leaf area development of onion Red Creole in relation to growing degree days (GDD).

Daylength	Temperature	Model with i^{th} GDD	Point of Inflection (t)		% of Variation accounted for	F probability for Regression
			GDD	Est. Y		
11.5 h	25/12°C	200	197.3	96.8	79.8	<0.001**
	30/15°C	240	389.6	60.4	95.7	<0.001**
	35/18°C	300	-297.3	3.6	67.8	<0.001**
12 h	25/12°C	200	405	161.5	68.2	<0.001**
	30/15°C	240	431.8	105.7	84.5	<0.001**
	35/18°C	320	431.2	82.3	79.6	<0.001**
12.5 h	25/12°C	200	140.1	59.6	82.5	<0.001**
	30/15°C	300	410.7	132.3	79	<0.001**
	35/18°C	320	579.4	79.6	80	<0.001**

With a 12 h daylength, temperature treatments induced only a slight variation in leaf area development. It was also found that the cultivars required almost the same number of GDD (Table 4.10) to increase the rate of leaf area development under the temperature treatments. The 25/12°C temperature was expected to further increase the leaf growth when the cultivars obtained more GDD for their growth. However, as the temperatures increased (30/15°C and 35/18°C), there was an increase in leaf development, but at a slow rate. At 35/18°C, the slow rate of leaf area development might be due to stress.

At a 12.5 h daylength, temperature induced variations in leaf development. At the 25/12°C temperature, the rate of leaf area increase occurred earlier than in the other two temperatures (Table 4.10) and declined after receiving certain number of GDD. This leaf area growth trend might be associated with bulb development. There was also an increment of leaf area at 30/15°C and 35/18°C later than with the cool temperature, but the highest temperature seems to be a supra-optimal condition for leaf growth.

In all the three cultivars, plants grown at the highest temperature showed a decline in leaf area (Figure 4.12). The decline at the highest temperature was caused by a rapid drop in leaf number in this treatment, while plants grown at the cooler temperature continued to produce leaves. Leaf growth was strongly dependent on temperature and this relationship implies that growth would be simply related to GDD. If the mean temperature does not exceed an optimum range, the relationship implies that leaf growth will be simply related to accumulated degree days (Brewster, 1994).

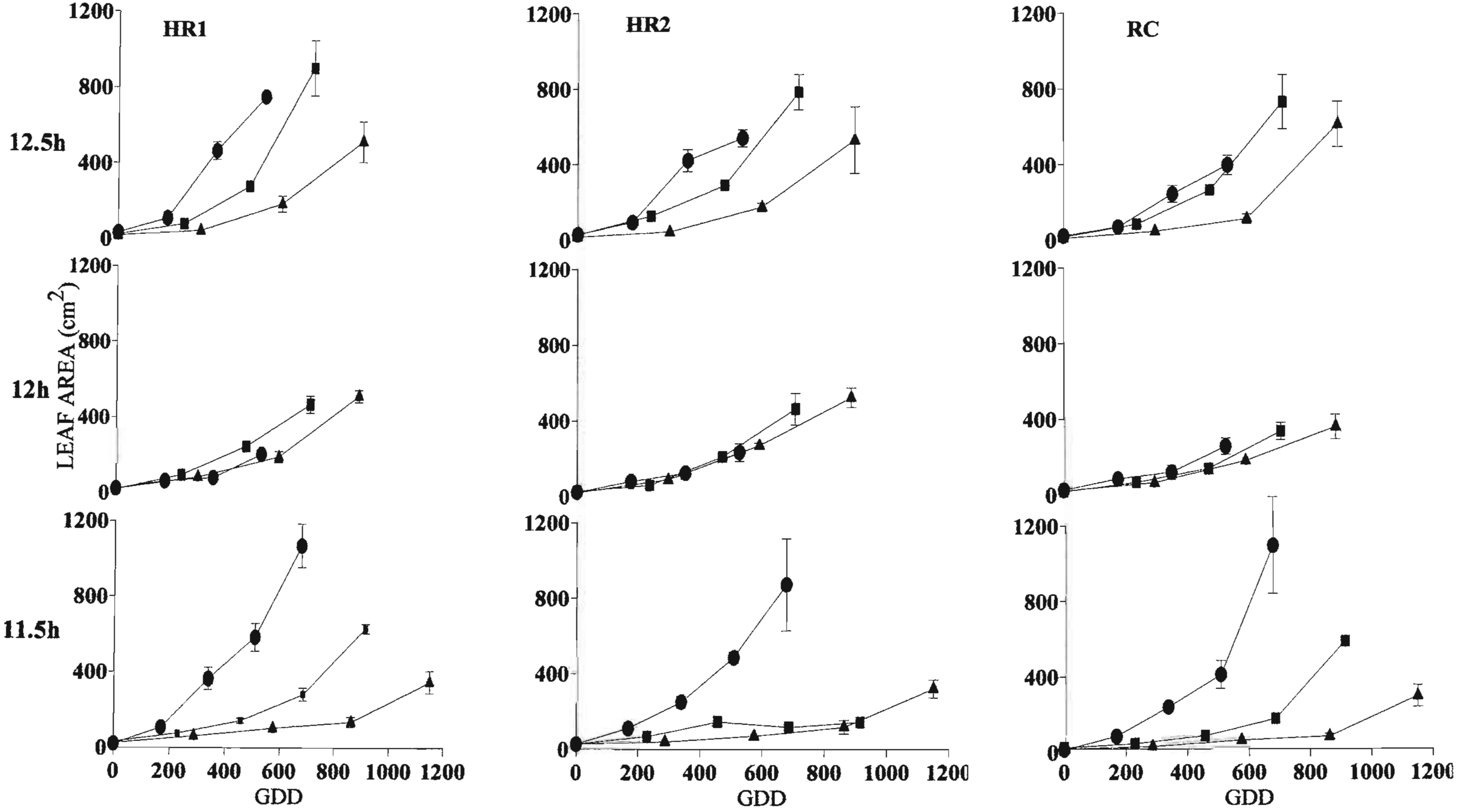


Figure 4.12 The growth response in terms of leaf area of the onion cultivars (Hagaz Red 1, Hagaz Red 2, and Red Creole), grown under three regimes of daylength (11.5 h, 12 h, 12.5 h) combined with three levels of temperature (25/12°C–●; 30/15°C–■; 35/18°C–▲) over growing degree days (GDD). Bars represent SED.

Leaf growth was uniform at the beginning of the experiment when the plant received 200–400 GDD (Figure 4.13). Variability in leaf growth increased as the number of growing degree days increased. This indicated the sensitivity of the leaf development in relation to the number of growing degree days. The regression line showing the relationship between the overall data on leaf area and degree days did not show a best fit (Figure 4.13) (Appendix 4.4). Alternatively, the non-linear standard curve fit, exponential (or asymptotic regression), was applied and the coefficient of determination (R^2) was 55.2%. It is evident from Figure 4.13 that leaf area was affected by the given temperature treatments.

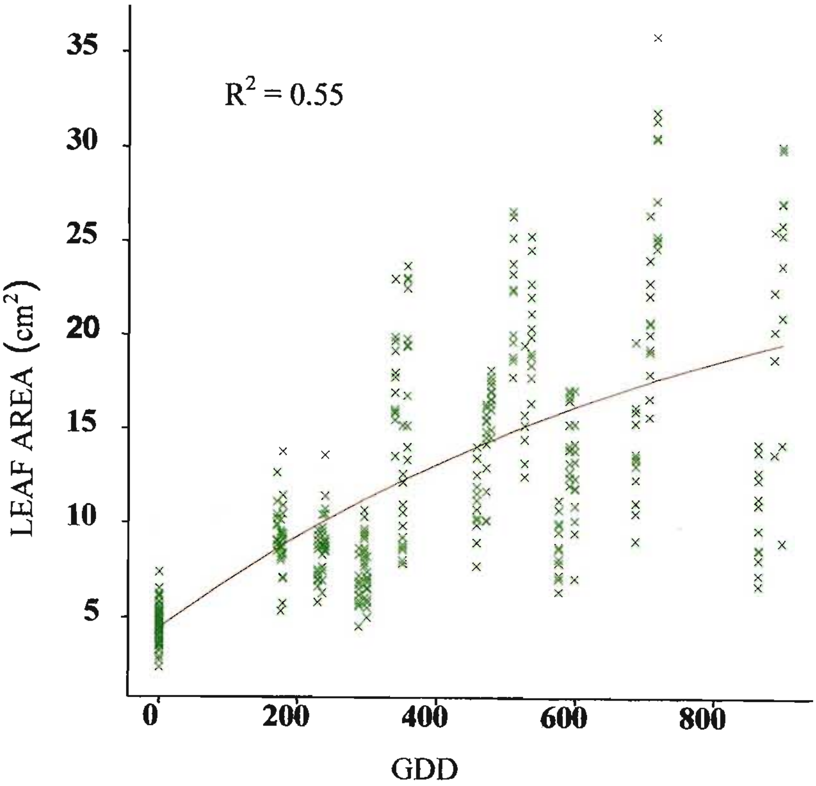


Figure 4.13 Regression line showing the relationship between the leaf area and GDD for the collected data. (n=417).

4.3.4 Height to Uppermost Leaf Tip

At the 11.5h and 12.5h daylengths, temperature induced more variation in plant height in all three cultivars (Figure 4.14) than at a 12 h photoperiod. However, the 35/18°C temperature decreased the plant height at the three daylengths (11.5 h, 12 h and 12.5 h). One might expect that supra-optimal temperature would induce stress-related physiological disorders and caused a shorter plant height. This was most likely associated with a decreased rate of leaf production under the hot temperature. This was observed on plants grown under the supra-optimal day temperature (35°C) which would have increased the rate of respiration and utilized carbohydrate reserves in order to strive to this particular condition. The temperature had a dominant role in determining plant height of all three cultivars. At a 12 h daylength, the temperature also produced less variability in plant height of the cultivars. It was also observed that under the neutral (12 h) daylength, the temperature had less effect in plant growth than the short (11.5 h) and long (12.5 h) daylengths. And at 12.5 h daylength, temperature also induced more variation in the cultivars. Temperature was a more significant factor in determining plant height under long daylength (12.5 h).

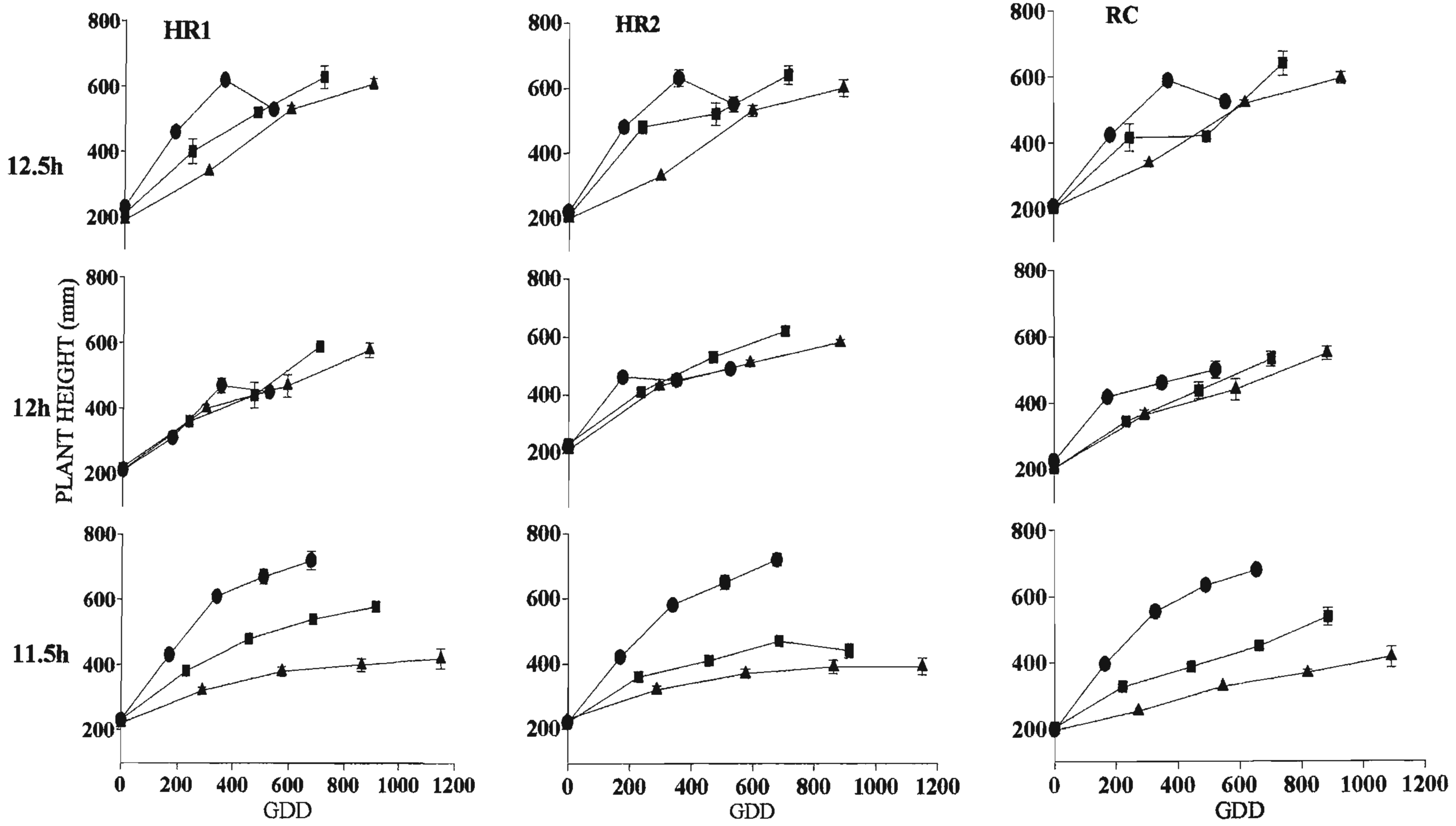


Figure 4.14 The growth response in terms of plant height of three onion cultivars (Hagaz Red 1, Hagaz Red 2, and Red Creole,), grown under three regimes of daylength (11.5 h, 12 h, 12.5 h) and three levels of temperature (25/12°C–●; 30/15°C–■; 35/18°C–▲) over growing degree days (GDD). Bars represent SED.

