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Full Length Research Paper

Growth responses of tropical onion cultivars to photoperiod and temperature based on growing degree days

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Onions (Allium cepa L.) are widely produced within the tropics, but little is known about the Eritrean cultivars Hagaz Red 1 and 2 (HR 1, and HR 2) and Red Creole (RC). Responses of the onion cvs. HR 1, HR 2 and RC to photoperiod and temperature on bulbing were compared. Plants were grown in growth rooms under combinations of photoperiod (11.5, 12, and 12.5 h) and day/night temperatures (25/12, 30/15 and 35/18°C). Growth responses were determined by growing degree day (GDD) base and the broken-stick regression model. There were relationships between bulb initiation and rate of leaf area growth under 12 and 12.5 h. Under the 12 h photoperiod, cultivars needed 343, 482, and 597 GDD before bulb initiation and 405, 432, and 431 GDD to increase rate of leaf area development at 25/12, 30/15, and 35/18°C, respectively. Under a 12.5 h photoperiod, cultivars needed 344, 423, and 432.2 GDD to initiate bulbing and 140, 411, and 579 GDD to increase leaf growth rates at 25/12, 30/15, and 35/18°C, respectively. Temperature induces variations in leaf number, plant height, leaf area, and affect bulbing and these responses may be used in the development of superior cultivars for tropical conditions.

Key words: Growing degree days (GDD), onion, bulb, broken-stick analysis.

INTRODUCTION

Reports in literature suggest that tropical plants may respond to variations in day length under natural short day conditions (Adam, 2006); which may determine critical day length for bulb initiation and formation. For example, Uzo and Currah (1990) observed that under short day conditions, onion plants produced new leaves indefinitely without bulb formation while at longer day lengths, bulbs were formed.

Temperature also plays an important role in bulb initiation and formation in onions. Temperature variations have been shown to influence the rate of vegetative growth (Butt, 1968; Brewster, 1979; Seabrook, 2005), leaf initiation, and emergence (de Ruiter, 1986). It is probable that the response of tropical onions to short day variations in day length may be further influenced by temperature. Topical onion varieties can be classified as “short day onions” because these plants will initiate and form bulbs in less than 12 h photoperiods (day length) and are suitable for warm climates (Rabinowitch and Currah, 2002).

The determination of short day variations in day length in “short day onions” using chronological age may not provide insightful information because of temperature variations which may occur during the growing season. Instead, growing degree days (GDD) which are based on actual temperatures may provide a simple and accurate way to determine the relationship between short day variations in day length (photoperiod) and bulb initiation and formation in onion. 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).

This study investigated the effects of short day variations in day length (photoperiod), and temperature on the growth and ‘onset of bulbing’ in three tropical onion cultivars. The thermal presentation of plant development was used to determine the growing degree days required to compare bulbing and leaf growth of the cultivars to

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relate growth and time of initiation of bulbing under different short day lengths.

MATERIALS AND METHODS

Two Eritrean cultivars (HR 1, HR 2), from the Hagaz location in Keren, Eritrea (Latitude 15° 46′ 40″ N and Longitude 38° 27′ 29″ E; altitude 960 m above sea level) and a third cultivar, Red Creole (RC) cultivated in Eritrea and widely grown in South Africa were used in the study. These cultivars can be classified as tropical and "short day onions" because they flower in less than 12 h photoperiods. The experiment 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). 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 two to three 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/photoperiod treatments. After eight weeks, three uniform seedlings were transferred to plastic pots of 200 mm diameter. Before treatment, 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.

The experiment was conducted under simulated tropical conditions with day lengths of 11.5, 12, and 12.5 h and day/night temperatures of 25/12, 30/15 and 35/18°C, which are suitable conditions for bulb initiation under natural short day conditions. The choice of night temperature levels was based on the findings of Steer (1980) who 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.

Experiment design

The split plot design of three levels of photoperiod and three levels of temperature resulted in nine treatment combinations. The experimental units were subjected to a constant relative humidity of 70% over the experimental period. The single replication and series plantings were done for the growth rooms because it is not feasible to do the experiment simultaneously. 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 were transferred to each growth room treatment following the week of transplant adjustment. Growing degree days (GDD) were calculated according to Holen and Dexter (1996).

