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Flowering of *Heliconia angusta*

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University of Hawaii, 1992

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Ann Arbor, MI 48106

FLOWERING OF *HELICONIA ANGUSTA*

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF

THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT

OF THE REQUIREMENT FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN HORTICULTURE

DECEMBER 1992

By

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I would like to thank Mrs. Charlotte Yamane of Koolau Ranch Farm for providing her monthly harvest data of *H. angusta* without which I could not validate model for flower initiation and flowering of *H. angusta* in Honolulu.

ABSTRACT

The minimum daylength requirement for flower bud initiation in H. angusta was 13 hr for 7 weeks. Anatomical analysis of shoot apex also confirmed transformation of vegetative apex to reproductive apex under daylengths 13 hr or longer. In daylengths longer than 13 hr, the differences in daylength had no significant effect on flowering time which was 16 weeks after long-day treatment. Longer duration of treatment produced more flowers. The number of shoots per pot had negative relationship with number of flowers showing mutual shading effects of leaves and pseudostems. Length of flower stalk had a positive correlation with the number of bracts.

The effect of environmental factors on flower development was investigated. Daylengths of 12, 14, 16, 18 hr had no effect on time to flower after initiation or number of flowers, but plants grown in 18 hr produced longer flower stalks. Night temperature had a significant effect on the number of flowers, or flower quality. Differences in light intensity during flower development had no effect on flowering time, but flower numbers per pot and length of flower stalk were increased with an increase in light intensity.

Leaf elongation pattern was analyzed using growing degree day (GDD) units. An S-curve equation

($y=a/(1+e^{-b-k*x})$) better described the leaf elongation patterns than linear and negative exponential curves. The GDD unit requirement based on daily average temperature with a base temperature at 14°C from shoot emergence to leaf 3 and 4 expansion was 677-745 (42-54 days) and 930-992 (66-72 days) respectively. The average of elongation rates in leaves 1 to 5 was 25.4 mm/GDD and 3.8 cm/day.

A model based on Honolulu daylength conditions including civil twilight showed that potential flower bud initiation under daylengths 13 hr or longer would be March 28-July 30, flower development would be May 16-December 5, and flowering time would be August 30-January 7. Validation with monthly harvest data from a commercial grower showed that 99.6% of flowers were harvested within the predicted flowering period. Based on Honolulu daylength and accumulation of GDD units calculated from weather data (from January 1, 1962 to December 31, 1991), the late possible shoot emergence dates for stems with fully expanded leaf 3 to initiate flower bud under daylengths of 13 hr or longer would be June 16-28.

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CHAPTER 1. INTRODUCTION

1.1. Botany and horticulture

Heliconias in the family Heliconiaceae in the order of Zingiberales (Tomlinson, 1969) are perennials with a sympodially branched rhizome system having distichous scale leaves. Leaves are alternate and their overlapping bases and sheathes form a pseudostem. Inflorescences are borne terminally on these erect shoots (Criley, 1985).

Most of heliconia species are found in the tropics and subtropics where they are pollinated mostly by nectar-feeding hummingbird or by bats (Kress, 1985 and 1990). The phenology of flowering, nectar, and color or shape recognition by these pollinators were used for identification of the pollinator species or of the heliconia species (Stiles, 1979; Wooton and Sun, 1990).

Heliconias can be propagated by seeds (Montgomery, 1986; Carle, 1990). In practice, they are usually propagated vegetatively by dividing pseudostem clumps into smaller clumps of 1 or 2 pseudostems (Broschat and Donselman, 1983a; Donselman and Broschat, 1986 and 1987; Criley, 1989a).

Insects give serious problems. Aphids are the most common pest on H. psittacorum feeding on nectar (Broschat and Donselman, 1983a). Recently heliconias were discovered

to be a carrier of one pathover of P. solanacearum which can cause Moko disease of banana (Ferreira, 1990).

Postharvest life of cut heliconia flowers differs among species. H. psittacorum has about 2-3 week postharvest life (Tjia and Sheehan, 1984). No further opening is to be expected once the flowers are cut (Nau, 1991). Various types of floral preservatives supplied to cut heliconia flowers did not improve postharvest life (Tjia, 1985; Ka-ipo et al., 1989)

The bracts contain liquid, so insects can easily infest flowers. Thorough cleaning with some chemicals before shipping was recommended (Hansen et al., 1990). Bract liquids in H. imbricata are actively secreted by plant (Bronstein, 1988) and may protect submerged flowers from herbivory (Wootton and Sun, 1990).

1.2. Status of heliconias in cut flower industry

Heliconias, having colorful bracts and florets, are grown for cut flowers, potted plants, and interiorscape and landscape materials. The number of commercial growers in Hawaii increased gradually during 1980's. The high prices in the flower market and fast growth rate of heliconias led to this increase. In 1990, the wholesale value of heliconias in state of Hawaii was 1.34 million dollars which was 1071 % of the value in 1985 (Hawaii Agr. Stats. Serv.,

1991), the year production of heliconias was first separated out as an individual cut flower crop.

1.3. Research

Heliconia angusta shows a seasonal flowering pattern which has a peak of bloom around Christmas season and so is called Christmas heliconia or Holiday heliconia, although shoot emergence is not seasonal.

It was first suggested by Criley(1985) that there might be a photoresponse in 'Holiday' heliconia. The work of Lekawatana(1986) indicated that flower initiation occurred under long-day (LD) conditions. The minimum number of leaves to respond to photoperiodic stimulus was three.

This LD requirement for flower bud initiation was further confirmed by Sakai et al.(1990a). In their study on the relationship between time of shoot emergence and flowering, only those shoots which emerged before August flowered. Based on this, they suggested that the critical day-length required for flower bud initiation be 13.3 hr because the day-length near the end of July is about 13.3 hr including morning and evening civil twilight.

Several environmental factors may affect flower development process of heliconias. In H. angusta, flower development seemed not to be affected by daylength (Lekawatana, 1986). Although Lekawatana(1986) and Sakai et al.(1990a) reported some aspects about flowering in H.

angusta, the minimum LD requirement for flower bud initiation and the effect of environmental factors such as light intensity or temperature on flower bud development have not been fully studied so far.

The objectives of this study were to investigate:

1. The minimum LD requirement for flower bud initiation.
2. The effect of environmental factors on flower bud development.
3. Potential flower initiation and flower development and flowering period in Honolulu.

The results of this study may be helpful for commercial growers to predict flowering time or plan off-season flower production because H. angusta blooms over too short a period and growers want to extend the flowering period.

CHAPTER 2. LITERATURE REVIEW

2.1. Introduction

From the point of basic biology, plant scientists have given much attention to flowering because this is the first step towards reproduction. Interest in this developmental process has a strong economic basis, too, since many aspects of agronomic and horticultural crop production are intimately associated with flowering (Jacob, 1977).

The strong seasonal flowering pattern in heliconias led scientists to suggest a dry-wet cycle control of flowering (Stiles, 1979). But in Hawaii, where no distinctive dry-wet cycle is present, there are still seasonal flowering patterns. Other environmental factors might be involved in this process (Criley, 1985).

2.2. Environmental factors affecting flowering

2.2.1. Light intensity

2.2.1.1. Effect of light on heliconias

Most heliconias are grown commercially in open field situations. In the USA, Hawaii and Florida are the major production states. Flower production can be achieved throughout the year in heated greenhouse in Florida (Broschat et al., 1984).

In their natural environmental habitat condition, heliconias grow best in forest clearings, with the number of flowering stalks decreasing as light intensity decreases (Stiles, 1979). Although most heliconias are grown commercially in open field situations, bract color in some species may be stronger under light shade (Criley, 1989).

In case of H. psittacorum, light intensity is a limiting factor in flower production. H. psittacorum grown in full sun produced three to four times more flowers than plants in 63 % shade (Broschat and Donselman, 1983a). Mutual shading by leaves and pseudostems reduces the light intensity and limits flower production in this species. Annual flower production of this species in heated green houses having about 80 % light transmittance in Florida was actually lower than that produced outdoors under suboptimal temperature conditions due to the reduced light intensity in the greenhouses during the fall through spring months (Broschat and Donselman, 1988).