The regression analysis of plant height over GDD showed that the coefficient of determination (R^2) was 58.3% (Figure 4.15) (Appendix 4.3). Even though the amount of thermal heat had an effect on plant height, it was difficult to decipher the response based on GDD for the collected data. However, the graph is shown for the sake of interest. The regression line did not show a best fit.

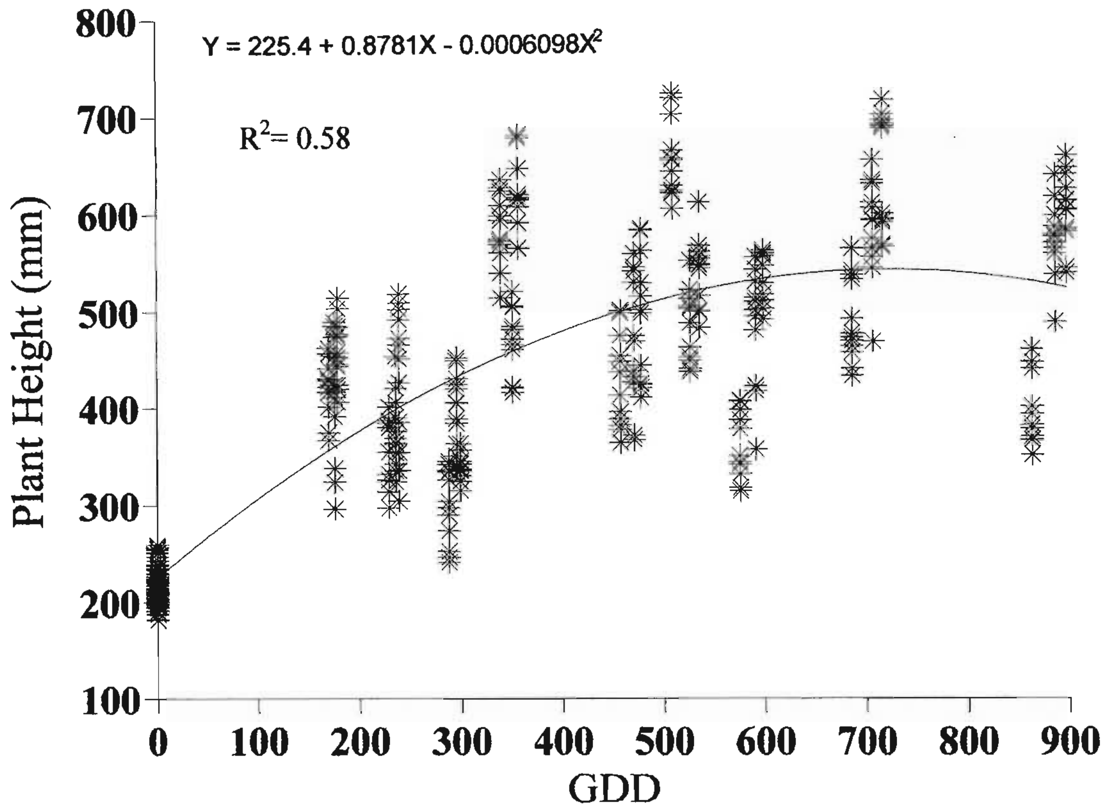


Figure 4.15 The regression line showing the relationship between plant height and GDD for the duration of the experiment. (n= 433)

4.3.5 Bulbing Ratio

Under the 11.5 h daylength, temperature induced variation of bulb growth for all the cultivars (Figure 4.16). The broken-stick regression model 'broke' the growth curve into two linear-linear curves with different interceptions and gradients. There were significant regressions ($P<0.05$)

when modeling growth curves of the three onion cultivars on the GDD values (200, 240, 300, 320). This means that the intercepts and/or gradients of the two linear curves obtained were significantly different (Tables 4.11, 4.12, 4.13). The high percentage variations accounted for, and significant F-probability, were instrumental in the establishment of the point of inflection (Appendix 3.3).

The 25/12°C temperature induced bulb initiation at earlier GDD as compared to 30/15°C and 35/18°C temperatures (Table 4.11). However, the growth trend of bulb ratio was similar for all cultivars. It was not surprising that there was early bulb initiation under the 11.5 h daylength. The plants can start bulbing under short daylengths, but would not form a bulb. Instead they remain vegetative and produce thick-neck bulbs. In daylenghts shorter than a certain minimum value plants remain continually vegetative and no bulbing occurs. However, because of variation in the photoperiodic response within a cultivar, behaviour of plants is variable in photoperiods close to the minimum with some plants remaining vegetative but others bulbing (Magruder and Allard, 1937).

Table 4.11 Broken-stick analysis of bulb initiation of three onion cultivars (HR1, HR2 and RC) over increasing GDD.

Cultivars	Daylength	Temperature	Model with i^{th} GDD	Point of Inflection (t)		% of Variation accounted for	F probability. for Regression
				GDD	Est. Y		
HR1	11.5 h	25/12°C	200	319.93	1.1	94.5	<0.001**
		30/15°C	240	432.8	1.06	99.7	<0.001**
		35/18°C	300	539.9	1.09	96.3	<0.001**
HR2		25/12°C	200	318.8	1.06	93.2	<0.001**
		30/15°C	240	439.04	1.06	94.1	<0.001**
		35/18°C	300	575.5	1.12	93	<0.001**
RC		25/12°C	200	336.8	1.1	91.9	<0.001**
		30/15°C	240	413.02	1.06	84.9	<0.001**
		35/18°C	300	499.6	1.07	99.1	<0.001**

At the 12 h daylength, temperature induced significant variations in bulb growth of the cultivars. The 25/12°C temperature resulted in quicker induction of bulbing as compared to 30/15°C and 35/18°C. The bulb induction was distinctively significant in HR 1 under the cooler temperature.

The HR 1 cultivar recorded earliest bulbing at 353 GDD (bulb ratio of 1.8), earlier than HR 2 and RC (Table 4.12). In this case, once the bulbing process was initiated, temperature increased the rate of development. The 12 h daylength was a photoperiodic inductive phase for Eritrean cultivars. There were significant regressions ($P < 0.05$) when modeling growth curves of the three onion cultivars on the GDD values (200, 240, 320) (Table 4.12).

Table 4.12 Broken-stick analysis of bulb initiation of three onion cultivars (HR 1, HR 2 and RC) over increasing GDD.

Cultivars	**Daylength**	**Temperature**	**Model with i^{th} GDD**	**Point of Inflection (t)**		**% of Variation accounted for**	**F probability for Regression**
				GDD	Est. Y		
HR 1	12 h	25/12°C	200	352.6	1.8	84	<0.001**
		30/15°C	240	484.7	1.3	98.5	<0.001**
		35/18°C	320	581.2	1.3	93.5	<0.001**
HR 2		25/12°C	200	329.04	1.3	98.1	<0.001**
		30/15°C	240	465.3	1.3	97.5	<0.001**
		35/18°C	320	599.2	1.3	88.6	<0.001**
RC		25/12°C	200	345.9	1.3	98	<0.001**
		30/15°C	240	496.8	1.3	95.9	<0.001**
		35/18°C	320	610.8	1.3	95.1	<0.001**

At the 12.5 h daylength, temperature induced variations in bulb growth of cultivars. The growth trend of the cultivars was similar for the different temperature treatments. The cultivars started bulbing at 346 GDD. Generally, under cool temperatures, the photoperiodic response of the cultivars to onset of bulbing occurred more rapidly at 12 h daylength than at 12.5 h daylength. It is not surprising that the 12.5 h daylength did not switch bulbing quicker than at 12 h daylength. This might be due to interaction effects between daylength and temperature which affect the readiness of onions to respond to external stimuli (Jones and Mann, 1963b). There were significant regressions (P< 0.05) when modeling growth curves of the three onion cultivars on the GDD values (200, 300, 320) (Table 4.13).

Table 4.13 Broken-stick analysis of bulb initiation of three onion cultivars (HR 1, HR 2 and RC) over increasing GDD.

Cultivars	Daylength	Temperature	Model with i^{th} GDD	Point of Inflection (t)		% of Variation accounted for	F probability for Regression
				GDD	Est. Y		
HR1	12.5 h	25/12°C	200	345.8	1.2	96.4	<0.001**
		30/15°C	300	434.6	1.28	93.4	<0.001**
		35/18°C	320	512.8	1.3	93.5	<0.001**
HR 2		25/12°C	200	323.2	1.16	82.9	<0.001**
		30/15°C	300	417.9	1.3	91.0	<0.001**
		35/18°C	320	368.9	1.13	88.9	<0.001**
RC		25/12°C	200	362.9	1.3	68.2	<0.001**
		30/15°C	300	415.8	1.4	85.7	<0.001**
		35/18°C	320	414.9	1.2	93.8	<0.001**

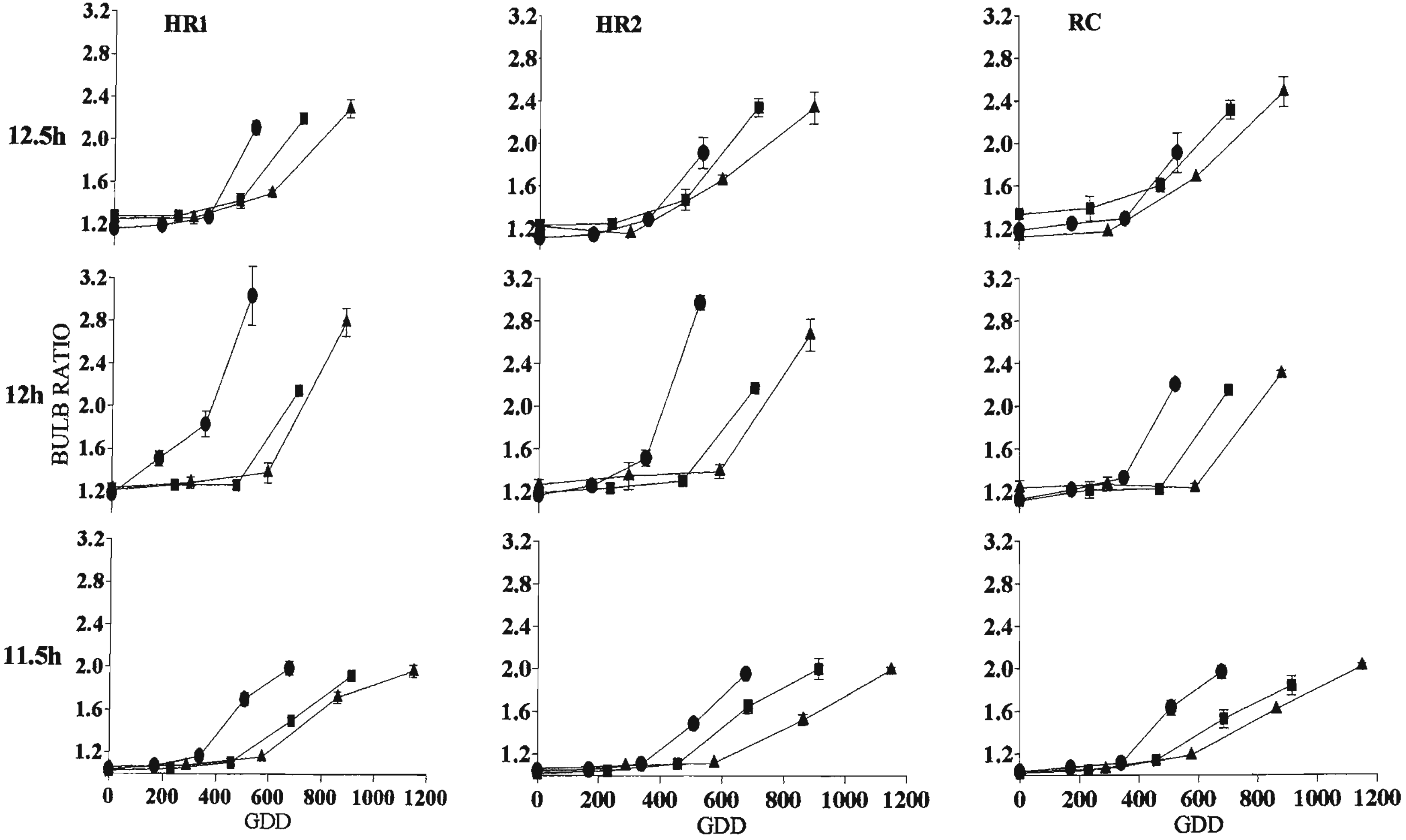


Figure 4.16 The growth response of bulb ratio of three onion cultivars (Hagaz Red 1, Hagaz Red 2, and Red Creole,), grown under three regimes of daylength (11.5 h, 12 h, 12.5 h) combined with three levels of temperature (25/12°C–●; 30/15°C–■; 35/18°C–▲) over different growing degree days (GDD). Bars represent SED.