Measurements

Numbers of green leaves; leaf area (as split and spread blades), bulb diameter (taken at the widest part of the base of the pseudostem), and neck diameter (minimum diameter of pseudostem above the swollen stem) were determined. Measurements of bulb and neck diameter, leaf number, leaf area and plant height were taken fortnightly until onset of bulbing with an absolute digimatic digital caliper (CD-S6"C, Micro Precision Calibration Inc., Grass Valley, CA, USA). A bulbing ratio of >2 characterises the onset of bulbing (Clark and Heath, 1962).

Growing degree days (GDD)

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

Where, GDD is the growing degree days; T_{day} is the day temperature; T_{night}, is the night temperature; DL is the daylength; NL is the night length; T_b is the base temperature.

Statistical analysis

Analyses of variance were performed using GenStat version 9.1 (VSN International, Hemel, Hempstead, UK). The broken-stick regression model was used to find the point of inflection on growth and this provided an appropriate point to evaluate bulb initiation and rate of leaf area growth. Broken-stick regression is a modeling procedure of the GenStat statistical package that breaks a non-linear curve into two linear components.

RESULTS AND DISCUSSION

Leaf number

At the 11.5 and 12.5 h day lengths, temperature induced more variation in leaf production in response to GDD in all cultivars than at a 12 h photoperiod (Figure 1). The 35/18°C temperatures decreased leaf number at the 11.5 and 12.5 h day lengths. High temperatures may induce stress-related physiological disorders and cause a decreased in the rate of leaf initiation and final number. The development of leaf primordia and consequently leaf initiation has been shown to be influenced by temperature (Wiles, 1989; Gough et al., 2010). This was observed on all plants grown at the supra-optimal temperature of 35°C. The high variability in leaf production under 11.5 h indicatethat temperature treatments had a greater affect on leaf production than did photoperiod. However, under 12 h photoperiod, temperature treatments did not influence thermal time responses. It is expected that the photoperiod response of the cultivars will change with temperature increment as leaves age (Salisbury, 1955). Once the photoperiod induced bulbing, leaf production in an onion plant will be gradually terminated. Under the 12.5 h photoperiod, the 35/18°C temperature decreased the rate of leaf production over GDD as they did under the short day length (11.5 h). This might occur when plants, induced by stress conditions to develop bulbing, hasten the growth cycle and start to accumulate stored carbohydrate for bulb development. Temperature treatments affected leaf production more at the 12.5 h photoperiod.

Leaf area

At the 11.5 and 12.5 h day lengths, temperature induced more variation in leaf area in all cultivars than at the 12 h photoperiod (Figure 2). The 25/12°C temperature induced increased rate of leaf area production in all cultivars