Shoots of H. psittacorum x 'Parrot' in Hawaii were produced more in July to September than the other months of the year. Shoots which developed during summer produced more flowers. Greater production of flowers in summer appeared to result from a factor of greater total sunlight or higher temperature or accumulation of both factors (Manarangi et al., 1988).

In the case of container culture for heliconias, Ball (1987) recommended 30 to 40 % shading for H. angusta cv. Holiday in contrast to H. psittacorum X latispatha or H. psittacorum cv. Andromeda because 'Holiday' burns under full sun.

As there is no report regarding direct relationship between light intensity and flower bud initiation in heliconias, greater flower production might be due to increased overall number of stems and growth of whole plants under the stronger light intensity.

2.2.1.2. Effect of light on other ornamental plants

There have been various reports regarding effect of light intensity on different ornamental plants. In contrast to heliconia plants, a direct relationship between light intensity and flower bud initiation was reported in some other plants.

In woody perennials, flower initiation occurs towards the exterior of the leaf canopy, rarely at the interior: e.g., flower initiation was inhibited in apples when the incident light was reduced by 80 %. a level normally found about 1 meter into the canopy (Cain, 1971). The minimum radiant energy requirement for flower initiation varies widely among species. Flower initiation in day-neutral W-38 tobacco cultivar requires a radiant energy input about

1/20 that for the SDP, bougainvillea, and about 1/2 that of the LDP, fuchsia (Sachs, 1987)

Light intensity has also been implicated in the control of flowering in Leucospermum. Heavy shading during summer prevented flower bud initiation while factors leading to flower bud initiation were suggested to be prevalent at high light intensities (Jacobs, 1983). Low light intensity reduced flower quality (Jacobs and Minnar, 1980), and floret initials began to develop under the influence of high light intensities and short daylengths (Jacobs et al., 1986). Shading plants during the reproductive phase caused a rapid loss in responsiveness to inductive short days, but this shade induced loss in responsiveness was enhanced by growth regulator GA_3 and ethephon treatment (Napier and Jacobs, 1989).

In case of cut flowers, shade affected yield and stem length in field grown plants and responses within a species differed among cultivars. Plants grown in 55 % or 67 % shade treatments for 3 to 5 years had longer flower stems than those grown in ambient irradiance: however, yield was dependent on species (Armitage, 1991). Yield of annual species Centaurea americana Nutt. 'Jolly Joker', cultivars of bulbous plant Zantedeschia, and perennial Eryngium planum declined linearly with reduction in irradiance. In contrast to these plants, yield of

Echinops ritro L. 'Taplow Blue' was higher in 67 % shade condition. Flower yield of some cultivars of Anemone coronaria L. 'De Caen' were not affected at all by shading.

High irradiation is associated with increased flower production in most self-inductive plants in which flowers are initiated autonomously in every growing shoot after a certain number of leaves have been formed (Halevy, 1987). Flowering in roses (Halevy, 1987), geranium (Armitage and Weltzstein, 1984), and carnations (Bunt, 1973) is increased or hastened as irradiance was increased. In the case of roses (Halevy, 1987), low irradiance causes a reduction in flowering mainly because of an increase in flower abortion. This response has generally been attributed to the effect of light on photosynthesis. Light was also shown to increase sink strength of rose flower buds (Zieslin and Halevy, 1975)

In Achimenes, three cultivars, 'Flamenco', 'Hilda', and 'Rosenlife' grown in 8, 6, or 24 hours of irradiance (213 μ mol $s^{-1}m^{-2}$) showed that increasing duration of illumination increased rhizome dry and fresh weight and did not much affect on flower weight (Vlahos, 1991b). In case of pot chrysanthemum production, supplemental lighting using high intensity discharge lamps was used often in greenhouses (Hickleton, 1984). Photosynthetically active radiation (PAR: 77, 148 and 231

μ mol $s^{-1}m^{-2}$) provided in commercial greenhouses has improved quality and productivity of flowers grown (Hickleton, 1985).

Providing shade is an effective means of reducing irradiance, but low irradiance has also been shown to increase internode elongation (Armitage et al., 1990).

2.2.2. Temperature

2.2.2.1. Effect of temperature on heliconias

As tropical plants, heliconias are found from sea level to 2000 m with the greatest numbers of species occurring at middle elevations (500 to 1000 m), and there is considerable latitudinal distribution of heliconia species representing a range of 20 to 28 °C (Smith, 1968 and 1977; Stiles, 1979).

Optimum temperature for cut flower production varies, but it was suggested by Broschat et al.(1984) that 21 °C was minimum temperature for H. psittacorum species, with increased production up to 35 °C. H. stricta cv. Dwarf Jamaican and H. angusta cv. Holiday will grow and flower at 15 °C although plants grow better at higher temperature than 15 °C (Lekawatana, 1986; Ball, 1987).

In Florida, temperature is a major limiting factor in the production of H.psittacorum. Decreasing temperature from 21 to 10 °C decreased growth and flower production, and at 10 °C, plant growth and flower production all stop.

At this temperature, cold injury symptoms first appear on the floral rachis, but the entire inflorescence blackens and necrosis on the foliage follows if the temperature becomes cooler than 10 °C. Pseudostems are apt to be injured at freezing temperature, but rhizomes may survive 1-2 °C colder temperature than pseudostems (Broschat and Donselman, 1983a).

While no heliconia species is reported to start flower bud initiation in response to a temperature stimulus, increasing temperature indirectly increases flowering rate due to an increased overall growth rate of plants. In H. psittacorum, increasing the minimum temperature from 15 to 21 °C produced more stems as well as the number of flowering stems per unit area in Denmark. In addition, flower quality and stem length was also improved markedly (Geertsen, 1989). A similar result was obtained in H. aurantiaca Ghiesbr. ex. Lemaire. Raising the temperate increased the flowering percentage by 20 % and length of flowering stems by 20 cm (Geertsen, 1990).

In the study of relationship between time of pseudostem emergence and flowering for seasonality of flowering in H. angusta cv. Holiday, the rainfall pattern and mean monthly temperature in Hawaii did not show any significant effects, therefore, these two environmental factors were excluded as possible determinators of flowering in H. angusta in Hawaii (Sakai et al., 1990a).

2.2.2.2. Effect of temperature on other ornamental plants

In some tropical plants, flowering occurs subsequent to rainfall wherein significant decreases in leaf temperature have been recorded. It has been suggested that an internal hormone is triggered to overcome dormancy (Alvim, 1960) or through a relief of water stress (Croat, 1969; Opler et al., 1976). Alternatively, it was suggested that rainfall may make possible of culmination of flower development processes initiated by photoperiod (Criley, 1985).

In some other plants, soil temperature rather than air temperature plays more important role in flowering. In case of Alstroemeria hybrida, cool air temperature (20 °C) increased flower yield more than warm temperature (24 °C), but a combination of warm air temperature and cooled gravel substrate around rhizome area produced the highest yield of flower in cultivar 'Monika' (Keil-Gunderson et al., 1989), and 'Regina' (Healy and Wilkins, 1986).

In case of Aeschynanthus, constant temperature promoted rapid flowering but fluctuation of temperature enhanced the flowering percentage (number of stems flowered per total number of stems) in cultivar 'Koral' (Whitton and Healy, 1990). But fluctuating temperature did not show any significant effect on time to flower or number of flowers in geranium (Gagnon and Dansereau,

1992). In case of Achimenes, an increase in temperature from 17 to 25 °C increased plant height, number of nodes, number of flowers, and shortened time to anthesis (Vlahos, 1991b) but increased daylength had no effect (Vlahos, 1991a).

2.2.3. Daylength

2.2.3.1. Effect of daylength on heliconia

Species such as H. psittacorum, H. hirsuta, H. chartacea, H. episcopalis and some cultivars of H. stricta and H. bihai show year round flowering under suitable light intensity condition and are not generally considered to be photoperiodic plants (Broschat and Donselman, 1983b; Criley, 1989). But, many other species show seasonal flowering patterns and photoperiod might be involved in controlling of flowering.