Generally, in this experiment bulbing of the three onion cultivars was regulated more by temperature than daylength. Similarly Abdalla (1967), Robinson (1973) and Currah (1985) reported that bulbing of onions in the tropics is regulated more by temperature than daylength.

A regression analysis was done to examine the growth trend of bulb ratio in response to changing growing degree days during the experiment. The regression line did not show a best fit, (R^2 =54.8%) (Figure 4.17) (Appendix 4.4). However, since the amount of thermal heat had an effect on bulb initiation, the bulbing process was also affected by GDD factors. The non-linear standard curve fit, exponential (or asymptotic regression), was applied for the regression analysis because of its best fit.

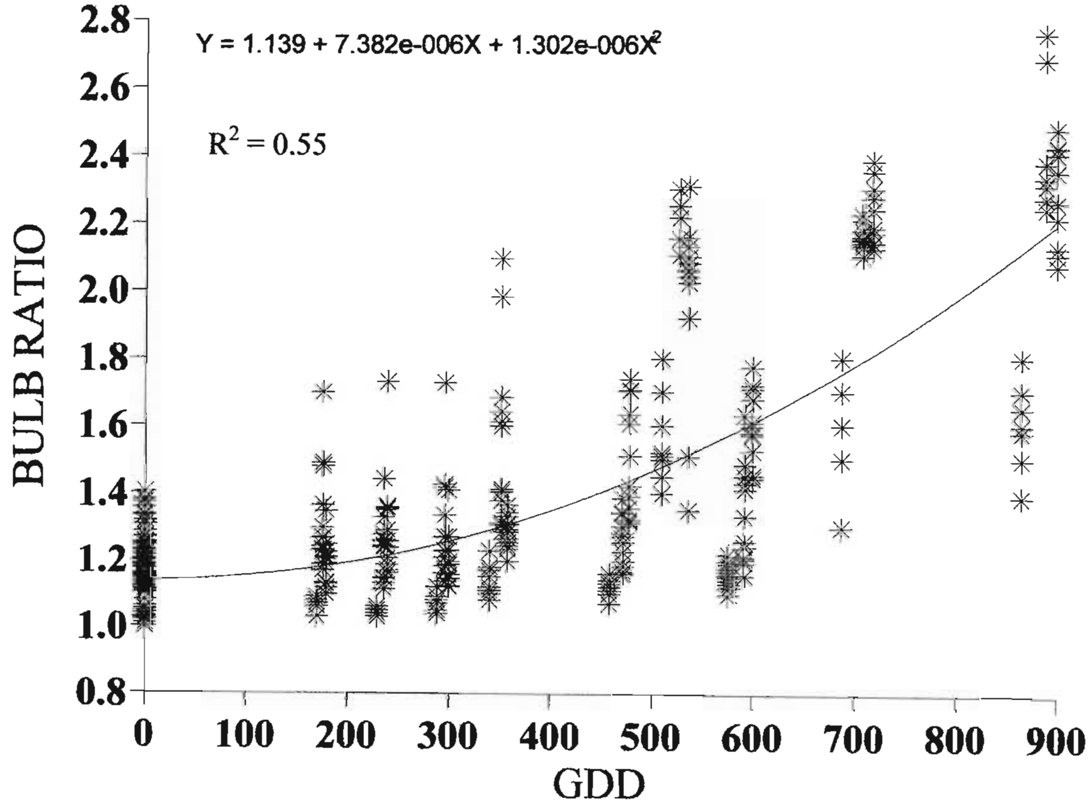


Figure 4.17 The regression line showing the relationship between bulb ratio and GDD for the collected data. (n=417)

4.3.6 Discussion

At a 11.5 h photoperiod, a supposedly non-inductive environment for bulbing, temperature induced significant variations in plant growth. It was observed that leaf number, plant height and leaf area were increased per unit GDD as the cultivars were grown under the cool temperatures (25/12°C) (Figure 4.24). The bulb ratio seemingly increased at the 25/12°C earlier than at the 30/15°C and 35/18°C. It was expected that growth under cooler conditions (25/12°C) would result in the production of thick-necked (poor quality) onions. Wickramasinghe *et al.* (2000) found that at the lowest (17–22°C) temperatures tested, bigger bulbs with thick necks were produced. This may be due to changes in bulb structure at low temperature. It was also observed in this study that the bulb initiation was accompanied by an increased leaf area and leaf number, but plant height slightly declined at the cooler (25/12°C) temperatures. It is interesting that the increased bulb ratio was positively associated with increased leaf area. The leaf area might have an influence on the supply of carbohydrates to the apical meristem for the formation of bulbs. Also, as the temperature increased, the growth of plant components decreased or alternatively, was retarded due to a temperature-stress related physiological response. However, under a 12 h daylength, an inductive environment for bulbing, there were consistent growth increments in leaf number, plant height and leaf area in relation to GDD under the various temperature treatments. The temperatures did not affect these growth parameters significantly. At the 12 h daylength, bulbing was induced earlier at the cooler temperature (25/12°C) than the other temperatures. Under a 12.5 h daylength, a supposedly inductive environment for bulbing, temperature again induced significant variation in plant growth. It was observed that leaf number, plant height and leaf area increased per unit GDD under the cooler temperature (25/12°C) and further, decreased as temperatures increased from 30/15°C to 35/18°C. The increase in leaf area seemed to be associated with bulbing (Figure 4.24). However, a further increment of temperature from 30/15°C to 35/18°C decreased the plant growth and bulbing, due to a stress-related physiological response. Under this daylength, the temperature effects were significant on the development of plant parts, including bulbing. The rapid decline at the highest temperature was caused by a rapid drop in leaf number in this experiment. The plant responses are discussed relative to GDD rather than elapsed time.

The thermal time presentation of the development of bulb ratio indicated that the cultivars were sensitive to temperature. However, plants should be exposed to a minimum daylength to produce bulbs. Thus, the combined effect of daylengths and temperatures induced bulbing of the cultivars, as indicated by the inflection points using a broken-stick regression technique, before a bulb ratio of 2.0 was achieved (Figure 4.18). There was no clear variability in initiation of onion bulbing between the cultivars tested.

At a 11.5 h daylength, a supposedly non-inducing environment for bulbing, there was initiation of bulbing under the temperature treatments tested. The 25/12°C (GDD value of 325) temperature induced bulb initiation earlier than at the 30/15°C (GDD value of 428) and 35/18°C (GDD value of 538) temperatures (Tables 4.11; mean values). The bulb initiation seemed to be associated with the rate of growth of leaf area under the temperature treatments. The 25/12°C temperature increased leaf area most at 197 GDD, followed by 30/15°C (GDD value of 390) and 35/18°C. The GDD data indicated that the rate of leaf area increased and was followed by bulb initiation.

At a 12 h daylength, an inductive environment for bulbing, the 25/12°C temperature induced initiation of bulbing (GDD value of 343) earlier than 30/15°C (GDD value of 482) and 35/18°C (GDD value of 597). There were no clear variations in leaf area, plant height and leaf area caused by the temperature treatments. The GDD was applied to investigate a relation between a growth component, particularly leaf area and bulb initiation. The rate of leaf area increased most at 25/12°C (GDD value of 405) and followed by similar values at 30/15°C (GDD value of 432) and 35/18°C (GDD value of 431), respectively. The GDD data indicated that at the cooler (25/12°C) temperature the rate of leaf area increased most after bulb initiation, but under warm and hot temperatures, it was the rate of leaf area which increased first. It seems that the bulb initiation of the cultivars was highly sensitive to this daylength when they were under cool temperature.

At a 12.5 h daylength, an inducing environment for bulbing, there was initiation of bulbing under all temperature treatments. The 25/12°C (GDD value of 344) temperatures induced bulb initiation earlier than the 30/15°C (GDD value of 423) and 35/18°C (GDD value of 432.2) temperatures (Table 4.13; mean values). The bulb initiation seemed to be associated with the growth of leaf area under the temperature treatments. The temperature increased leaf area soonest at 25/12°C

(GDD value of 140), followed by 30/15°C (GDD value of 411) and 35/18°C (GDD value of 579). The GDD data indicated that the increased rate of leaf area increase was followed by bulb initiation.

The switch in growth to bulbing was earlier under the cool (25/12°C) temperature (GDD ranges from 329 to 353) (HR 1). Plants showed rapid bulb growth while they were grown under cool temperatures and a slower rate of bulb growth when they were grown under the hot (35/18°C) temperature. Hot temperatures have a negative impact on plant development. Since the cultivars were able to adapt to the hot temperature, it is possible they used stored carbohydrate for their survival. As a result, the bulb ratio was negatively affected and a slower growth rate was observed.

The process of bulbing started before the 'onset of bulbing' at a fixed thermal time, when the bulb ratio reached 1.5 to 1.6. The cultivars did not reach the bulb ratio of 2.0 until they had a thermal time average of 643.3. They initiated bulbing in about 4 weeks after transfer to the given daylengths (Appendix 4.2). In all cases the estimate of thermal time from the start of bulb initiation to the 'onset of bulbing' was 160–180, 220–240 and 280–300 degree-days at 25/12°C, 30/15°C and 35/18°C for the three levels of daylength, respectively. Bulbing within each temperature regime took place over a narrow range of GDD, irrespective of daylength.

An interaction between growing room temperature and daylength on days to 'onset of bulbing' was observed, such that the shorter daylength (11.5h), with all levels of temperature, resulted in bulbing 15 days later than 12 h and 12.5 h daylengths. The days from transplanting to onset of bulbing are presented for interest (Table 4.10).

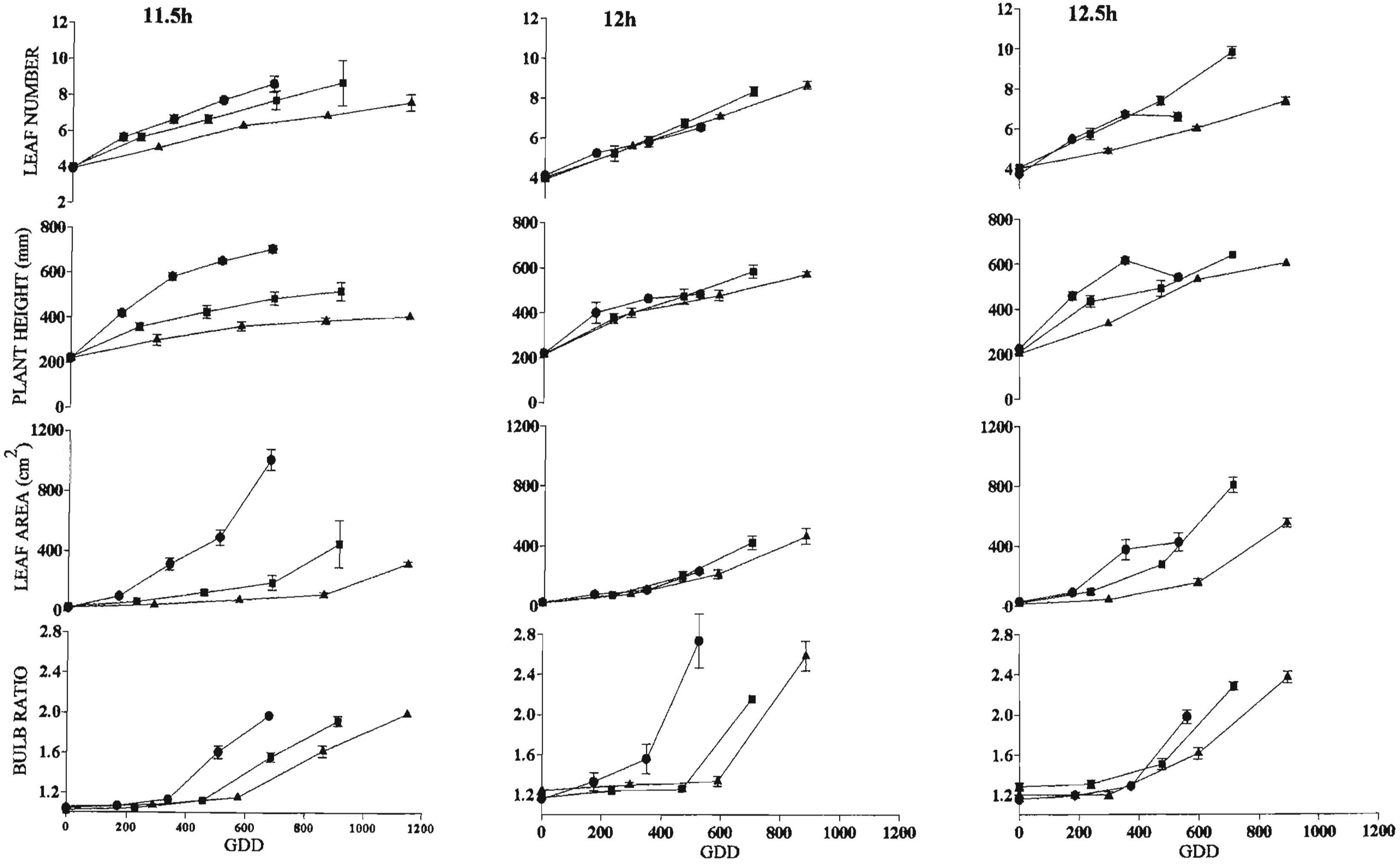


Figure 4.18 The response of growth components (leaf number, leaf area, plant height, and bulb ratio) of the onion cultivars grown under three regimes of daylength (11.5 h, 12 h, 12.5 h) combined with three levels of temperature (25/12°C–●; 30/15°C–■; 35/18°C–▲) over increasing growing degree days GDD. Bars represent SED.