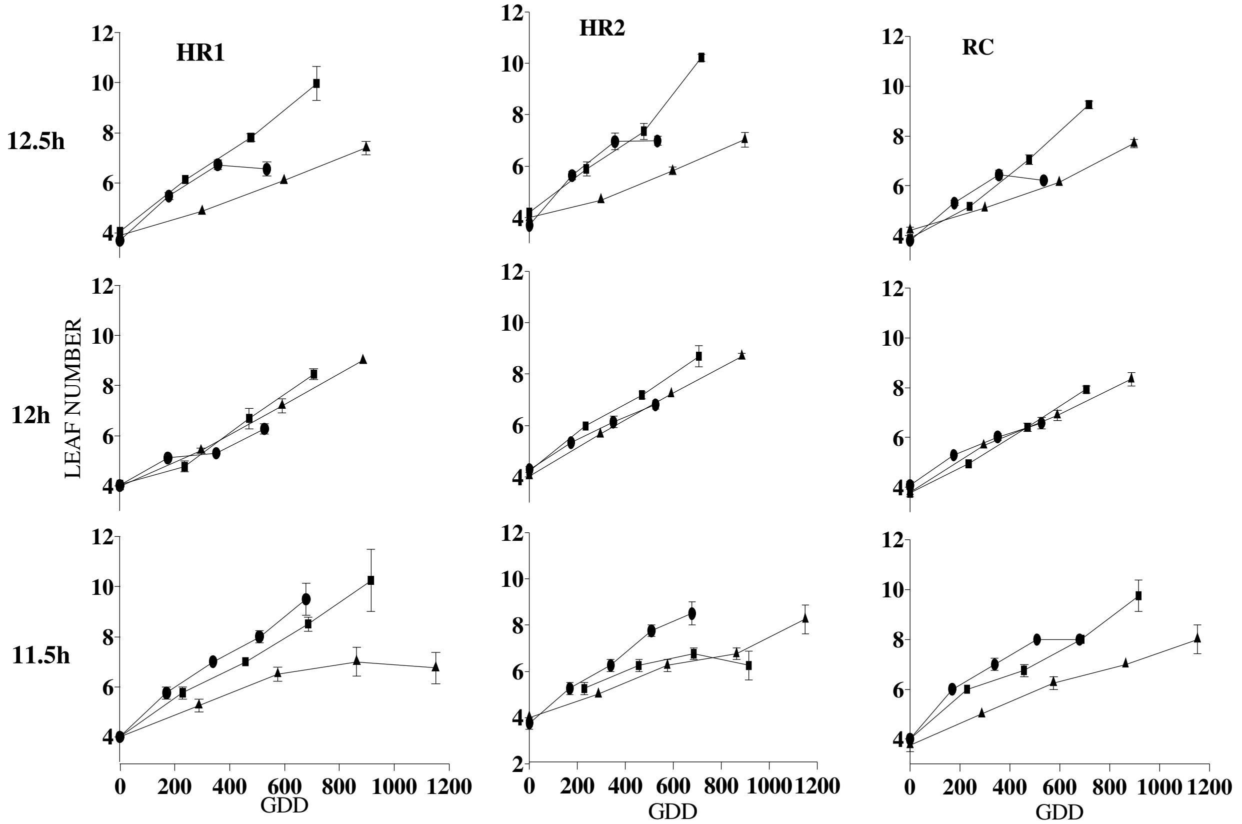

Figure 1. Leaf number of onion cvs. HR 1, HR 2, and RC grown under photoperiods of 11.5, 12, and 12.5 h and temperature regimes of 25/12 (●); 30/15 (■); and 35/18 (▲) over growing degree days (GDD). Bars represent SED.