Observation of seasonal flowering pattern of Heliconia angusta led to Criley(1985) to suggest a possible photoresponse to this species. Lekawatana(1986) indicated that flower bud initiation occurred under long-day condition. Differences in daylength had no significant effect on the time to flower or number of flowers. A minimum of 3 leaves per pseudostem was required to respond to LD photoperiodic stimulus. Sakai et al.(1990b) found that H. angusta initiated flowers during the longest days of the year. As no significant

difference in monthly rainfall or mean monthly temperature pattern was present in Hawaii, only photoperiodic stimulus was suggested for flower bud initiation. The study on the relationship between time of pseudostem emergence and flowering showed that only those pseudostems that emerged before August flowered in the winter. Based on these results, it was suggested that critical daylength required for initiation of flowering to be 13.3 hr because the daylength near the end of July is about 13.3 hr including morning and evening civil twilight (Sakai et al., 1990a).

The effects of photoperiod treatment on flower development in H. angusta were not significant on time to flower, length of peduncle and inflorescence (Lekawatana, 1986). Rather, time to flower had inverse relationship with the number of initial leaves per pseudostem. Shoots with fewer leaves flowered later than the shoots with more leaves.

In contrast to long-day plants such as H. angusta species, H. stricta cv. Dwarf Jamaican, H. wagneriana, and H. aurantiaca have been shown to initiate flowers under short days. In H. stricta Huber cv. Dwarf Jamaican, pseudostems with at least 3 leaves responded to 8 hr short daylength treatment (Criley and Kawabata, 1986).

In H. aurantiaca Ghiesbr. ex. Lemaire, plants subjected to 8 hr of short photoperiod had a greater

flowering percentage than plants subjected to 12 or 16 hr photoperiod (Geertsen, 1990), but the minimum photoperiod requirement for flower initiation was not studied.

2.2.3.2. Effect of daylength on other ornamental plants

Even when plants are subjected to otherwise favorable condition for flower bud initiation, there are many cases plants are unable to flower. The reasons why plants do not initiate flowers are insufficient leaf area in Cardamine pratensis (Pierik, 1967), unfavorable ratio of immature to mature leaves in tomato (Hussey, 1963), leaf insensitivity to daylength in beans, influence of the root system in apple, or meristem insensitivity to floral promoters in citrus (Kinet et al., 1985).

2.3. Modelling of plant growth and development

2.3.1. Introduction

In developmental studies, even such a simple measurement as dry matter weight can not be obtained without killing the plant, and one obviously can not cut microtome sections of a stem more than once. So many samples or parallel samples are used, and this procedure is very time consuming. The plastochron index concept was introduced to predict a certain phase of development of plant, but it was only applicable to vegetative shoot growth (Erickson and Michelini, 1957).

Biological systems are complicated, but their study becomes more tractable if they can be divided into main components and expressed in mathematics. Mathematical equations are essential tools in understanding of process of plant growth and development. They are simply formal, symbolic statement of a relationship between those quantities (Charles-Edwards et al., 1986).

2.3.2. Mathematical equations for modelling

Much biological research data are evaluated in the manner which one variable (y:dependent) depends on another (x:independent) variable. If this evaluation can be done by linear regression, it has advantage of being simple to fit to data and easy to understand causes and effects. However, linear relations seldom occur in nature, so nonlinear curve fitting was suggested (Landsberg, 1977). The exponential relationship of length, volume, area, weight with time continue until after emergence of the enclosing sheaths (cereals and grasses) and then decline, giving the familiar characteristic S-shaped curve. A number of useful mathematical equations have been used to describe the change of plant growth (y) with time (t); these include a modified monomolecular relation (Constable and Rawson, 1980), Gompertz equation (Amer and Williams, 1957), simple logistic equation (Clough and Milthorpe,

1975), generalized logistic equation (Landsberg, 1977; Dennett et al., 1978; Causton and Venus, 1981).

With personal computers within everyone's reach, crop modelling has become an acceptable and even a fashionable research activity in USA in last 10 years (Acock, 1988). Modelling of plant growth in horticulture gives us two major advantages: 1) economic gains for the crop manager and 2) increased information regarding plant growth (Hammer and Langhans, 1978).

In given time and resources, it is not possible to include all environmental factors such as light intensity, temperature, daylength, CO_2 concentration etc. in most models. Therefore, only a few important major parameters are being used in modeling (Weiss, 1981) in such ways of response surface technique or 3 dimensional analysis of interaction of many factors (Karlsson and Heins, 1986; Kraszewski and Ormond, 1986; Hopper and Hammer, 1991).

The concept of heat unit accumulation was introduced on the assumption that next phase of growth or development in plant occurs when the first heat accumulation reaches a certain level. The temperature giving the smallest coefficient of variation from a heat accumulation was chosen as an adequate base temperature (Arnold, 1959).

To increase the accuracy of this heat accumulation model, a series of modifications have been made. Inclusion of daylength (Madariaga and Knott, 1951; Reath

and Wittwer, 1952), measurement of air temperature at the crop height rather than ambient air temperature (Katz, 1952), and summation of hourly temperature instead of daily temperature (Lana and Harber, 1952) were introduced.

In addition to these modifications, temperature ceiling or so called temperature threshold was introduced (Madariaga and Knott, 1951; Perry et al., 1986). When maximum is greater than the given ceiling, then maximum was set equal to ceiling before summing the heat units.

When daily maximum and minimum temperatures are given, daily behavior patterns of temperature in air or soil were calculated through use of a truncated sine wave model (Parton and Logan, 1981) and the model was improved (Logan and Boyland, 1983; Wann et al., 1985). Various modified methods of growing degree day (GDD) were also used in the study to predict harvest time in collard (Dufault et al., 1989).

In ornamental plants, effect of temperature or irradiation integral on floral development was studied in Senecio x Hybridus (Larsen, 1988), in chrysanthemum (Karlsson and Heins, 1986), Tagetes patula (Armitage et al., 1981a), geranium (Armitage et al., 1981b; White and Warrington, 1984 and 1988), Alstroemeria (Healy et al., 1982; Lin, 1985), H. chartacea cv. Sexy Pink (Criley and Lekawatana, 1991), Leucospermum cordifolium cv. Vlam (Criley et al., 1990), and in bird of paradise (Kawabata,

1989). In vegetables, harvest time of collard (Dufault et al., 1989) and cucumber (Perry et al., 1989) was studied.

In addition of time prediction, leaf area in cherry (Eisensmith et al., 1982), chill requirement for completion of rest in peach trees (Richardson et al., 1974), plant growth rate in Zea mays (Aspiazu and Shaw, 1972) and Lycopersicon esculentum (Warnock, 1973), pest control and management (Wilson and Barnett, 1983), and yield of Solanum tuberosum (Yandell et al., 1988) have been studied using GDD models.

CHAPTER 3. MINIMUM LONG-DAY REQUIREMENT FOR FLOWER BUD INITIATION

3.1. Abstract

Five daylength treatments and five durations of each daylength treatment were combined to study the effects of daylength and duration on flower bud initiation. Daylength of 12.5, 13, 13.5, 14 hr, and natural daylength (11.6-12.4 hr) were used. Each daylength treatment was provided for 5, 6, 7, 8, and 9 weeks. The minimum daylength requirement for flower bud initiation was 13 hr for 7 wks. In this condition, anatomical analysis of shoot apex also confirmed flower bud initiation by showing the earliest transformation from vegetative apex to reproductive one. In daylengths longer than 13 hrs, the different daylengths had no significant effect on time to flower which was 16 wks after the end of LD treatment. Significantly more flowers were produced after 8 or 9 than 7 wks duration of LD. When durations of daylength treatment and flower development were combined, there was no significant difference in flowering times. The minimum number of initial leaves for flower bud initiation was three. Pseudostems with more initial leaves flowered earlier. There was a significant inverse linear relationship between number of pseudostems in pots and flowers produced indicating mutual shoot shading density

effect. The earlier initiation and longer duration of flower development enhanced the quality of flower in terms of length of flower stalk and number of bracts.

3.2. Introduction

Several heliconia species exhibit seasonal flowering patterns. It has been discovered that H. angusta initiates flower bud under LD photoperiod condition (Lekawatana, 1986). Sakai et al. (1990a) suggested that critical daylength for H. angusta to initiate flower bud in Hawaii was 13.3 hr.

The objective of this experiment was to study the minimum LD requirement in terms of daylength and duration of LD for flower bud initiation. The results from this experiment can be used as a basis to expand flowering period in H. angusta with artificial lighting.