Table 4.14 Days from transplanting to 'onset of bulbing' in onion Hagaz Red 1 (HR 1), Hagaz Red 2 (HR2) and Red Creole grown in a controlled environment.

Photoperiod	**25°C/12°C**			**30°C/15°C**			**35°C/18°C**		
	HR1	HR2	Red Creole	HR1	HR2	Red Creole	HR1	HR2	Red Creole
11.5 h	>45	>45	>45	>45	>45	>45	>45	>45	>45
12 h	>30	>30	>30	>30	>30	>30	>30	>30	>30
12.5 h	>30	>30	>30	>30	>30	>30	>30	>30	>30

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

A comparison of the daylength and temperature responses of Eritrean cultivars (HR 1 and HR 2) and RC in controlled conditions was done in two ways. Firstly, the response to combinations of temperature and daylength was tested statistically at 108 days after transplanting of the seedlings. The results confirmed that there was a significant interaction between daylength and temperature on all plant growth components (leaf number, plant height, and leaf area and bulb ratio). Secondly, to assess the photoperiodic sensitivity of the cultivars in the absence of a phenological response to temperature, a developmental base of GDD was used. The results confirmed that temperatures affected the growth of plants more dominantly than daylengths. Where response to temperature can be expressed as the rate of progress towards a morphogenetic change, temperature fluctuations can be allowed by employing the concept of day-degrees (Roberts and Summerfield, 1987).

In this experiment, the single replication and series plantings in the growth rooms were done because it was not feasible to do the experiment simultaneously as the Controlled Environment Research Unit (CERU) has only three growth rooms, and 36 rooms would be required to run the treatments and replications simultaneously. It was assumed that each growth room had the same environmental conditions, other than the variable of daylength and temperature that was changed, and replication was within rooms. There will always be speculation on source of variations on the growth responses other than the set values. Since no scientific monitoring on moisture content of the soil was done, the soil moisture, nutrition, and other possible factors, supposedly could have an in-chamber effect on the growth of the plants. However, statistically, it was assumed that these variations were uniformly distributed between treatments and within each pot.

The results reported herein confirm that leaf number, plant height and leaf area decreased as the temperature increased in excess of 30/15°C at an 11.5 h daylength (supposedly non-inductive growth environment). The further increase in temperature in excess of 25/12°C decreased vegetative growth under the short daylength without development of bulbing as assessed by a bulbing ratio greater than 2.0 (Roberts *et al.* 1988). This result also agrees with the findings of Wiles (1989). He found that the number of leaves emerging before bulb scale formation is also affected by temperature, and the temperature response depends on cultivar. In this study, it was found that the cool temperatures (25/12°C) induced more vegetative growth at the 11.5 h daylength. Bertaud (1986) hypothesized that in short days the allocation of carbohydrates to form bladed leaves, rather than scale leaves, would be expected. The delay of onset of bulbing (bulb ratio ≥ 2.0) resulting from shorter daylengths might also produce more bladed leaves immediately after production of the first bulb scales and may account for the observations of Abdalla (1967), Robinson (1973) and Wiles (1989) that bladed leaves continue to emerge after bulb initiation.

Since the cultivars would be expected to take approximately the same thermal time to start bulb initiation under the same growth conditions, it must be concluded that temperatures induced significant variations on growth components (leaf number, plant height, leaf area), and affected this response. The cultivars received a fixed thermal time value of 325, 428 and 538 GDD units before bulb initiation at 25/12°C, 30/15°C and 35/18°C, respectively, under an 11.5 h daylength. This result indicated that the cultivars required only a certain fixed amount of thermal time for their development at a particular temperature, and that, if anything, the slow growth rate at the higher temperature must be due to supra-optimal temperatures.

The results of the photoperiod experiment clearly showed that the cultivars needed a minimum 12 h photoperiod for bulb formation. This also confirms the early findings of Magruder and Allard (1937) that, physiologically, onion is an obligate long-day plant notwithstanding whether it is, in relative terms, an obligate long- or short-day cultivar. These results challenge the suggestion that photoperiod is not important for bulb formation in the tropics (Abdalla, 1967; Robinson, 1971). The plant size also has an effect on the time of onset of bulbing and further development of bulbing (Mettananda and Fordham, 1999). Under a 12 h daylength, the growth components decreased as the temperature increased in excess of 30/15°C. It is probable that the highest temperatures (35/18°C) stimulated bulbing resulting in rapid leaf senescence and, because of a small leaf area, small bulbs. This agrees with the observations of Mondal *et al.* (1986a) and Brewster (1990). They reported that the effect of temperature on growth in leaf area, and therefore leaf area index, would also be expected to affect the within-crop R:FR ratio, which is believed to affect the timing of bulb initiation. Wickramasinghe *et al.* (2000) also reported that plants grown at a high temperature (29–34°C) showed a rapid decline in leaf area. The effect of temperature on leaf area is complex. Initially high temperatures result in high rates of plant growth (Butt, 1968; Brewster, 1979) and therefore growth in leaf area (Brewster and Barnes, 1981) but the rate of leaf senescence increases at high temperatures (Thompson and Smith, 1938) and supra-optimal temperature reduces the size of individual leaves (Butt, 1968). At the lowest temperature, a 12 h photoperiod may not have been sufficient to stimulate bulbing at an early stage of plant development; however, as the plants grew they became more sensitive to the bulbing stimulus. Wright and Sobeih (1986) reported that sensitivity to photoperiodic stimulation increased with plant age.

Under the 12 h daylength, the cultivars needed 343, 482 and 597 GDD units before a bulbing ratio > 2.0 was exceeded and 405, 432 and 431 GDD to increase the growth rate of leaf area at 25/12°C, 30/15°C and 35/18°C, respectively. This result confirmed that the daylength induced bulb initiation and its further rate of development was affected by temperature. It can also be concluded that the 25/12°C and 30/15°C temperatures would be expected to be a conducive environment for onion production. However, the 35/18°C are supra-optimal temperatures whereby the temperature hastens the development cycle of the cultivars and the production of small bulbs (poor quality) would likely ensue with the relatively poorly developed LAI, due to a stress-related response. The production of small bulbs is also associated with the short length of time that cultivars can translocate photoassimilates from leaf blade to storage organs. It is also a mechanism which is developed by the cultivars to escape the temperatures.

The 12.5 h daylength was inductive for bulbing in all treatments; the 25/12°C temperatures increased the growth components (plant height and leaf area) as compared to the 12 h daylength. The result confirmed that the cultivars would be expected to produce larger bulbs at this temperature. The production of larger bulbs is associated with higher leaf area of the cultivars, which would produce larger amounts of photosynthates to be transported to the plant storage organ (bulb) in an extended period of growth. The production of larger bulbs loses market interest from the consumers' side. The temperatures of 30/15°C were also expected to produce relatively larger onion bulbs, and this growth condition would probably be an ideal condition for onion production. Such plants are able to produce greater leaf carbohydrate to be assimilated in a longer period of time from the plant canopy into a growing bulb and hence delay foliage collapse (Daymond *et al.*, 1997).

Temperature is known to affect a number of plant growth responses which have been implicated in controlling plant response to photoperiod (Table 5.1).

Table 5.1 Plant processes and characterstics controlled by temperature in onion (Wiles, 1989).

Process/character	Source
Rate of leaf initiation and emergence	De Ruiter (1986)
Rate of leaf senescence	Thompson and Smith (1938)
Leaf shape/ specific leaf area	Butt (1968)
Rate of growth in plant weight and leaf area	Butt (1968), Brewster (1977, 1979), Brewster and Barnes (1981)
Carbohydrate content of the plant	Butt (1968)

Under the 12.5 h daylength, the cultivars needed 344, 423 and 432.2 GDD units before a bulbing ratio of > 2.0 was achieved and 140, 411 and 579 GDD units to increase growth rates of leaf area at 25/12°C, 30/15°C and 35/18°C, respectively. This result showed that the increased rate of leaf development preceded bulb initiation at the 25/12°C temperature. With the substantial leaf area achieved prior to bulb initiation, it can be expected that large onion bulbs would be produced.

Generally, it was confirmed that the 35/18°C temperatures are supra-optimal for growth of all of the cultivars under all three daylengths. The 25/12°C and 30/15°C temperatures are more ideal temperature conditions under the inductive growing daylengths (12 h, 12.5 h), particularly for bulb production.

The three cultivars (HR 1, HR 2 and RC) showed very similar growth response to the daylength and temperature interactions. One might expect the Eritrean cultivars (HR 1 and HR 2), being fairly closely genetically related, respond similarly to environmental conditions. It is interesting that the RC responded similarly to the Eritrean cultivars. The three cultivars may have a similar genetic origin. This aspect needs to be supported by looking at the genetic backgrounds of Eritrean cultivars and RC. This information would also help to improve the Eritrean onion cultivar development programme.

The photoperiodic response of cultivars is crucial in determining timing of transplanting and of bulb initiation, as cultivar differences in photoperiodic response control the earliness and susceptibility to premature bulbing in onions. Nevertheless, temperature also plays an important role in plant development and both photoperiod and temperature, and their interactions, control the rate and extent of plant and bulb growth and development.

The experiment was conducted under simulated tropical conditions by daylengths (11.5 h, 12 h, and 12.5 h) and temperatures (25/12°C, 30/15°C and 35/18°C) which are suitable for bulb initiation under tropical field conditions. The GDD values presented in this research might help to predict the time of bulb initiation which is a determinant feature for bulb yield (Appendix 4.2). Accurately predicting harvesting date and the crop's developmental stage has widespread application for improving crop management, e.g., scheduling labour, machinery, integrated pest management practices, and timely production at high market pricing. A base temperature of 6.4°C, was determined for these onion cultivars. So it should now be possible to use environmental data to assist growers to schedule planting dates and harvesting times. Hence the results presented here are hopefully applicable to field conditions for the production of onions in Eritrea.

Onions require cool temperatures during the seedling stage and moderately high temperatures during bulbing. Moderately high temperatures, particularly when combined with a dry atmosphere and low relative humidity facilitate harvesting and curing of bulbs (Edmond *et al.,* 1957). The climate in Eritrea is largely influenced by the topography. Hot and arid conditions are prevalent in the lowlands, particularly in the eastern part of the country, while temperatures in the highlands are cooler. Mean maximum day temperature during late summer (April-May) in the lowlands, where the production area (Hagaz) is situated, is 35°C. This is the period when the onion bulbs are ready for harvesting. Eritrean growers, traditionally, do not grow onion seedlings at this temperature in this locality. In this study, it was found that high temperature is a supra-optimal condition for young plant growth. However, onions are produced in the Eritrean highlands during this period on a small scale. There is speculation possibly by growing onion seedlings in the cooler highlands until transplants reach the appropriate size, that they could be transplanted to grow the crop for bulb production in the lowlands (hot temperature) to enhance productivity of the crop.

It will be apparent from the results presented in this study that there are still many gaps to investigate in the environmental physiology of tropical onions in order to enhance understanding. Some of them are:

1. To find the minimum light intensity that is effective in triggering the photoperiodic and temperature response of bulbing in Eritrean cultivars. Experimental evidence shows that as light intensity increases 'onset of bulbing' occurs earlier (Heath and Hollies, 1965; Butt, 1968; Terabun, 1971a; Mondal *et al.*, 1986b) and the rate of bulb swelling is greater (Kato, 1964).

2. To conduct the same experiment under field conditions to support the results which were obtained in the controlled environment.

3. To investigate the effect of the daylength and temperature on post-initiation stages of bulb development.

4. Since it is not evident, the origin of the Eritrean cultivars and their genetic background need to be investigated. The results showed that the Eritrean cultivars (HR 1 and HR 2) had similar growth characteristics as compared to American (Louisiana) cultivar grown in South Africa (RC). It is expected all the three cultivars might be genetically related.

5. It seemed to be more meaningful if this kind of experiment is conducted in respect to growing degree days (GDD) than a time factor. The concept of a broken-stick regression model was also found to be logical in determining the point of inflection of growth responses. The growth switch would have a direct implication in physiological response of the plants under a given growth condition, so that it might be appropriate to incorporate the concept of multiple regression model in this type of study.

REFERENCES

Abdalla, A. A. (1967). Effect of temperature and photoperiod on bulbing of common onion (*Allium cepa* L.) under arid tropical conditions of the Sudan. *Experimental Agriculture* **3**: 137-142.

Anonymous (1978). The management of pot experiments for fertility studies. Department of Crop Science: University of Natal, Pietermaritzburg, South Africa, 17 pp.

Anonymous (1996). **PlotIT** for Windows 95/NT, Version 3.20b Copyright© 1996 Scientific Programming Enterprises.

Anonymous (2001). Annual Report on crop production of Sub-Zone Hagaz, Keren, Eritrea.

Anonymous (2003). **GenStat** – Seventh Edition, Version – 7.1.0.198, Copyright© 2003, Lawes Agricultural Trust.