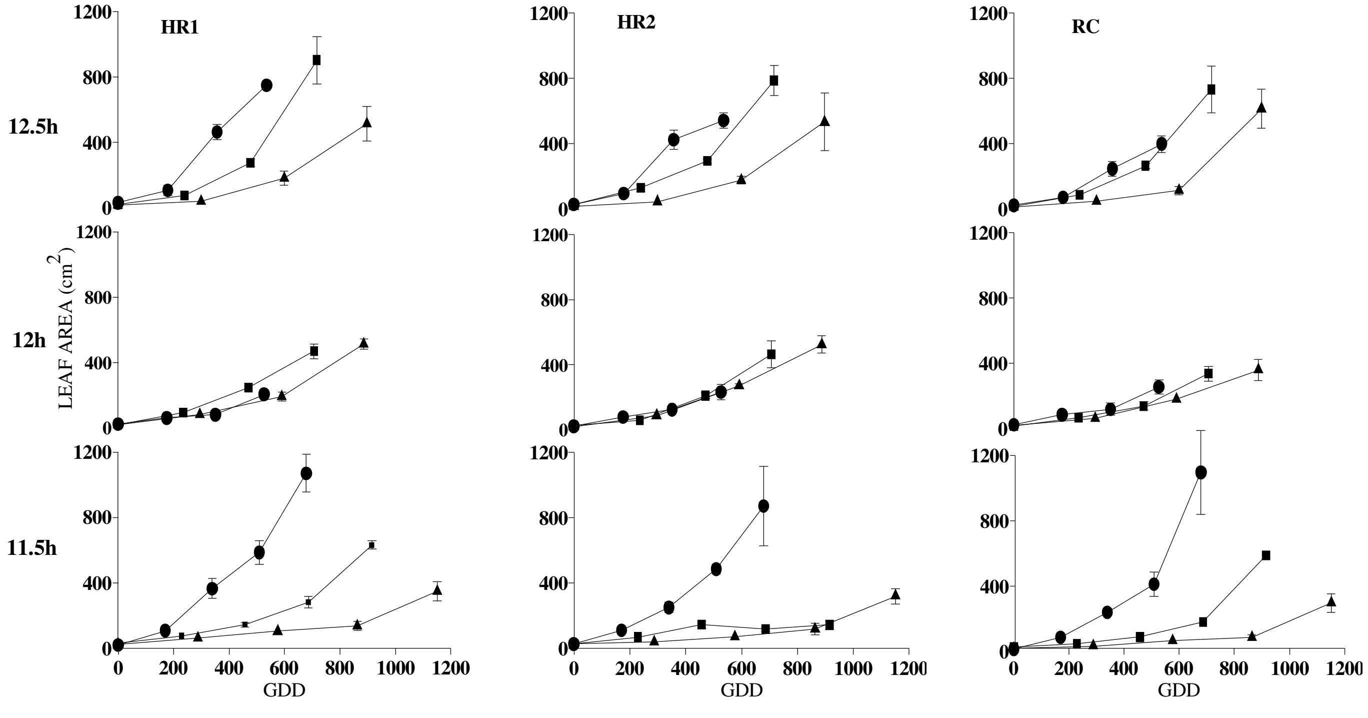

Figure 2. Leaf area of onion cvs. HR 1, HR 2, and RC grown under photoperiods of 11.5, 12, and 12.5 h and temperature regimes of 25/12 (●); 30/15 (■); and 35/18°C (▲) over growing degree days (GDD). Bars represent SED.

Table 1. Broken-stick analysis for leaf area development of tropical onions in relation to GDD.

Photoperiod (h)	Temperature (°C)	Model with i^{th} GDD	Point of inflection (t) GDD	Point of inflection (t) Est. Y	% of variation accounted for	F probability for regression
11.5	25/12	200	201.5	89.4	74.3	<0.001**
	30/15	240	360.2	64.8	91.7	<0.001**
	35/18	300	245.5	47.4	58.8	<0.001**
12	25/12	200	399.9	156.2	70.2	<0.001**
	30/15	240	420.4	115.1	81.6	<0.001**
	35/18	320	427.8	78.5	73.5	<0.001**
12.5	25/12	200	155.7	56.6	79.1	<0.001**
	30/15	300	389.8	125.4	71.4	<0.001**
	35/18	320	569.2	68.9	74.2	<0.001**

**-highly significant at P = 0.05; analysis was done on pooled data for all cultivars.

earlier in comparison to 30/15 and 35/18°C. This seemed to particularly occur under the 11.5 h photoperiod. The cultivars produced a higher leaf area when grown under the lower temperature at the 11.5 h photoperiod than the warmer temperatures. The 25/12°C temperature seemed to be the most suitable for vegetative growth under short photoperiod (11.5 h). At this temperature, plants required fewer GDD for leaf development than at the other two temperatures. Leaf area decreased as temperature increased (30/15 to 35/18°C). High leaf area production might be associated with rapid induction of bulbing under the lower temperature (25/12°C). Leaf area strongly affects response to bulbing stimulus in onion (Mettananda and Fordham, 1999). Plant size (Jones and Mann, 1963) or plant age (Butt, 1968) have also been implicated in regulating 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 detect the induction of bulbing (Table 1). Since there were no significant differences between cultivars, the analysis was done on pooled data for the three cultivars.

With a 12 h photoperiod, temperature treatments induced only a slight variation in leaf area development. The cultivars also required almost the same number of GDD (Table 1) to increase the rate of leaf area development regardless of temperature. The 25/12°C temperature was expected to further increase leaf growth when the cultivars obtained more GDD for their growth. As temperature increased (30/15 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 the stress.

At a 12.5 h photoperiod, temperature induced variations in leaf development. There was an increase in the rate of leaf area development at 25/12°C temperature, than for 30/15°C and 35/18°C (Table 1), which declined after receiving certain number of GDD. The highest temperature seems to be a supra-optimal condition for leaf growth.

In all cultivars, plants grown at the highest temperature (35/18°C) exhibited a decline in leaf area (Figure 2). This decline could probably be attributed to a rapid drop in leaf number; however, plants grown at the cooler temperature continued to produce leaves. This clearly shows that leaf growth was dependent on temperature and this relationship implies that growth may be related to GDD.

Height to uppermost leaf tip

At the 11.5 and 12.5 h day lengths, temperature induced more variation in plant height in all cultivars (Figure 3) than for a 12 h photoperiod. However, the 35/18°C temperature decreased the plant height at 11.5, 12 and 12.5 h photoperiods. A supra-optimal temperature could induce stress-related physiological disorders. This was most likely associated with a decreased rate of leaf production under high temperature. Temperature had a dominant role in determining plant height in all cultivars. At a 12 h photoperiod, temperature produced less variability in plant height. Under the neutral (12 h) photoperiod, the temperature had less effect in plant growth than the short (11.5 h) and long (12.5 h) day lengths and at 12.5 h photoperiod, temperature also induced more variation in the cultivars. Temperature was a more significant factor in determining plant height under the longer photoperiod (12.5 h).