3.3. Materials and Methods

This experiment was conducted at the Magoon greenhouse and Pope laboratory glasshouse facilities of the University of Hawaii. H. angusta plants were divided and potted in 16 X 13 cm pots in May, 1990. Eighty pots were used. The potting medium was a mixture of peat moss and perlite in 1:1 ratio in volume and amended with dolomite, Micromax (minor elements) and treble superphosphate at the rates of 6.0, 1.0, and 0.6 kg / m^3

respectively. These plants were again divided and potted in 200 16 X 13 cm pots in August, 1990. Plants were drip-irrigated automatically with nutrient solution. The fertilizer ratio in this irrigation was 200N-0P-223K (ppm), at the rate of 1000 ml per pot per day. When these repotted plants rooted and grew well, 147 pots with healthy and uniform plants were selected in October, 1990. The pseudostems with more than 3 leaves were cut off, so pseudostems with 1, 2, or 3 leaves could grow under daylength condition shorter than 12.5 hr including morning and evening civil twilight.

For the daylength treatments, plants were moved in Pope lab glasshouse on December 18, 1990, 2 weeks before long day treatment because the condition in Pope lab and Magoon greenhouse are a little different because Pope lab glasshouse had less paint on glass. Daylength treatments of 12.5, 13, 13.5, 14 hr and natural daylength were provided in five 170 x 150 x 180 cm compartments made of cardboard and black plastic film. Seven pots were placed in each daylength and duration combination, and 7 pots in natural daylength. The long days were given by supplementing natural daylength with incandescent illumination with 60 W lamp (470 lux) placed 1.6 m above the pots. The on and off time settings were 6:00 AM -6:30 PM for 12.5 hr, 6:00 AM-7:00 PM for 13 hr, 6:00 AM-7:00 PM for 13.5 hr, and 6:00 AM-8:00 PM for 14 hr of photoperiod.

The sides of compartments were raised only when supplementary light was given during night time. To enable the plants to receive equal amount of supplementary light, plants were regularly rotated within each compartment.

The LD treatments began January 4, 1991. Each daylength treatment was provided for 5, 6, 7, 8, and 9 weeks. After LD treatment for flower bud initiation, these treated plants were moved to Magoon greenhouse again. The results were analyzed as a factorial design of 5 factors of daylength and duration. As it was not possible to make compartments for each replication, each pot selected at one time in a combination of daylength x duration was considered as replication.

The number of initial leaves per pseudostem at beginning of daylength treatment), number of flowers (number of inflorescences), time to flower (flower appearance in the lowest bracts), number of stems per pot at flowering, number of bracts, and flower stalk length (length of total peduncle + inflorescence) were recorded.

An anatomical analysis of shoot apex (10 in each daylength and duration combination) was made to see when shoot apex became reproductive after LD treatment. FAA (formalin-acetoalcohol) was used for fixation. After FAA treatment, specimens were subjected to a tertiary butyl alcohol dehydration series and embedded in paraffin. The

thickness of materials cut with microtome was 20 μ m. For slide preparation, Haupt's solution with formalin was used as an adhesive and toluidine blue as a staining agent (Berlyn and Miksche, 1976).

3.4. Results

3.4.1. Daylength and number of flowers

There was a final population of 1344 pseudostems produced out of 1464 pseudostems because 120 pseudostems died during the experiment. Among these 1344 shoots, there were 754 shoots which had an initial leaf count of 3 or more and out of these 754 stems, 253 stems flowered. The average flowering percentage (# of stems flowered /# of stems with 3 or more initial leaves) was 35.9 %.

The effect of daylength on flower bud initiation as evidenced by number of flowers per pot is shown in Figure 1. The minimum daylength required for flower initiation was 13 hr for 7 wks. In daylength longer than 13 hr, the difference in daylengths had no significant effect on the number of pseudostems which flowered (Appendix Table 1).

Increased duration of LD treatment showed a tendency for higher numbers of inflorescences per pot. Flowers were not initiated with only 6 wks LD, while 7 or more wks provided sufficient stimulus. Flowering was not significantly affected by 8 or 9 wks of LD (Appendix Table 2).

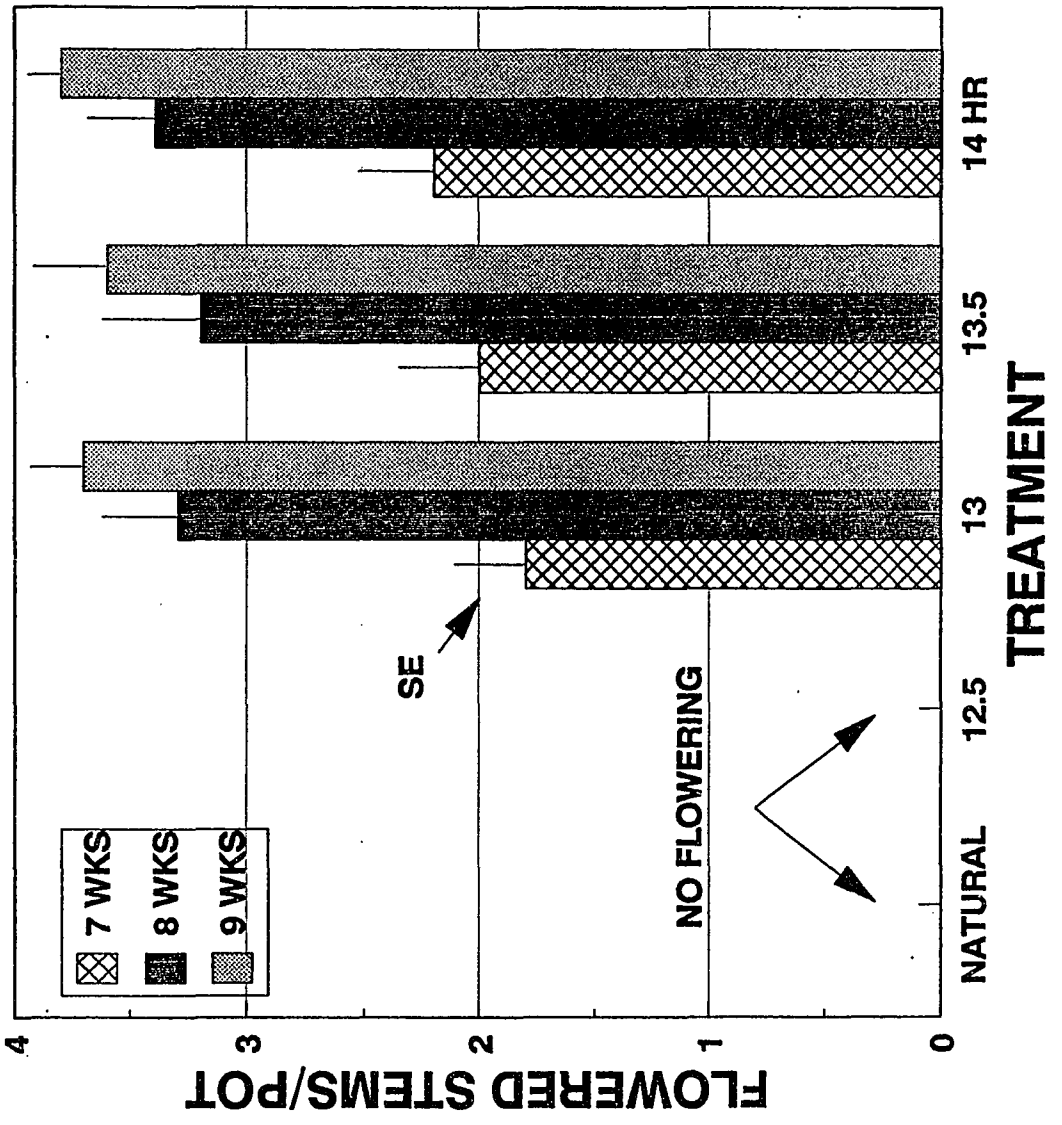

Figure 1. Effect of daylength and duration for flower initiation on number of flowers (inflorescence) per pot (16 x 13 cm) in H. angusta in Pope lab. (natural condition: 11.6-12.4 hr daylength)

3.4.2. Daylength and time to flower

The effect of daylength during flower bud initiation on flowering time is shown in Figure 2. No flowers were produced at natural daylength or the 12.5 hr daylength treatment. The average time to flower was 16.1 weeks after the end of treatment.