Anonymous (2005). Agricultural Data: FAOSTAT. Available from: http://faostat.fao.org/faostat/collections?version=ext&hasbulk=0. Accessed on: 16/03/2006

Arnold, C. Y. (1959). The determination and significance of the base temperature in a linear heat unit system. *Proceedings of the American Society for Horticultural Science* **4:** 430-445.

Austin, R. B. (1972). Bulb formation in onions as affected by photoperiod and spectral quality of light. *Journal of Horticultural Science* **47**: 493-504.

Ben-Gad, D. Y., Altman, A., and Monselise, S.P. (1979). Interrelationships of vegetative growth and assimilate distributions of *Citrus limettioides* seedlings in response to root-applied GA_3 and SADH. *Canadian Journal of Botany* **57**: 484-490.

Bertaud, D. S. (1986). The effect of light on bulbing in onions. *Proceedings of the Agronomy Society of New Zealand* **16**: 79-86.

Bertaud, D. S. (1990). Photoperiod and temperature affect sprouting of onion bulbs (*Allium cepa* L.). *Annals of Botany* **66**: 179-181.

Boniolo, A. and Ramina, A. (1976). Assimilate distribution and apical dominance in *Pisum sativum* L. *Rivista della Ortofloro Frutticoltura Italiana* **60**: 213-223.

Brewster, J. L. (1977). The physiology of the onion. Part one. *Horticultural Abstracts* **47**: 103-112.

Brewster, J. L. (1979). The response of growth rate to temperature in seedlings of several *Allium* crop species. *Annals of Applied Biology* **93**: 351-357.

Brewster, J. L. (1982). Growth, dry matter partitioning and radiation interception in an overwintered bulb onion (*Allium cepa*) crop. *Annals of Botany* **49**: 609-617.

Brewster, J. L. (1987). The phenology of onion bulb development at different sites and its irrelevance to incomplete bulbing ('thick-necking'). *Journal of Horticultural Science* **62**: 371-378.

Brewster, J. L. (1990). Physiology of crop growth and bulbing. In: *Onions and Allied Crops* (Rabinowitch, H. D. and Brewster, J. L. Volume 1, eds.). Florida: Boca Raton, CRC Press, pp. 53-88.

Brewster, J. L. (1994). Onions and other vegetable alliums. CAB International, Wallingford, Oxon, UK.

Brewster, J. L. (1997). Environmental physiology of the onion: Towards quantitative models for the effects of photoperiod, temperature and irradiance on bulbing, flowering and growth. In: *Proceedings of the First International Symposium on Edible Alliaceae* (Burba, J. L. and Galmarini, C. R. eds.). *Acta Horticulturae* **433**: 347-362.

Brewster, J. L. and Barnes, A. (1981). A comparison of the relative growth rates of different individual plants and different cultivars of onion at two temperatures and two light intensities. *Journal of Applied Ecology* **18**: 589-608.

Brewster, J. L., Mondal, M. F. and Morris, G. E. L. (1986). Bulb development in onion. IV. Influence on yield of radiation interception, its efficiency of conversion, the duration of growth and dry matter partitioning. *Annals of Botany* **58**: 221-233.

Brewster, J. L., Lawes, W. and Whitlock, A. J. (1987). The phenology of onion bulb development at different sites and its relevance to incomplete bulbing ('thick-necking'). *Journal of Horticultural Science* **62**: 371-378.

Brewster, J. L. and Rabinowitch, H. D. (1990). Onions and allied crops (Volume III). Florida: Boca Raton, CRC press, 265 pp.

Brewster, J. L., Salter, P. J. and Darby, R. J. (1977). Analysis of the growth and yield of overwintered onions. *Journal of Horticultural Science* **52**: 335-346.

Butt, A. M. (1968). Vegetative growth, morphogenesis and carbohydrate content of the onion plant as a function of light and temperature under field and controlled conditions. *Mededelingen Landbouwhogeschool te Wageningen* **68**: 211 pp.

Clark, J. E. and Heath, O. V. S. (1962). Studies in the physiology of the onion plant. V. An investigation into the growth substance content of bulbing onions. *Journal of Experimental Botany* **13**: 227-249.

Clough, J. M., Peet, M. M. and Kramer, P. J. (1981). Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of a soyabean cultivar. *Plant Physiology* **67**: 1007-1010.

Cober, E. R. and Curtis, D. F. (2003). Both promoters and inhibitors affected flowering time to grafted soybean flowering-time isolines. *Crop Science* **43**: 886-891.

Cook, M. G. and Evans, L. T. (1978). Effect of relative size and distance of competing sinks on the distribution of photosynthetic assimilates in wheat. *Australian Journal of Plant physiology* **5**: 495-509.

Currah, L. (1985). Review of three onion improvement schemes in the tropics. *Tropical Agriculture* **62**: 131-136.

Currah, L. and Proctor, F. J. (1990a). The genetic base and the cultivars grown in the tropics. In: *Onions in tropical regions*. Natural Resource Institute, Bulletin No. 35, xiii + 232 pp.

Currah, L. and Proctor, F. J. (1990b). The onion and the environment. In: *Onions in tropical regions*. Natural Resource Institute, Bulletin No. 35, xiii + 232 pp.

Daymond, A. J., Wheeler, T. R., Hadley, P., Ellis, R. H., and Morison, J. I. L. (1997). The growth, development and yield of onion (*Allium cepa* L.) in response to temperature and CO_2. *Journal of Horticultural Science* **72**: 135-145.

de Ruiter, J. M. (1986). The effect of temperature and photoperiod on onion bulb growth and development. *Proceedings Agronomy Society New Zealand* **16**: 93-100.

Dragland, S. (1972). Effect of temperature and daylength on growth, bulb formation and bolting in leeks (*Allium porrum* L.). Meldinger fra Norges Landbrukshogskole, **51**, Agricultural University, Norway.

Duvick, D. N. (1967). Influence of morphology and sterility on breeding morphology. In: *Plant Breeding* (Fry, K. J. ed.). Ames, Iowa: University press, 85 pp.

Edmond, J. B., Musser, A. M., and Andrews, F. S. (1957). *Fundamentals of horticulture*. New York: McGraw-Hill Book Company, Inc., pp. 360-361.

Evans, L. T. (1969). *The induction of flowering*. Melbourne: MacMillan.

Garforth, C. (2001). *Agricultural Knowledge and information system in Hagaz, Eritrea.* London: International and Rural Development Department, The University of Reading.

Garner, W. W. and Allard, H. A. (1923). Further studies in photoperiodism: The response of the plant to relative length of day and night. *Journal of Agricultural Research* **23**: 871-920.

Ginzburg, C. (1974). The effect of gibberelin A_3 and (2-chloroethyl) trimethylammonium chloride on assimilate distribution in gladiolus in relation to corm growth. *Journal of Experimental Botany* **25**: 995-1003.

Gray, D. and Steckel, J. R. A. (1993). Effect of plant raising environment, transplant weight and date of transplanting on the subsequent growth and development of leeks (*Allium porrum* L.) grown for early production. *Journal of Horticultural Science* **68**: 955-965.

Halfacre, R. G. and Barden, J. A. (1979). *Horticulture*. New York: McGraw-Hill Book Company, Inc., pp. 538-539.

Hartmann, H. T., Flocker, W. J., and Kafranek, A. M. (1981). *Plant Science-growth, development and utilization of cultivated plants*. New Jersey: Prentice-Hall, Inc., 676pp.

Heath, O. V. S. (1943). Studies in the physiology of the onion plant. I. An investigation of factors concerned in the flowering ('bolting') of onions grown from sets and its prevention. Part II. Effects of daylength and temperature on onions grown from sets, and general discussion. *Annals of Applied Biology* **30**: 308-319.

Heath, O. V. S. (1945). Formative effects of environmental factors as exemplified in the development of the onion plant. *Nature* (London), **155**: 623-626.

Heath, O. V. S., and Holdsworth, M. (1948). Morphogenic factors as exemplified by the onion plant. *Symp. Soc. Exp. Biol.* **2**: 326-350.

Hoffman, (1933). Developmental morphology of *Allium cepa. Botanical Gazette* **95**: 279-299.

Holen, C. D. and Dexter, A. G. (1996). A growing degree day equation for early sugar beet leaf stages. *Sugar Beet Research and Extension Reports* **27**: 152-157.

Houghton, J. T., Callander, B. A. and Varney, S. K. (1992). Climate change 1992: The supplementary report to the IPCC scientific assessment. Cambridge: University Press.

Isenberg, F. M. R., Ludford, P. M. and Thomas, T. H. (1987). Hormonal alterations during the postharvest period. In: *Postharvest physiology of vegetables* (Weichmann, J., ed.). New York: Marcel-Dekker, Inc.

Johnson, I. R. and Thornley, J. H. M. (1985). Temperature dependence of plant and crop processes. *Annals of Botany* **55**: 1-24.

Jones, H. A., and Davis, G. N. (1944). Inbreeding and heterosis and their relation to the development of new varieties of onions. U.S. Dept. Agr. Tech Bul. 874. 28 pp.

Jones, H. A. and Mann, L. K. (1963a). Morphology and development. *In: Onions and their allies: botany, cultivation and utilization.* London: World Crops Books, Leonard Hill, xviii +286 pp.

Jones, H. A. and Mann, L. K. (1963b). Growing the crop. In*: Onions and Their Allies: botany, cultivation and utilization.* London: World Crops Books, Leonard Hill, xviii +286 pp.

Kato, T. (1964). Physiological studies on bulbing and dormancy of onion plants. III. Effects of external factors on the bulb formation and development. *Journal of the Japanese Society for Horticultural Science* **33**: 53-61.

Kato, T. (1965). Physiological studies on bulb formation and dormancy in the onion plant. V. The relation between the metabolism of carbohydrates, nitrogen compounds and auxin and bulbing phenomenon. *Journal of the Japanese Society for Horticultural Science* **34**: 187-195.

Kedar, N., Levy, D., and Goldschmidt, E. E. (1975). Photoperiodic regulation of bulbing and maturation of Beta Alpha onions (*Allium cepa* L.) under decreasing daylength condition. *Journal of Horticultural Science* **50**: 373-380.

Lady, E. L. (2002). Max-min problems for functions of two variables. Available from: http://www.math.hawaii.edu/~lee/calculus/MaxMin2.pdf. Accessed on: 10/05/2005.

Lancaster, J. E., Triggs, C. M., de Ruiter, J. M., and Gandar, P. W. (1996). Bulbing in onions: Photoperiod and temperature requirements and prediction of bulb size and maturity. *Annals of Botany* **78**: 423-430.

Lercari, B. (1982). The promotion effect of far-red light on bulb formation in the long-day plant *Allium cepa* L. *Plant Science Letters* **27**: 243-254.

Lercari, B. (1984). Role of phytochrome in photoperiodic regulation of bulbing and growth in the long day plant *Allium cepa*. *Physiologia Plantarum* **60**: 433-436.

Lercari, B. and Micheli, P. (1981). Photoperiodic regulation of cytokinin levels in leaf blades of *Allium cepa* L. *Plant and Cell Physiology* **22**: 501-505.

Lipe, W. N. (1975). Influence of growth regulators on growth, bulbing, maturity and yield in onions. *HortScience* **10**: 20-21.

Magruder, R. and Allard, H. A. (1937). Bulb formation in some American and European varieties of onions as affected by length of day. *Journal of Agricultural Research* **54**: 719-52.

Mettananda, K. A., and Fordham, R. (1997). The effects of 12 and 16 hour daylength treatments on the onset of bulbing in 21 onion cultivars (*Allium cepa* L.) and its application to screening germplasm for use in the tropics. *Journal of Horticultural Science* **72**: 981-988.

Mettananda, K. A., and Fordham, R. (1999). The effects of plant size and leaf number on the bulbing of tropical short day onion cultivars (*Allium cepa* L.) under controlled environments in the United Kingdom and tropical field conditions in Sri Lanka. *Journal of Horticultural Science and Biotechnology* **74**: 622-631.

Mondal, M. F., Brewster, J. L., Morris, G. E. L. and Butler, H. A. (1986a). Bulb development in onion. I. Effects of plant density and sowing date in field conditions. *Annals of Botany* **58**: 187-195.

Mondal, M. F., Brewster, J. L., Morris, G. E. L., and Butler, H. A. (1986b). Bulb development in onion (*Allium cepa* L.) II. The influence of red:far-red spectral ratio and of photon flux density. *Annals of Botany* **58**: 197-206.

Mor, Y., Spiegelstein, H. and Halevy, A. H. (1981). Translocation of ^{14}C-assimilates in roses. II. The effect of shoot darkening and cytokinin application. *Physiologia Plantarum* **52**: 197-200.

Morris, G .E. L. and Tucker, W. G. (1985). A study of the components of growth of the spring-sown onion and their relationships with meteorological data. *Journal of Horticultural Science* **60**: 341-351.

Moss, D. N. and Peaslee, D. F. (1965). Photosynthesis of maize leaves as affected by age and nutrient status. *Crop Science* **5**: 280-281.

Nojiri, H., Yamane, H., Seta, H., Yamaguchi, I., Murofushi, N., Yoshihara, T., and Shibaoka, H. (1992). Qualitative and quantitative analysis of endogenous Jasmonic acid in bulbing and non-bulbing onion plants. *Plant Cell Physiology* **33**: 1225-1231.