Bulbing ratio

The 25/12°C temperature induced bulb initiation at lower GDD compared to the 30/15°C and 35/18°C temperatures (Table 2). However, the growth trend of bulb ratio was similar for all cultivars. Early bulb initiation under the

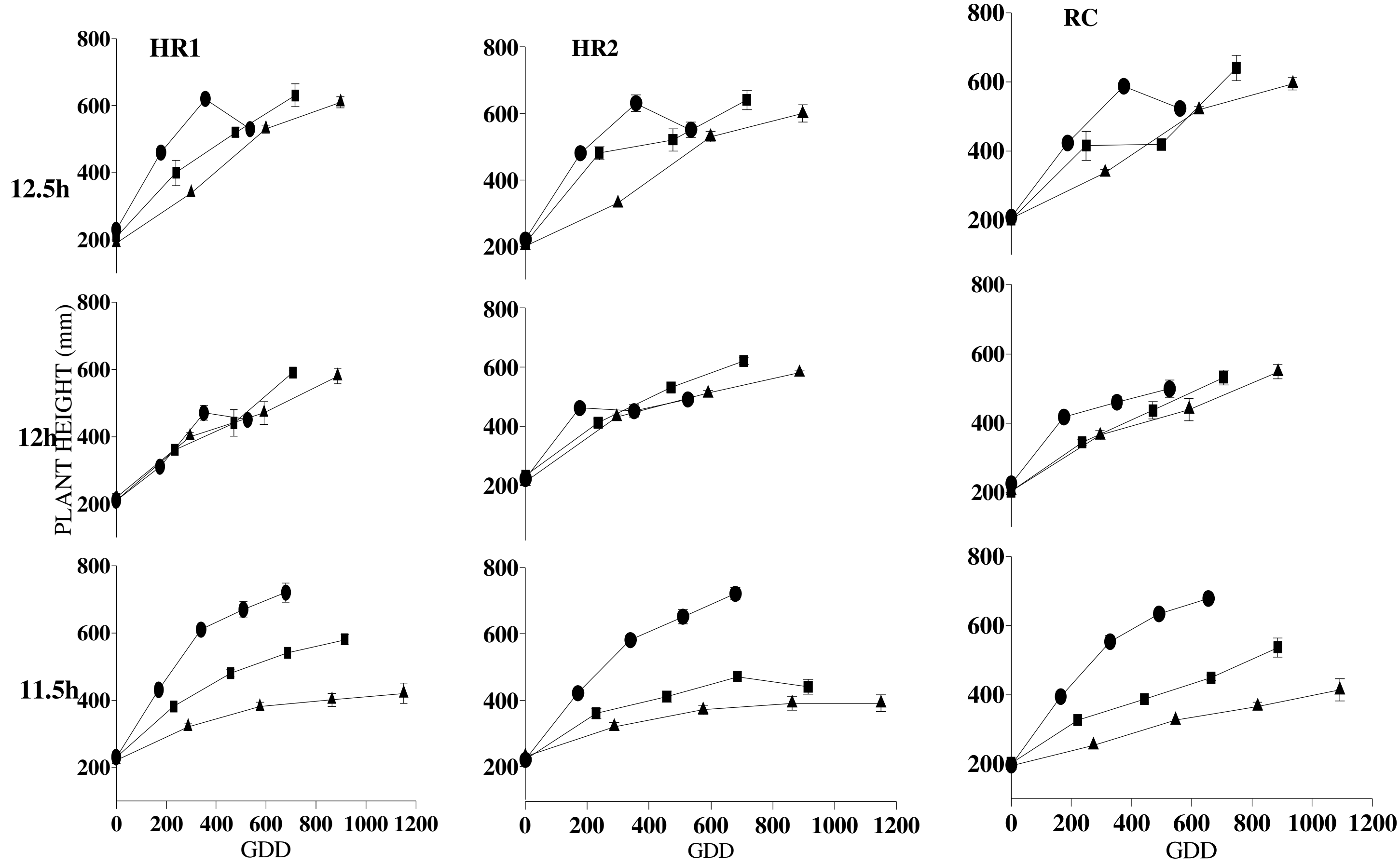

Figure 3. Plant height of onion cvs HR 1, HR 2, and RC grown under photoperiods of 11.5, 12, 12.5 h and temperature regimes of 25/12 (●); 30/15 (■); and 35/18°C (▲) over growing degree days (GDD). Bars represent SED.