The earliest flowering time was 15.9 wks in 13 hr daylength. The difference in daylengths had no significant effect on time to flower (Appendix Table 3). This indicated that type of response of H. angusta to photo stimulus might be an absolute (qualitative) long day plant rather than facultative (quantitative) one because once daylength was longer than 13 hr, there was no significant difference in effect of daylength on flowering time.

The effect of daylength duration for flower initiation on flowering time is shown in Figure 3. In the conditions of 5 and 6 wks of daylength duration, pseudostems did not flower at all. The minimum daylength duration required for flower bud initiation in H. angusta was 7 wks. Among the LD treatments, duration of LD for 7 weeks or longer showed a inverse relationship between time to flower and duration of LD treatment (Appendix Table 4). As the weeks of daylength treatment increased, the time to flower became shorter. When weeks of daylength treatment

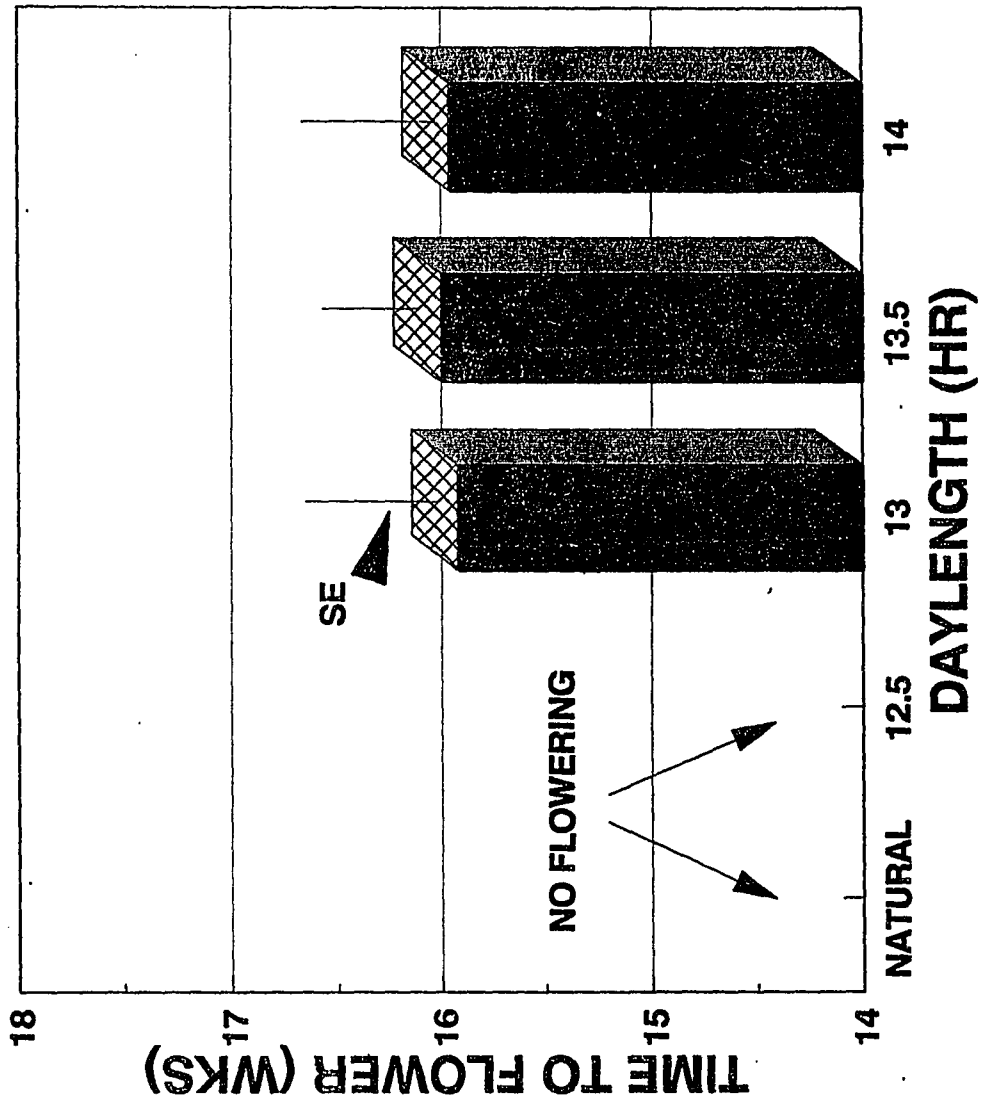

Figure 2. Effect of daylength for flower initiation on time to flower (appearance of flower in the lowest bract) after LD treatments in H. angusta in Pope lab.

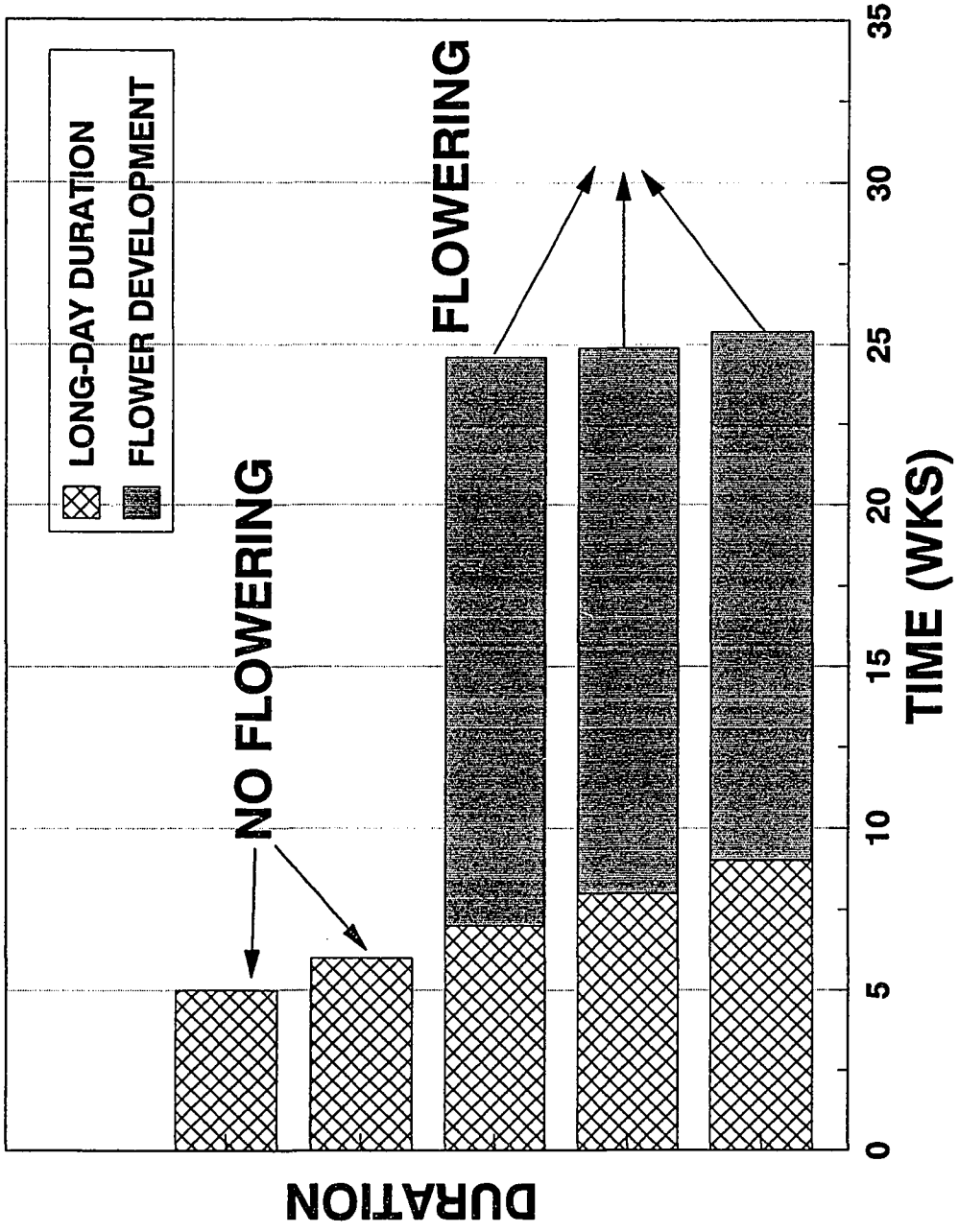

Figure 3. Effect of daylength duration for flower initiation on flower development period and flowering time in H. angusta.

and flower development were combined, there was no significant difference in flowering times.