Ochuodho, J. O. (2005). Physiological basis of seed germination in *Cleome gynandra* L. PhD Thesis, University of KwaZulu Natal, Pietermaritzburg, South Africa.

Parry, M. L. and Carter, T. R. (1990). An assessment of the effects of climatic change on agriculture. In: Climate change and plant genetic resources (Jackson, M.T., Ford-Lloyd, B.V. and Parry, M.L., eds). London: Belhaven, pp. 61-84.

Patrick, J. W. (1982). Hormonal control of assimilate transport. In: *Plant growth substances* (Wareing, P.F. ed.). London: Acadamic Press, pp. 669-678.

Purseglove, J. W. (1972). *Tropical crops monocotyledons*. London: Longman Group Limited. pp. 42-44, 47, 49.

Roberts, E. H. and Summerfield, R. J. (1987). Measurement and prediction of flowering in annual crops. In: *The manipulation of flowering* (Atherton, J.G. ed.). London: Butterworths, pp. 17-50.

Roberts, E. H., Hadley, P., Ellis, R. H. and Summerfield, R. J. (1988). Quantitative relations between photoperiod, temperature and rates of development and their implications for screening germplasm, in *4th Eucarpia Allium Symposium, Institute of Horticultural Research,* Wellesbourne, Warwickshire, pp. 139-148.

Robinson, J. C. (1971). Studies on the performance and growth of various short-day onion varieties in the Rhodesian Lowveld in relation to date of sowing. 1. Yield and quality analysis. *Rhodesian Journal of Agricultural Research* **9**: 31-38.

Robinson, J. C. (1973). Studies on the performance and growth of various short-day onion varieties (*Allium cepa* L.) in the Rhodesian Lowveld in relation to date of sowing. 2. Growth analysis. *Rhodesian Journal of Agricultural Research* **11**: 51-68.

Roderick, M. L. (1992). Methods for calculating solar position and daylength including computer programs and subroutines. Western Australian Department of Agriculture, Western Australia. Resource Management Technical Report No. **137**: iv + 81 pp.

Salisbury, F. B. (1955). The dual role of auxin in flowering. *Plant Physiology* **30**: 327-34.

Sanders, D. C. and Cure, J. D. (1996). Control of bolting in Autumn-sown sweet onions through undercutting. *Journal of American Society of Horticultural Science* **121**: 1147-1151.

Scully, N. J., Parker, M. W. and Borthwick, H. A. (1945). Interaction of nitrogen nutrition and photoperiod as expressed in bulbing and flower-stalk development of onion. *Botanical Gazette,* illus, **107**: 52-61.

Sobeih, W. Y. (1988). The photoperiodic regulation of bulbing in onions (*Allium cepa* L.). IV.The translocation of ^{14}C–assimilate during bulbing in response to light and hormonal factors. *Journal of Horticultural Science* **63**: 109-118.

Sobeih, W. Y. and Wright, C. I. (1986). The photoperiodic regulation of bulbing in onions. II. Effects of plant age and size. *Journal of Horticultural Science* **61**: 337-341.

Steer, B. T. (1980a). The bulbing response to daylength and temperature of some Australian cultivars of onion. *Australian Journal of Agricultural Research* **31**: 511-518.

Steer, B. T. (1980b). The role of night temperature in the bulbing of onion (*Allium cepa* L.). *Australian Journal of Agricultural Research* **31**: 519-523.

Summerfield, R. J. and Roberts, E. H. (1987). Effects of illuminance on flowering in long-and short-day grain legumes: A reappraisal and unifying model In: *Manipulation of Flowering* (J. G. Atherton ed). London: Butterworths, pp. 203-223.

Tarakanov, J. G. (2002). Environmental control of morphogenesis in onion: Possible role of phytohormone metabolism. Available from: http:// www.ueb.cas.cz/eng/rawanto2002. Accessed on: 26/02/2005.

Terabun, M. (1971a). Studies on the bulb formation in onion plants. VII. Photo environmental factors influencing bulb formation of onion plants. *Journal of the Japanese Society for Horticultural Science* **40**: 17-22.

Terabun, M. (1971b). Studies on the bulb formation in onion plants. VIII. Internal factors in reference to bulb formation. *Journal of the Japanese Society of Horticultural Science* **40**: 50-56.

Terabun, M. (1981). Effect of low temperature on the bulb formation in onion plants. *Journal of the Japanese Society for Horticultural Science* **50**: 53-59.

Thompson, H. C. and Smith, O. (1938). Seedstalk and bulb development in the onion (*Allium cepa* L.). *Bulletin of the Cornell Experimental Station* **708**: 1-21.

Vince-Prue, D. (1975). *Photoperiodism in plants.* London: McGraw-Hill Book Company, 444 pp.

Viner, D. and Hulme, M. (1993). *What carbon dioxide concentrations should be used with climate change scenarios?* Technical Note No. 3. Climate Research Unit, University of East Anglia, UK.

Waycott, W. (1995). Photoperiodic response of genetically diverse lettuce accessions. *Journal of American Society for Horticultural Science* **120**:460-467.

Wickramasinghe, U. L., Wright, C. J., and Currah, L. (2000). Bulbing responses of two cultivars of red tropical onions to photoperiod, light integral and temperature under controlled growth conditions. *Journal of Horticultural Science and Biotechnology* **75**: 304-311.

Wiebe, H. J. (1990). Vernalization of vegetable crops-a review. *Acta Horticulturae* **267**: 323-328.

Wiles, G. C. (1989). The effect of light and temperature on bulb initiation and development in tropical cultivars of onion (*Allium cepa* L.). PhD Thesis, Wye College, University of London, UK.

Wiles, G. C. (1994). The Effect of different photoperiods and temperatures following bulb initiation on bulb development in tropical onion cultivars. *Acta Horticulturae* **358**: 123-126.

Williams, C. N., Uzo, J. O., and Peregrine, W. T. H. (1991). *Vegetable production in the tropics*. Malaysia: Longman Group UK Limited, pp. 142-143.

Woodbury, G. W. and Ridley, J. R. (1969). The influence of incandescent and florescent light on the bulbing response of three onion varieties. *Journal of the American Society of Horticultural Science* **94**: 365-367.

Wright, C. J., and Sobeih, W. Y. (1986). The photoperiod regulation of bulbing in onions (*Allium cepa* L.). I. Effects of irradiance. *Journal of Horticultural Science* **61**: 331-335.

Yamaguchi, M., Paulson, K. N., Krusella, M. N., and Bernhard, R. A. (1975). Effects of soil temperature on growth and quality of onion bulbs (*Allium cepa* L) used for dehydration. *Journal of the American Society of Horticultural Science* **100**: 415-419.

INDEX OF APPENDICES

APPENDIX 3.1 Analysis of variance table: Response of cultivars grown under different temperatures and daylengths at 108 days.

Variate: Leaf number

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Reps stratum	3	1.6660	0.5553	2.04	
Reps.*Units* stratum					
daylength	2	3.8077	1.9038	7.01	0.002
Temperature	2	49.6108	24.8054	91.34	<.001
cultivars	2	0.8053	0.4026	1.48	0.233
daylength.Temperature	4	56.0668	14.0167	51.61	<.001
daylength.cultivars	4	4.3888	1.0972	4.04	0.005
Temperature.cultivars	4	2.6129	0.6532	2.41	0.057
daylength.Temperature.cultivars	8	5.7686	0.7211	2.66	0.012
Residual	78	21.1828	0.2716		
Total	107	145.9097			

GRAND MEAN 7.76 **CV 6.7%**

Total number of observations 108

APPENDIX 3.1 (continued)

Variate: Leaf area

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Reps stratum	3	394398.	131466.	7.22	
Reps.*Units* stratum					
daylength	2	2031158.	1015579.	55.75	<.001
Temperature	2	210471.	105235.	5.78	0.005
cultivars	2	82542.	41271.	2.27	0.111
daylength.Temperature	4	2033969.	508492.	27.91	<.001
daylength.cultivars	4	72180.	18045.	0.99	0.418
Temperature.cultivars	4	73820.	18455.	1.01	0.406
daylength.Temperature.cultivars	8	184083.	23010.	1.26	0.275
Residual	78	1420857.	18216.		
Total	107	6503478.			

GRAND MEAN 412. CV 32.7%

Total number of observations 108

Variate: Plant height

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Reps stratum	3	93.83	31.28	2.11	
Reps.*Units* stratum					
daylength	2	1242.69	621.35	41.97	<.001
Temperature	2	474.84	237.42	16.04	<.001
cultivars	2	200.57	100.28	6.77	0.002
daylength.Temperature	4	5147.33	1286.83	86.92	<.001
daylength.cultivars	4	136.10	34.03	2.30	0.066
Temperature.cultivars	4	66.03	16.51	1.12	0.355
daylength.Temperature.cultivars	8	153.63	19.20	1.30	0.257
Residual	78	1154.74	14.80		
Total	107	8669.76			

GRAND MEAN 55.11 CV 7.0%

Total number of observations 108

APPENDIX 3.1 (continued)

Variate: Bulb ratio

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Reps stratum	3	0.23343	0.07781	1.94	
Reps.*Units* stratum					
daylength	2	15.27289	7.63644	190.61	<.001
Temperature	2	0.66645	0.33323	8.32	<.001
cultivars	2	0.44826	0.22413	5.59	0.005
daylength.Temperature	4	2.55488	0.63872	15.94	<.001
daylength.cultivars	4	1.01229	0.25307	6.32	<.001
Temperature.cultivars	4	0.55891	0.13973	3.49	0.011
daylength.Temperature.cultivars	8	0.69028	0.08629	2.15	0.040
Residual	78	3.12500	0.04006		
Total	107	24.56240			

GRAND MEAN 2.101 **CV 9.5%**

Total number of observations 108

APPENDIX 3.2 Broken-stick Regression analysis table: The leaf area of the onion cultivars regressed on GDD.

11.5 h×25/12°C

```
Model with I = 200.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                    d.f.          s.s.          m.s.      v.r.   F pr.
Regression            3       373948.       124649.      20.75   <.001
Residual             12        72078.         6006.
Total                15       446026.        29735.

Percentage variance accounted for 79.8
Standard error of observations is estimated to be 77.5
          Gdd         y_Est
      197.2747      96.7783
```

11.5h×30/15°C

```
Model with I = 240.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                    d.f.          s.s.          m.s.      v.r.   F pr.
Regression            3        55323.       18441.1     112.62   <.001
Residual             12         1965.         163.7
Total                15        57288.        3819.2

Percentage variance accounted for 95.7
Standard error of observations is estimated to be 12.8
            Gdd         y_Est
       389.6453       60.4454
```

APPENDIX 3.2 (continued)

11.5h×35/18°C

```
Model with I = 300.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis
                   d.f.         s.s.         m.s.      v.r.   F pr.
Regression            3       11057.       3685.6     11.51   <.001
Residual             12        3841.        320.1
Total                15       14898.        993.2

Percentage variance accounted for 67.8
Standard error of observations is estimated to be 17.9
             Gdd        y_Est
       -297.3403       3.6195
```

12h×25/12°C

```
Model with I = 200.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis
                   d.f.         s.s.         m.s.      v.r.   F pr.
Regression            3      114995.       38332.     11.74   <.001
Residual             12       39180.        3265.
Total                15      154175.       10278.

Percentage variance accounted for 68.2
Standard error of observations is estimated to be 57.1
            Gdd        y_Est
       404.9901     161.5125
```

APPENDIX 3.2 (continued)

12h×30/15°C

```
Model with I = 240.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                   d.f.         s.s.          m.s.       v.r.   F pr.

Regression          3        236144.        78715.      28.23  <.001
Residual           12         33459.         2788.

Total              15        269603.        17974.


Percentage variance accounted for 84.5
Standard error of observations is estimated to be 52.8
          Gdd        y_Est
      431.8243    105.6961
```

12h×35/18°C

```
 Model with I = 320.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                   d.f.         s.s.          m.s.       v.r.   F pr.

Regression          3        275424.        91808.      20.53  <.001
Residual           12         53665.         4472.

Total              15        329089.        21939.


Percentage variance accounted for 79.6
Standard error of observations is estimated to be 66.9
           Gdd        y_Est
       431.1512     82.2862
```

APPENDIX 3.2 (continued)

12.5h×25/12°C

```
Model with I = 200.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis
                   d.f.          s.s.          m.s.       v.r.   F pr.
Regression          3         354130.        118043.      24.60  <.001
Residual           12          57574.          4798.
Total              15         411704.         27447.

Percentage variance accounted for 82.5
Standard error of observations is estimated to be 69.3
          Gdd        y_Est
      140.1153     59.6001
```

12.5h×30/15°C

```
Model with I = 300.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis
                   d.f.          s.s.          m.s.       v.r.   F pr.
Regression          3        1245632.        415211.      19.80  <.001
Residual           12         251684.         20974.
Total              15        1497316.         99821.

Percentage variance accounted for 79.0
Standard error of observations is estimated to be 145.
            Gdd        y_Est
        410.6645    132.2729
```

APPENDIX 3.2 (continued)

12.5h×35/18°C

```
Model with I = 320.0
Regression Analysis
Response variate: Leaf area (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis ***
```

	d.f.	s.s.	m.s.	v.r.	F pr.
Regression	3	953753.	317918.	21.03	<.001
Residual	12	181423.	15119.		
Total	*15*	*1135176.*	*75678.*		

```
Percentage variance accounted for 80.0
Standard error of observations is estimated to be 123.
```

Gdd	**y_Est**
579.3884	79.5963

APPENDIX 3.3 Broken-stick Regression analysis table: The bulb ratio of the onion cultivars regressed on GDD.