Table 2. Broken-stick analysis of bulb initiation of three onion cultivars (HR1, HR2 and RC) over increasing growing degree days (GDD).

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

11.5 h photoperiod suggests that variations may exist with respect to bulb initiation and formation under natural short day conditions. The plants can start bulbing under short day lengths (11.5 h), but would not form a bulb unless a critical day length is attained. Instead, they remain vegetative and produce thick-neck bulbs. Similar observations were made by Uzo and Currah (1990) who reported that under short day conditions, onion plants produced new leaves indefinitely without bulb formation while at longer day lengths bulbs were formed. Thus,

Table 3. Broken-stick analysis of bulb initiation of three onion cultivars (HR 1, HR 2 and RC) over increasing GDD.

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

Table 4. Broken-stick analysis of bulb initiation of three onion cultivars (HR 1, HR 2 and RC) over increasing GDD.

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

under natural short day conditions, day lengths shorter than a certain minimum value may cause plants to remain continually vegetative and no bulbing will occur. The bulb ratio increased at the 25/12°C earlier than at the 30/15 and 35/18°C. It would be expected that growth under cooler conditions (25/12°C) would result in production of thick-necked (poor quality) onions. Wickramasinghe et al. (2000) found that at the lowest (17 to 22°C) temperatures tested, bigger bulbs with thick necks were produced. This may be due to changes in bulb structure at low temperature.

At the 12 h photoperiod, temperature induced variation in bulb growth (Table 3). The 25/12°C temperature resulted in quicker induction of bulbing compared to 30/15 and 35/18°C. Bulb induction was significant in HR 1 under the cooler temperature. The HR 1 cultivar had earliest bulbing at 353 GDD (bulb ratio of 1.8); earlier than HR 2 and RC (Table 3). Once the bulbing process was initiated, increased temperature increased rate of development. The 12 h photoperiod was a photoperiodic inductive phase for Eritrean cultivars. There were significant regressions ($P< 0.05$) when modeling growth curves of the onion cultivars on the GDD values (200, 240, 320) (Table 3).

At the 12.5 h photoperiod, temperature induced variation in bulb growth of cultivars. The growth trend of cultivars was similar for the different temperatures (Table 4). The cultivars started bulbing at 346 GDD. Generally, under cool temperatures, the photoperiodic response of cultivars to onset of bulbing occurred more rapidly at 12 h photoperiod than at 12.5 h photoperiod. It is not surprising that the 12.5 h photoperiod did not cause bulbing to occur more quickly than at 12 h photoperiod. This might be due to interaction effects between Photoperiod and temperature which affect readiness of onions to respond to external stimuli (Jones and Mann, 1963). There were significant regressions ($P<0.05$) when modeling growth curves of the onion cultivars on the GDD values (200, 300, 320) (Table 4).

The thermal time presentation of development of bulb ratio indicate that the cultivars were sensitive to temperature. However, plants should be exposed to a