3.4.3. Number of leaves and flowering

The effect of number of initial leaves per pseudostem on flower initiation as evidenced by flowering time is shown in Figure 4. The minimum number of leaves per pseudostem required for flower initiation was three. As the number of leaves increased, the time to flower decreased. However, in pseudostems with 4 leaves or more, number of leaves had no significant effect on time to flower (Appendix Table 5).

The effect of initial number of leaves per pseudostem on flower initiation as evidenced by flowering percentage is shown in Figure 5. Flowering percentage was calculated as number of pseudostems flowered per number of pseudostems in each category of 3 leaves or more because only these pseudostems showed flowering. Pseudostems with 4 leaves had the highest flowering percentage, 39.2 %, while pseudostems with 3 leaves showed the lowest flowering percentage, 7.6 %. In pseudostems with 4 leaves or more, flowering percentages were lower as initial leaf number decreased. The pseudostems with 5 or 6 leaves were not significantly different at 5 % level (Appendix Table 6).

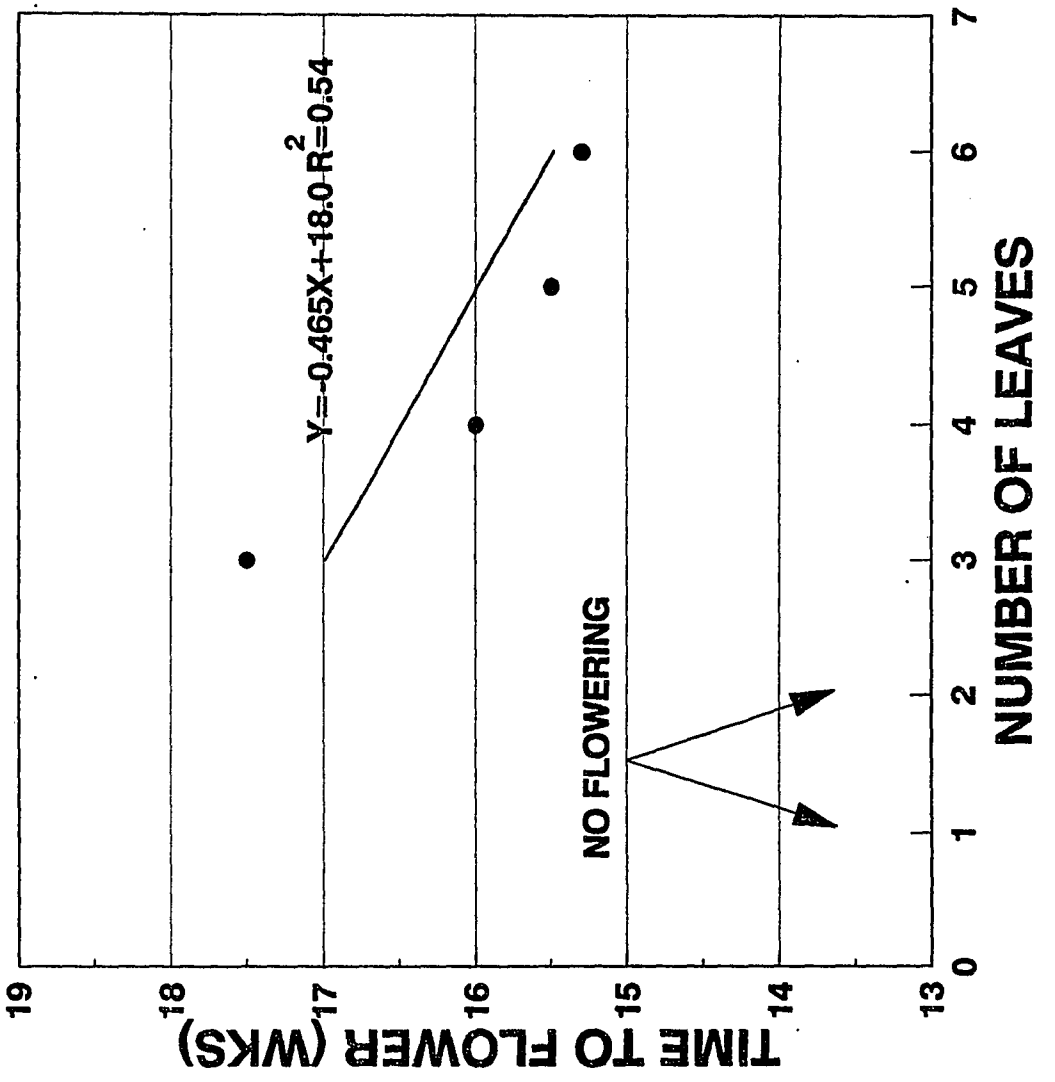

Figure 4. Effect of number of initial leaves per stem at beginning of LD treatment on flowering time (appearance of flower in the lowest bract) in H. angusta in Pope lab. (Leaf number: leaf 1=130, leaf 2=158, leaf 3=193, leaf 4=290, leaf 5=141, leaf 6=80)