11.5h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	0.95445	0.318150	57.45	<.001
Residual	12	0.06645	0.005537		
Total	*15*	*1.02090*	*0.068060*		

Percentage variance accounted for 91.9

Standard error of observations is estimated to be 0.0744

Gdd	**y_Est**
336.7980	1.1069

11.5h×30/15°C

Model with I = 240.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	0.65770	0.219233	29.04	<.001
Residual	12	0.09060	0.007550		
Total	*15*	*0.74830*	*0.049887*		

Percentage variance accounted for 84.9

Standard error of observations is estimated to be 0.0869

Gdd	**y_Est**
413.0208	1.0651

APPENDIX 3.3 (continued)

11.5h×35/18°C

Model with I = 300.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	0.859819	0.2866063	543.76	<.001
Residual	12	0.006325	0.0005271		
Total	*15*	*0.866144*	*0.0577429*		

Percentage variance accounted for 99.1

Standard error of observations is estimated to be 0.0230

Gdd	**y_Est**
499.6339	1.0722

11.5h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (HR 1)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	1.14492	0.381642	86.33	<.001
Residual	12	0.05305	0.004421		
Total	*15*	*1.19797*	*0.079865*		

Percentage variance accounted for 94.5

Standard error of observations is estimated to be 0.0665

Gdd	**y_Est**
319.9316	1.1035

APPENDIX 3.3 (continued)

11.5h×30/15°C

```
Model with I = 240.0
Regression Analysis
Response variate: Bulb ratio (HR 1)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                     d.f.          s.s.          m.s.       v.r.   F pr.

Regression             3      0.600725     0.2002417    1922.32   <.001
Residual              12      0.001250     0.0001042

Total                 15      0.601975     0.0401317


Percentage variance accounted for 99.7
Standard error of observations is estimated to be 0.0102
            Gdd        y_Est
        432.7703       1.0651
```

11.5h×35/18°C

```
Model with I = 300.0
Regression Analysis
Response variate: Bulb ratio (HR 1)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                     d.f.          s.s.          m.s.       v.r.   F pr.

Regression             3       1.17525      0.391750     130.04   <.001
Residual              12       0.03615      0.003012

Total                 15       1.21140      0.080760


Percentage variance accounted for 96.3
Standard error of observations is estimated to be 0.0549
            Gdd        y_Est
       539.9081       1.0906
```

APPENDIX 3.3 (continued)

11.5h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	0.53298	0.177659	69.89	<.001
Residual	12	0.03051	0.002542		
Total	*15*	*0.56348*	*0.037566*		

Percentage variance accounted for 93.2

Standard error of observations is estimated to be 0.0504

Gdd	**y_Est**
318.7687	1.0640

11.5h×30/15°C

Model with I = 240.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	1.06744	0.355814	80.42	<.001
Residual	12	0.05309	0.004424		
Total	*15*	*1.12054*	*0.074702*		

Percentage variance accounted for 94.1

Standard error of observations is estimated to be 0.0665

Gdd	**y_Est**
439.0434	1.0691

APPENDIX 3.3 (continued)

11.5h×35/18°C

Model with I = 300.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	0.56075	0.186917	67.06	<.001
Residual	12	0.03345	0.002787		
Total	*15*	*0.59420*	*0.039613*		

Percentage variance accounted for 93.0

Standard error of observations is estimated to be 0.0528

Gdd	**y_Est**
575.5500	1.1200

12h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	2.95972	0.986572	240.16	<.001
Residual	12	0.04930	0.004108		
Total	*15*	*3.00901*	*0.200601*		

Percentage variance accounted for 98.0

Standard error of observations is estimated to be 0.0641

Gdd	**y_Est**
345.8869	1.3051

APPENDIX 3.3 (continued)

12h×30/15°C

Model with I = 240.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	2.84415	0.948050	118.17	<.001
Residual	12	0.09627	0.008023		
Total	*15*	*2.94042*	*0.196028*		

Percentage variance accounted for 95.9

Standard error of observations is estimated to be 0.0896

Gdd	**y_Est**
496.8322	1.3224

12h×35/18°C

Model with I = 320.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	3.3371	1.11236	98.52	<.001
Residual	12	0.1355	0.01129		
Total	*15*	*3.4726*	*0.23150*		

Percentage variance accounted for 95.1

Standard error of observations is estimated to be 0.106

Gdd	**y_Est**
610.7885	1.3034

APPENDIX 3.3 (continued)

12h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (HR 1)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	7.911	2.63690	27.31	<.001
Residual	12	1.158	0.09654		
Total	*15*	*9.069*	*0.60461*		

Percentage variance accounted for 84.0

Standard error of observations is estimated to be 0.311

Gdd	**y_Est**
352.6263	1.8433

12h × 30/15°C

Model with I = 240.0

Regression Analysis

Response variate: Bulb ratio (HR 1)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	2.46132	0.820441	337.35	<.001
Residual	12	0.02918	0.002432		
Total	*15*	*2.49051*	*0.166034*		

Percentage variance accounted for 98.5

Standard error of observations is estimated to be 0.0493

Gdd	**y_Est**
484.6690	1.3126

APPENDIX 3.3 (continued)

12h×35/18°C

```
Model with I = 320.0

Regression Analysis

Response variate: Bulb ratio (HR 1)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

                  d.f.         s.s.         m.s.      v.r.  F pr.

Regression           3       6.7623      2.25411     73.27  <.001
Residual            12       0.3692      0.03076

Total               15       7.1315      0.47543


Percentage variance accounted for 93.5

Standard error of observations is estimated to be 0.175

             Gdd       y_Est

        581.1736      1.3324
```

12h×25/12°C

```
Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

                  d.f.         s.s.         m.s.      v.r.  F pr.

Regression           3       8.5248      2.84161    261.38  <.001
Residual            12       0.1305      0.01087

Total               15       8.6553      0.57702


Percentage variance accounted for 98.1

Standard error of observations is estimated to be 0.104

             Gdd       y_Est

        329.0410      1.3340
```

APPENDIX 3.3 (continued)

12h×30/15°C

```
Model with I = 240.0
Regression Analysis
Response variate: Bulb ratio (HR 2)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                d.f.        s.s.         m.s.       v.r.   F pr.

Regression        3      2.63689     0.878965     197.12  <.001
Residual         12      0.05351     0.004459

Total            15      2.69040     0.179360


Percentage variance accounted for 97.5
Standard error of observations is estimated to be 0.0668
            Gdd        y_Est
       465.2529       1.2800
```

12h×35/18°C

```
Model with I = 320.0
Regression Analysis
Response variate: Bulb ratio (HR 2)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                d.f.        s.s.         m.s.       v.r.   F pr.

Regression        3       5.3798      1.79325      39.82  <.001
Residual         12       0.5404      0.04503

Total            15       5.9201      0.39468


Percentage variance accounted for 88.6
Standard error of observations is estimated to be 0.212
             Gdd        y_Est
        599.2227       1.4286
```

APPENDIX 3.3 (continued)

12.5h×25/12°C

```
Model with I = 200.0
Regression Analysis
Response variate: Bulb ratio (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis
                  d.f.        s.s.         m.s.       v.r.   F pr.
Regression          3       1.3742      0.45806      11.74  <.001
Residual           12       0.4683      0.03903
Total              15       1.8425      0.12283

Percentage variance accounted for 68.2
Standard error of observations is estimated to be 0.198
          Gdd        y_Est
      362.9104      1.3139
```

12.5h×30/15°C

```
Model with I = 300.0
Regression Analysis
Response variate: Bulb ratio (RC)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis
                  d.f.        s.s.         m.s.       v.r.   F pr.
Regression          3       2.4453      0.81511      30.94  <.001
Residual           12       0.3161      0.02635
Total              15       2.7615      0.18410

Percentage variance accounted for 85.7
Standard error of observations is estimated to be 0.162
           Gdd        y_Est
       415.8103      1.4276
```

APPENDIX 3.3 (continued)

12.5h×35/18°C

Model with I = 320.0

Regression Analysis

Response variate: Bulb ratio (RC)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	4.7695	1.58982	77.16	<.001
Residual	12	0.2473	0.02060		
Total	*15*	*5.0167*	*0.33445*		

Percentage variance accounted for 93.8

Standard error of observations is estimated to be 0.144

Gdd	**y_Est**
414.8534	1.1892

12.5h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (HR 1)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	2.47720	0.825733	133.50	<.001
Residual	12	0.07422	0.006185		
Total	*15*	*2.55142*	*0.170095*		

Percentage variance accounted for 96.4

Standard error of observations is estimated to be 0.0786

Gdd	**y_Est**
345.8277	1.2238

APPENDIX 3.3 (continued)

12.5h×30/15°C

```
Model with I = 300.0
Regression Analysis
Response variate: Bulb ratio (HR 1)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                  d.f.        s.s.        m.s.      v.r.  F pr.
Regression           3      2.3510     0.78367     71.70  <.001
Residual            12      0.1312     0.01093
Total               15      2.4822     0.16548

Percentage variance accounted for 93.4
Standard error of observations is estimated to be 0.105
            Gdd        y_Est
    434.5737       1.2873
```

12.5h×35/18°C

```
Model with I = 320.0
Regression Analysis
Response variate: Bulb ratio (HR 1)
Fitted terms: Constant, GDD1, GDD2, dummy
Summary of analysis

                  d.f.        s.s.        m.s.      v.r.  F pr.
Regression           3      2.9155     0.97185     73.32  <.001
Residual            12      0.1591     0.01326
Total               15      3.0746     0.20497

Percentage variance accounted for 93.5
Standard error of observations is estimated to be 0.115
             Gdd         y_Est
       512.7952       1.2709
```

APPENDIX 3.3 (continued)

12.5h×25/12°C

Model with I = 200.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	1.6822	0.56074	25.18	<.001
Residual	12	0.2672	0.02227		
Total	*15*	*1.9494*	*0.12996*		

Percentage variance accounted for 82.9

Standard error of observations is estimated to be 0.149

Gdd	**y_Est**
323.2011	1.1699

12.5h×30/15°C

Model with I = 300.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	3.2828	1.09425	51.86	<.001
Residual	12	0.2532	0.02110		
Total	*15*	*3.5360*	*0.23573*		

Percentage variance accounted for 91.0

Standard error of observations is estimated to be 0.145

Gdd	**y_Est**
417.8697	1.2551

APPENDIX 3.3 (continued)

12.5h×35/18°C

Model with I = 320.0

Regression Analysis

Response variate: Bulb ratio (HR 2)

Fitted terms: Constant, GDD1, GDD2, dummy

Summary of analysis

	d.f.	*s.s.*	*m.s.*	*v.r.*	*F pr.*
Regression	3	3.5470	1.18233	41.13	<.001
Residual	12	0.3450	0.02875		
Total	*15*	*3.8920*	*0.25947*		

Percentage variance accounted for 88.9

Standard error of observations is estimated to be 0.170

Gdd	**y_Est**
368.9851	1.1385

APPENDIX 4.1 The GDD values calculated for different levels of base temperature (T_b) required to achieve the plant height (PH) of onion plants at the termination of growth recorded in 9 growth rooms set at three combinations of daylength and temperature

Growth conditions	**Days**	**GDD at 4°C T_b**	**GDD at 5°C T_b**	**GDD at 6°C T_b**	**GDD at 7°C T_b**	**GDD at 8°C T_b**	**Plant Height (mm)**
11.5h×25/12°C	60	882	822	762	702	642	**490.91**
11.5h×30/15°C	60	870	810	750	690	630	**520.37**
11.5h×35/18°C	60	846.9	786.9	726.9	666.9	606.9	**530.2**
12h×25/12°C	45	842.625	797.625	752.625	707.625	662.625	**670.85**
12h×30/15°C	45	832.5	787.5	742.5	697.5	652.5	**640.03**
12h×35/18°C	45	812.25	767.25	722.25	677.25	632.25	**540.8**
12.5h×25/12°C	45	1023.75	978.75	933.75	888.75	843.75	**590.5**
12.5h×30/15°C	45	1012.5	967.5	922.5	877.5	832.5	**530.62**
12.5h×35/18°C	45	989.325	944.325	899.325	854.325	809.325	**410.38**
R^2 of T_b (PH) are		73.57	73.24	73.48	73.45	72.84	

APPENDIX 4.2: Thermal time which was perceived by ‘Hagaz red 1’, ‘Hagaz red 2’ and ‘Red Creole’ on the means of leaf number over time per growth rooms.