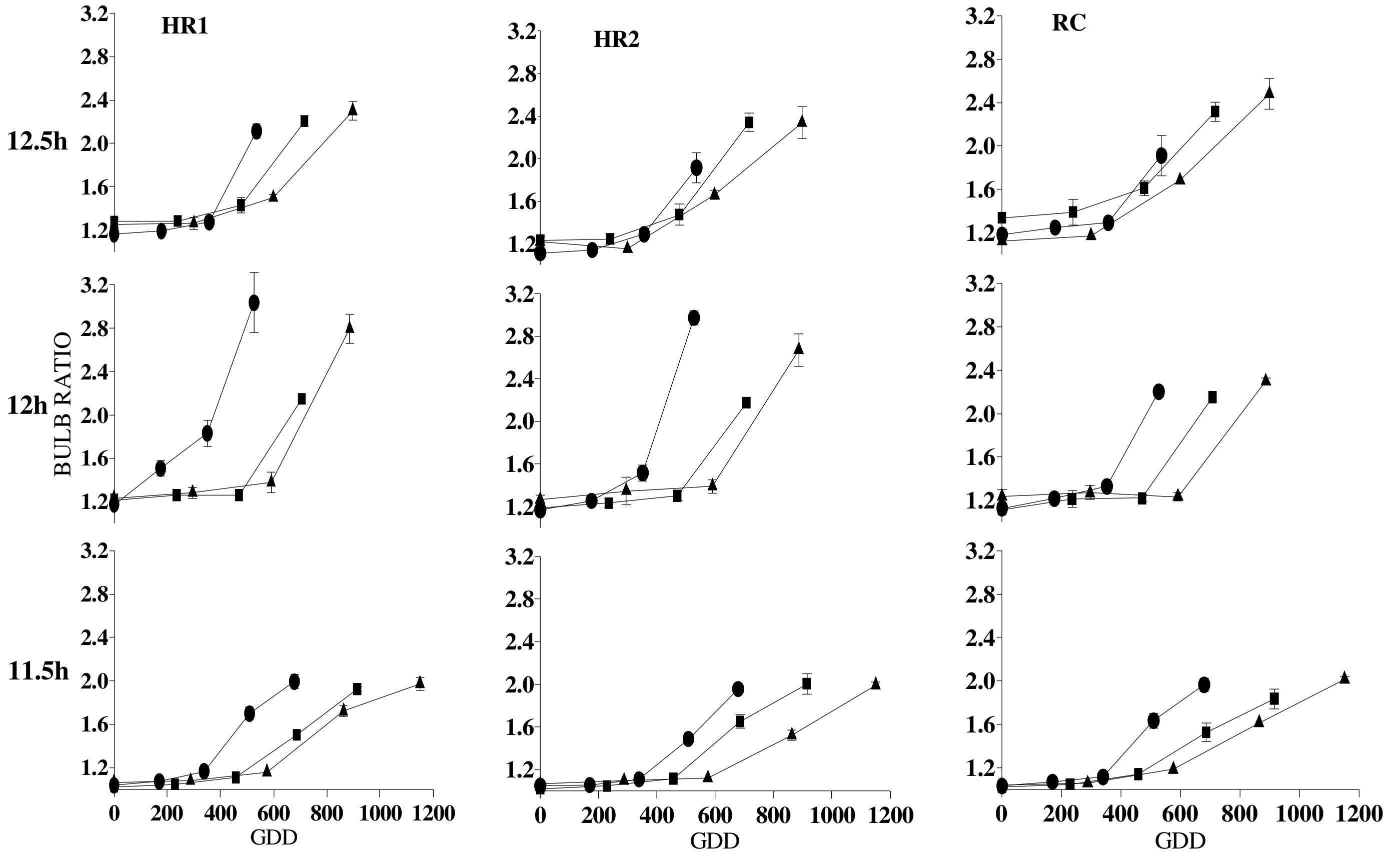

Figure 4. Bulb ratio of onion cvs. HR 1, HR 2, and RC grown under photoperiods of 11.5, 12, 12.5 h and temperature regimes of 25/12 (●); 30/15 (■); and 35/18°C (▲) over growing degree days (GDD). Bars represent SED.

minimum Photoperiod to produce bulbs. The combined effect of Photoperiod and temperature induced bulbing of cultivars, as indicated by the inflection points using a broken-stick regression technique, before a bulb ratio of 2.0 was achieved (Figure 4). There was no clear variability in initiation of onion bulbing between the cultivars tested.

Bulbing of the onion cultivars was regulated more by temperature than photoperiod as determined by GDD. This agrees with Abdalla (1967), Robinson (1973), and Currah (1985) who reported that bulbing of onions in the tropics is regulated more by temperature than day length. However, in those studies, temperature measurements did not consider the effect of base temperature. In addition, the broken-stick regression model was able to pinpoint the onset of bulbing with respect to GDD. All cultivars responded in a similar manner to the Photoperiod and temperature combinations. In conclusion, this study demonstrates that short day variations in day length under natural short day conditions may influence bulb initiation and development in "short day onion" plants. Growing degree days and the use of broken stick regression provide a novel approach that can be used to gain insights on the relationship between growing degree days, bulb initiation and development in "short day onion" plants under natural short day conditions.

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