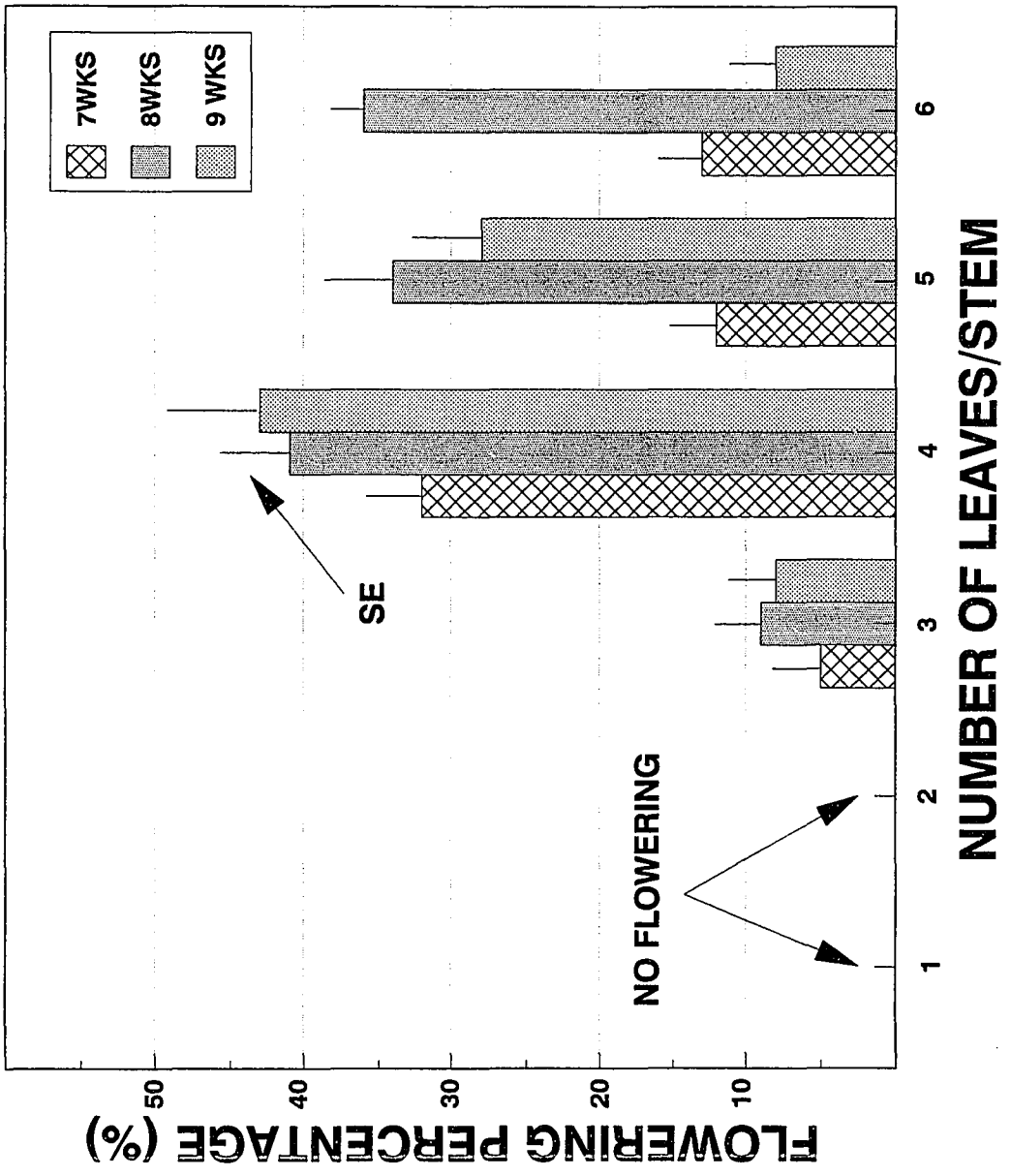

Figure 5. Effect daylength duration and number of initial expanded leaves per stem at beginning of daylength treatment on flowering percentage (number of stems flowered/number of stems with 3 or more leaves) in H. angusta.

3.4.4. Number of pseudostems per pot and flowering

The effect of number of pseudostems per pot at the beginning of LD treatment on flower count is shown in Figure 6. There was no significant effect of number of pseudostems on flowering in different daylength or duration of treatments. But within each treatment, the number of pseudostems per pot varied from 12 to 20. It was observed that pots with fewer pseudostems produced more flowers. Regression analysis showed that there was a negative linear relationship between number of stems and flowers (Appendix Table 7). A population of 20 pseudostems per 16 x 13 cm pot was very dense and may have caused severe competition among pseudostems resulting in insufficient amount of assimilates for full flower development.

3.4.5. Daylength and length of flower stalk

The effect of daylength on length of flower stalk in H. angusta is shown in Figure 7. Plants initiating flower buds under daylength of 13.5 hr had the longest flower stalk, 51.3 cm, whereas, plants initiated flower buds under 14 hr daylength had the shortest flower stalk, 48.5 cm. The difference of length of flower stalk among different treatment means was not significant at 5 % level (Appendix Table 8).

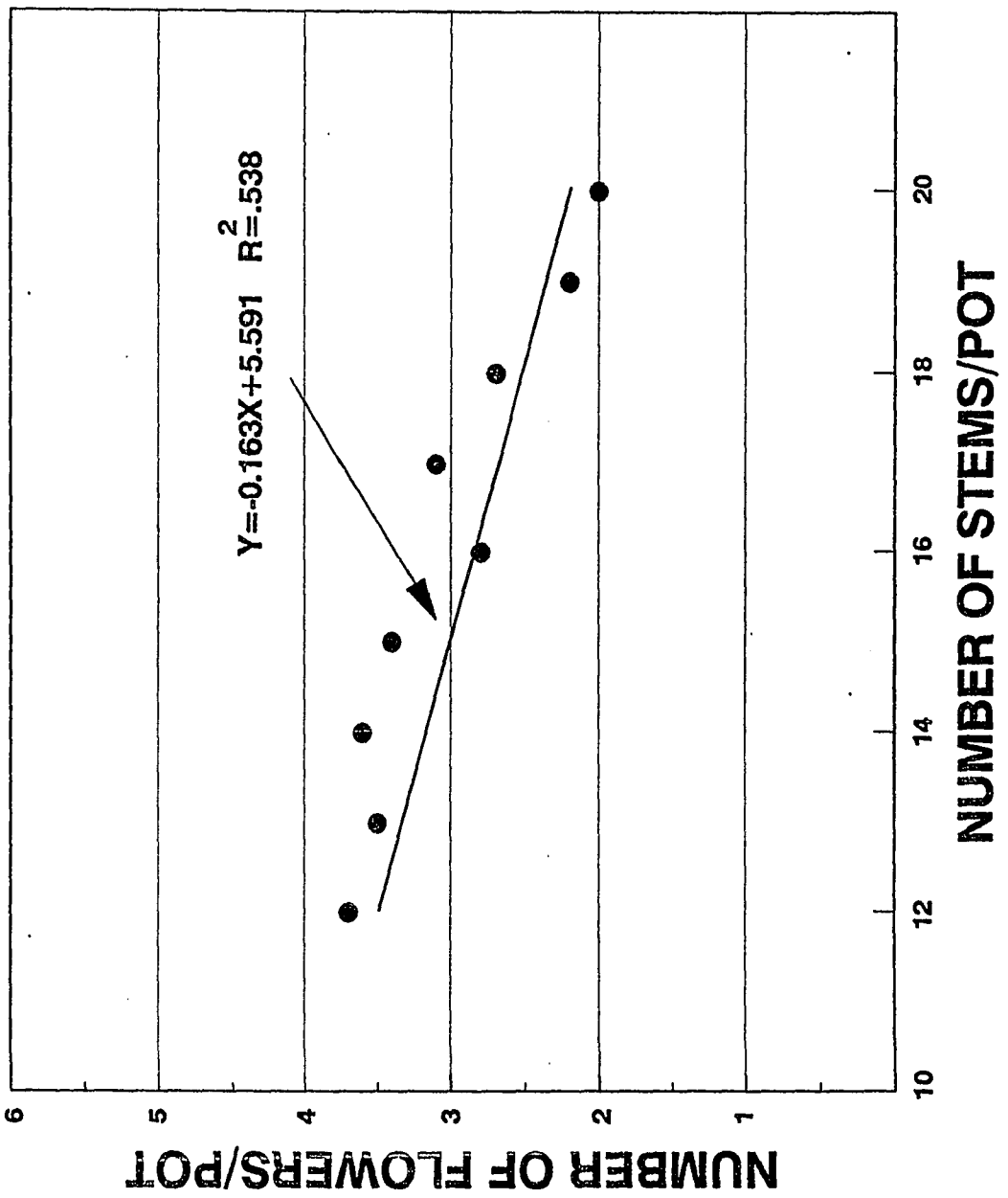

Figure 6. Effect of initial number of stems per pot (16 x 13 cm) at beginning of daylength treatment on flowering percentage in H. angusta.