Growth rooms	GDD	Red Creole	SED	Hagaz Red 1	SED	Hagaz Red 2	SED
11.5h×25/12°C	0	4.000	0.000	4.000	0.000	3.750	0.250
	175.725	6.000	0.000	5.750	0.250	5.250	0.250
	351.45	6.750	0.250	7.000	0.000	6.250	0.250
	527.175	8.000	0.000	7.500	0.250	7.750	0.250
	702.9	8.000	0.000	9.500	0.645	8.500	0.500
11.5h×30/15°C	0	4.000	0.000	4.000	0.000	4.000	0.000
	234.75	6.000	0.000	5.750	0.250	5.250	0.250
	469.5	6.750	0.250	7.000	0.000	6.250	0.250
	704.25	8.000	0.000	8.500	0.289	6.750	0.250
	939	9.750	0.629	10.250	1.250	6.250	0.629
11.5h×35/18°C	0	3.750	0.250	4.000	0.000	4.000	0.000
	293.775	5.000	0.000	5.250	0.250	5.000	0.000
	587.55	6.250	0.250	6.500	0.289	6.250	0.250
	881.325	7.000	0.000	7.000	0.577	6.750	0.250
	1175.1	8.000	0.577	6.750	0.629	8.250	0.629
12h×25/12°C	0	4.083	0.153	4.020	0.031	4.278	0.116
	181.5	5.300	0.083	5.120	0.072	5.332	0.072
	363	6.028	0.131	5.306	0.083	6.139	0.224
	544.5	6.583	0.224	6.278	0.196	6.806	0.153
12h×30/15°C	0	3.778	0.157	4.056	0.032	4.222	0.091
	241.5	4.954	0.060	4.769	0.218	5.978	0.091
	483	6.417	0.160	6.694	0.409	7.181	0.131
	724.5	7.931	0.142	8.458	0.208	8.694	0.417
12h×35/18°C	0	3.806	0.053	3.972	0.053	4.028	0.095
	301.5	5.686	0.050	5.409	0.106	5.667	0.045
	603	6.889	0.198	7.194	0.281	7.222	0.045
	904.5	8.347	0.276	9.000	0.064	8.694	0.115
12.5h×25/12°C	0	3.806	0.053	3.694	0.095	3.694	0.053
	184.5	5.306	0.105	5.472	0.139	5.639	0.160
	369	6.444	0.187	6.722	0.184	6.958	0.322
	553.5	6.222	0.079	6.556	0.272	6.986	0.170
12.5h×30/15°C	0	3.889	0.079	4.056	0.056	4.194	0.095
	244.875	5.176	0.070	6.135	0.098	5.886	0.271
	489.75	7.056	0.184	7.806	0.160	7.347	0.305
	734.625	9.250	0.166	9.972	0.676	10.222	0.136
12.5h×35/18°C	0	4.222	0.120	3.905	0.037	3.986	0.032
	305.25	5.111	0.000	4.861	0.028	4.667	0.045
	610.5	6.139	0.053	6.083	0.095	5.806	0.146
	915.75	7.694	0.166	7.389	0.266	7.028	0.288

APPENDIX 4.2 (continued)

Leaf area

Growth rooms	GDD	Red Creole	SED	Hagaz Red 1	SED	Hagaz Red 2	SED
11.5h×25/12°C	0	14.000	1.592	20.000	3.717	27.000	4.618
	175.725	85.000	8.147	107.000	10.001	111.000	17.196
	351.45	240.000	21.339	365.000	59.311	340.000	32.210
	527.175	412.000	74.042	585.000	73.782	485.000	29.673
	702.9	1096.000	255.556	1069.000	115.754	872.000	244.654
11.5h×30/15°C	0	25.800	3.878	31.800	7.664	26.900	0.810
	234.75	46.200	4.162	75.100	7.287	67.200	10.408
	469.5	87.500	10.941	143.100	13.776	144.500	21.294
	704.25	178.900	3.418	281.900	34.625	116.100	14.329
	939	587.700	12.391	630.600	25.109	142.900	27.602
11.5h×35/18°C	0	18.000	2.758	24.300	1.789	26.100	5.135
	293.775	31.900	4.457	60.900	6.578	39.300	2.334
	587.55	64.600	9.313	103.300	10.621	69.400	12.407
	881.325	84.700	14.348	135.700	26.650	117.700	35.524
	1175.1	296.800	56.949	347.100	58.936	319.300	47.235
12h×25/12°C	0	25.600	0.990	24.500	0.834	23.500	0.650
	181.5	84.500	3.452	62.500	12.596	80.300	7.875
	363	119.400	37.303	81.300	13.545	125.900	16.821
	544.5	256.400	43.135	206.900	13.694	234.500	47.585
12h×30/15°C	0	17.200	1.564	19.600	1.681	27.700	6.398
	241.5	65.500	8.691	95.200	4.806	60.200	6.191
	483	138.500	25.509	248.300	10.106	211.300	17.015
	724.5	336.000	45.382	470.600	45.853	465.300	83.689
12h×35/18°C	0	20.600	0.367	22.100	1.104	20.500	0.674
	301.5	62.900	11.643	83.900	3.323	89.800	11.844
	603	179.500	9.998	191.900	28.155	270.900	13.540
	904.5	359.200	65.088	514.500	32.786	525.400	51.884
12.5h×25/12°C	0	22.000	4.351	31.000	3.174	27.900	2.073
	184.5	69.900	12.884	107.200	31.126	93.700	17.527
	369	244.900	44.854	464.900	46.611	422.600	57.652
	553.5	397.400	51.001	341.100	10.701	541.300	45.177
12.5h×30/15°C	0	17.000	2.462	22.000	2.410	26.000	4.844
	244.875	84.000	8.612	77.000	2.363	128.000	21.572
	489.75	264.000	15.466	277.000	23.579	292.000	13.935
	734.625	731.000	143.716	904.000	145.413	786.000	92.896
12.5h×35/18°C	0	10.000	1.908	17.000	2.151	16.000	4.423
	305.25	46.000	7.734	41.000	7.037	44.000	3.059
	610.5	112.000	25.867	183.000	42.259	176.000	22.254
	915.75	613.000	119.942	515.000	107.344	532.000	176.905

APPENDIX 4.2: (continued)

Plant height

Growth rooms	GDD	Red Creole	SED	Hagaz Red 1	SED	Hagaz Red 2	SED
11.5h×25/12°C	0	19.640	0.478	23.820	0.971	22.510	0.373
	175.725	39.510	1.410	43.770	1.400	42.910	0.493
	351.45	55.380	1.733	61.140	1.366	58.840	1.418
	527.175	63.340	1.316	67.540	2.285	65.690	2.161
	702.9	67.850	1.261	72.620	2.839	72.130	1.853
11.5h×30/15°C	0	20.250	0.647	23.900	0.722	22.850	0.612
	234.75	32.580	0.682	38.460	0.171	36.700	1.487
	469.5	38.650	1.011	48.150	*1.105*	41.400	1.662
	704.25	44.890	0.826	54.270	0.700	47.530	0.596
	939	53.620	2.749	58.380	1.519	44.500	2.151
11.5h×35/18°C	0	19.530	0.120	22.650	0.143	23.710	0.629
	293.775	25.310	0.712	32.820	1.053	32.550	1.163
	587.55	32.680	0.702	38.960	1.328	37.810	1.345
	881.325	36.640	1.167	40.860	1.956	39.840	2.088
	1175.1	41.380	3.191	42.370	3.064	39.870	2.561
12h×25/12°C	0	22.550	0.503	21.050	0.688	22.490	0.784
	181.5	41.820	1.311	31.390	1.042	46.810	1.512
	363	46.040	1.590	47.800	2.219	45.420	2.047
	544.5	49.910	2.459	45.930	1.038	49.290	1.394
12h×30/15°C	0	20.230	0.748	21.770	0.471	23.200	0.962
	241.5	34.420	0.877	36.290	0.718	41.750	1.359
	483	43.660	2.465	44.680	3.959	53.910	0.339
	724.5	53.200	2.194	59.520	0.813	62.720	1.301
12h×35/18°C	0	20.390	0.342	22.050	1.078	21.920	0.673
	301.5	36.450	1.412	40.560	1.133	43.230	1.094
	603	43.940	3.229	47.660	3.418	51.870	1.064
	904.5	54.800	2.047	58.180	2.255	58.800	0.946
12.5h×25/12°C	0	21.000	0.359	23.650	0.312	22.590	1.174
	184.5	42.390	0.821	46.980	0.904	48.200	1.566
	369	58.800	1.357	62.460	0.752	63.530	2.561
	553.5	52.370	1.604	53.740	1.300	55.980	2.294
12.5h×30/15°C	0	20.230	0.586	21.110	0.324	21.510	0.427
	244.875	41.610	4.213	40.320	3.785	48.470	2.026
	489.75	41.950	0.331	52.570	1.358	52.770	3.410
	734.625	64.030	3.671	63.820	3.411	64.270	2.815
12.5h×35/18°C	0	20.610	0.626	19.680	0.573	20.370	0.574
	305.25	33.770	0.867	34.120	0.733	33.310	0.503
	610.5	51.870	0.959	53.920	1.225	53.330	1.582
	915.75	59.500	1.809	61.300	1.635	60.100	2.537

APPENDIX 4.2: (continued)

Bulb ratio

Growth rooms	GDD	Red Creole	SED	Hagaz Red 1	SED	Hagaz Red 2	SED
11.5h×25/12°C	0	1.033	0.016	1.038	0.009	1.045	0.009
	175.725	1.070	0.007	1.073	0.005	1.055	0.009
	351.45	1.115	0.014	1.165	0.031	1.110	0.024
	527.175	1.633	0.071	1.700	0.058	1.488	0.043
	702.9	1.966	0.061	1.993	0.064	1.955	0.026
11.5h×30/15°C	0	1.020	0.014	1.023	0.006	1.019	0.003
	234.75	1.045	0.005	1.045	0.006	1.045	0.003
	469.5	1.140	0.007	1.108	0.005	1.113	0.015
	704.25	1.525	0.085	1.500	0.000	1.650	0.065
	939	1.835	0.093	1.923	0.025	2.002	0.098
11.5h×35/18°C	0	1.038	0.005	1.063	0.006	1.065	0.005
	293.775	1.058	0.008	1.078	0.005	1.093	0.010
	587.55	1.185	0.017	1.160	0.015	1.120	0.012
	881.325	1.613	0.013	1.720	0.052	1.523	0.050
	1175.1	2.015	0.029	1.971	0.060	1.993	0.027
12h×25/12°C	0	1.126	0.029	1.175	0.025	1.169	0.029
	181.5	1.217	0.023	1.508	0.069	1.257	0.016
	363	1.330	0.028	1.832	0.121	1.516	0.074
	544.5	2.203	0.044	3.038	0.277	2.974	0.066
12h×30/15°C	0	1.112	0.033	1.213	0.020	1.189	0.026
	241.5	1.212	0.077	1.261	0.007	1.235	0.041
	483	1.220	0.031	1.261	0.038	1.301	0.042
	724.5	2.150	0.003	2.150	0.022	2.175	0.020
12h×35/18°C	0	1.234	0.069	1.233	0.040	1.268	0.043
	301.5	1.268	0.066	1.284	0.049	1.347	0.128
	603	1.232	0.038	1.380	0.095	1.393	0.063
	904.5	2.299	0.029	2.795	0.133	2.671	0.151
12.5h×25/12°C	0	1.182	0.045	1.163	0.015	1.110	0.023
	184.5	1.247	0.034	1.194	0.025	1.143	0.029
	369	1.293	0.028	1.276	0.032	1.288	0.018
	553.5	1.911	0.187	2.115	0.066	1.913	0.144
12.5h×30/15°C	0	1.335	0.011	1.280	0.040	1.231	0.037
	244.875	1.388	0.118	1.284	0.043	1.245	0.047
	489.75	1.610	0.067	1.428	0.071	1.472	0.099
	734.625	2.315	0.089	2.205	0.050	2.338	0.087
12.5h×35/18°C	0	1.123	0.011	1.254	0.046	1.221	0.060
	305.25	1.171	0.013	1.264	0.055	1.154	0.019
	610.5	1.680	0.024	1.500	0.030	1.658	0.045
	915.75	2.480	0.140	2.299	0.085	2.336	0.151

APPENDIX 4.3: Linear regression analysis table: The growth components of the onion cultivars regressed on growing degree days (GDD).

```
Response variate: leaf number

Fitted terms: Constant, GDD

Summary of analysis

                    d.f.         s.s.          m.s.       v.r.   F pr.

Regression            1         805.3      805.2760    1261.43   <.001
Residual            430         274.5        0.6384

Total               431        1079.8        2.5053


Percentage variance accounted for 74.5

Standard error of observations is estimated to be 0.799
```

```
Response variate: Plant height

Fitted terms: Constant, GDD

Summary of analysis

                    d.f.         s.s.          m.s.       v.r.   F pr.

Regression            1        53065.      53064.86     600.33   <.001
Residual            430        38009.         88.39

Total               431        91074.        211.31


Percentage variance accounted for 58.2

Standard error of observations is estimated to be 9.40
```

APPENDIX 4.4: Nonlinear regression analysis table: The growth components of the onion cultivars regressed on growing degree days (GDD).

Response variate: **bulb_ratio**

Explanatory: GDD

Fitted Curve: A + B*(R**X)

Constraints: R > 1

Summary of analysis

	d. f.	s. s.	m. s.	v. r.	F pr.
Regression	2	33. 35	16. 67715	252. 26	<. 001
Residual	413	27. 30	0. 06611		
Total	415	60. 66	0. 14616		

Percentage variance accounted for 54.8

Standard error of observations is estimated to be 0.257

Response variate: **leaf area (square root transformation)**

Explanatory: GDD

Fitted Curve: A + B*(R**X)

Constraints: R < 1

Summary of analysis

	d.f.	s.s.	m.s.	v.r.	F pr.
Regression	2	9960(6681242)	4979.76	256.75	<.001
Residual	413	8010(9614661)	19.40		
Total	415	17970.	43.30		

Percentage variance accounted for 55.2

Standard error of observations is estimated to be 4.40