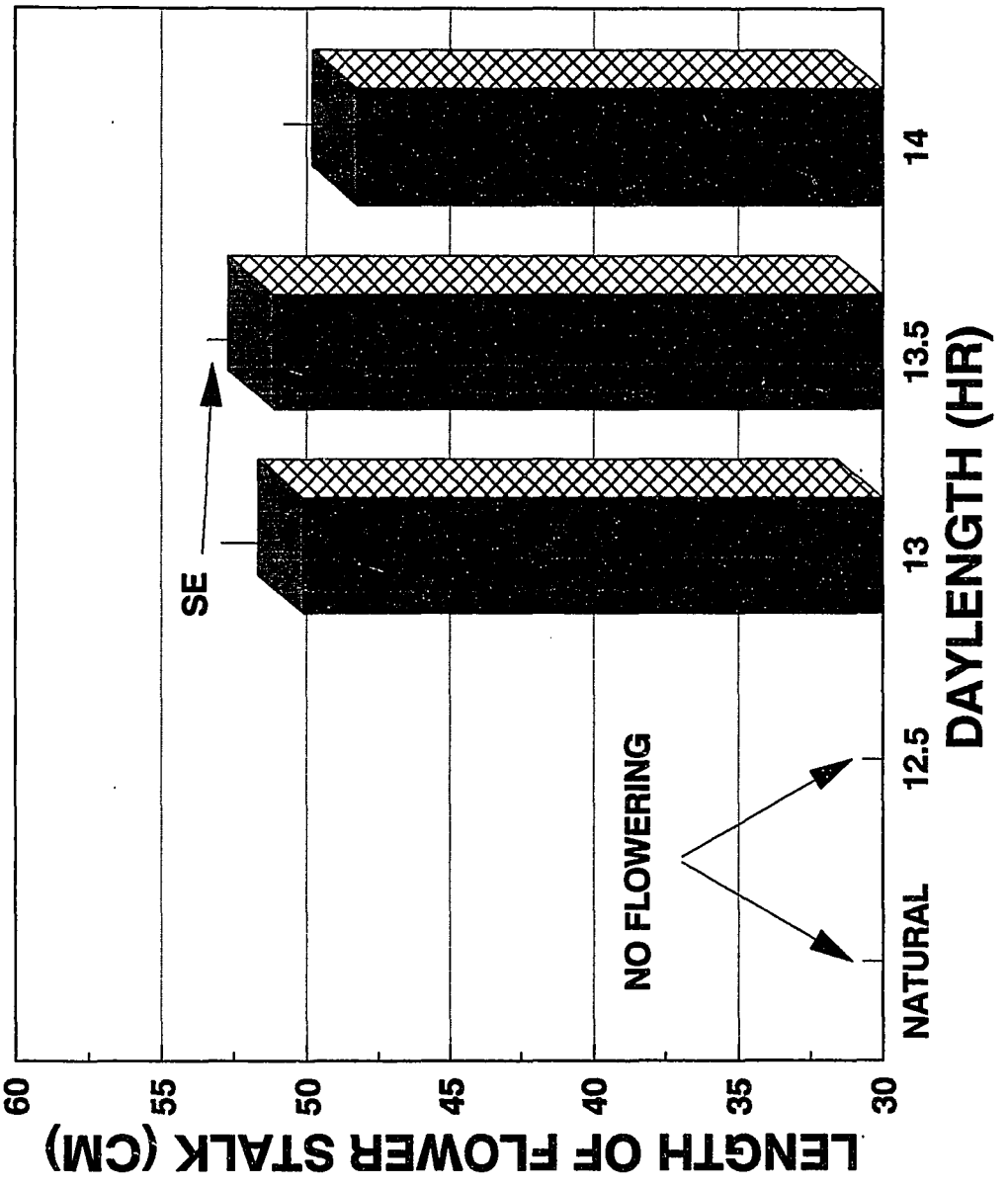

Figure 7. Effect of daylength for flower initiation on length of flower stalk (total length of peduncle + inflorescence) in H. angusta.

3.4.6. Relationships between duration of LD, flowering time, leaf number, and length of flower stalk

The effect of weeks of LD treatments for flower bud initiation on length of peduncle and inflorescence in H.angusta is shown in Figure 8a. Plants grown under 7 wks LD duration showed the longest flower stalk, 52.8 cm. As the duration of LD decreased, the length of flower stalk was significantly increased (Appendix Table 10).

The relationship between time to flower and length of flower stalk in H. angusta is shown in Figure 8b. The pseudostems which took longer time to flower had longer flower stalks as compared to those pseudostems which flowered earlier. The correlation analysis showed a significant positive relationship between length of flower stalk and flowering time at 5 % level (Appendix Table 10).

Number of leaves per stem had significant effect on length of flower stalk (Fig. 8c). There was a tendency that the stems with fewer initial leaves produced longer flower stalk than the stems with more initial leaves. The regression analysis showed a significant positive relationship between initial leaf number per stem and length of flower stalk at 5 % level (Appendix Table 11).

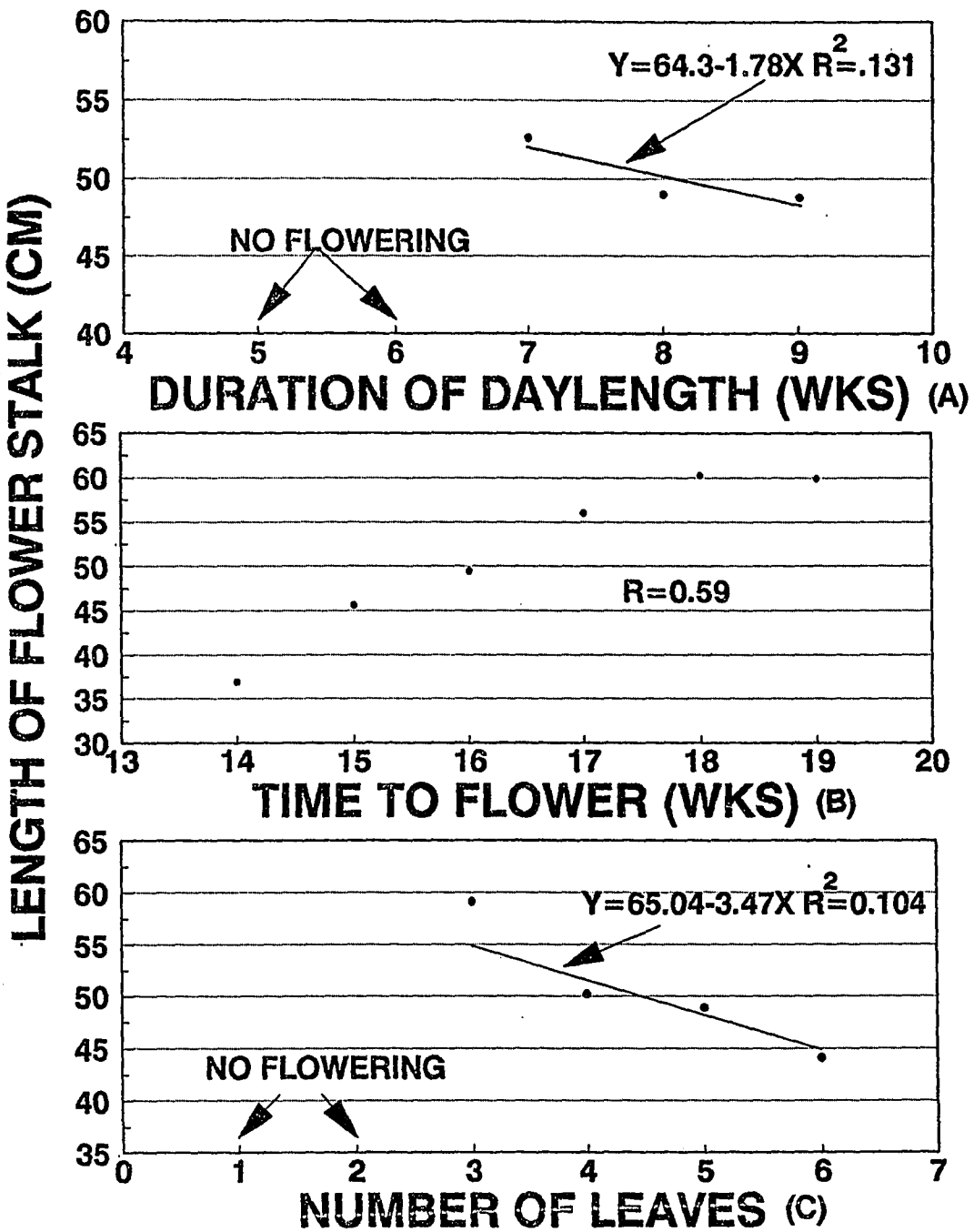

Figure 8. Effect of daylength duration(A), flowering time(B), and initial number of leaves(C) at beginning of LD treatment, on length of flower stalk (total length of peduncle + inflorescence) in H. angusta.

3.4.7. Relationship between flower stalk length and number of bracts

Relationship between length of flower stalk and number of bracts is shown in Figure 9. The longest flower stalks had approximately one more bracts than shorter ones. There was a significant linear correlation (Appendix Table 12).

3.4.8. Status of shoot apex

Results of anatomical analysis of shoot apexes collected from a combination of LD x duration treatment are shown in Table 1. Plants grown under daylength of 12.5 hr had only vegetative shoot apexes (Fig. 10A). In treatments with daylength longer than 13.0 hr, the earliest day which shoot apex showed flower bud initiation (Fig. 10B) was 7 wks after beginning of LD treatments, thus confirming the results in Figure 1 and 2.

3.5. Discussion

During flower bud development, the flower competes for current assimilates with various other plant parts. In case of iris (Elphinstone et al., 1987) and gladiolus (Halevy, 1987), once the flower bud initiated, the relative specific activity of leaves or daughter bulbs as sinks decreased. Under normal environmental conditions, most of the assimilates were distributed to the flower bud

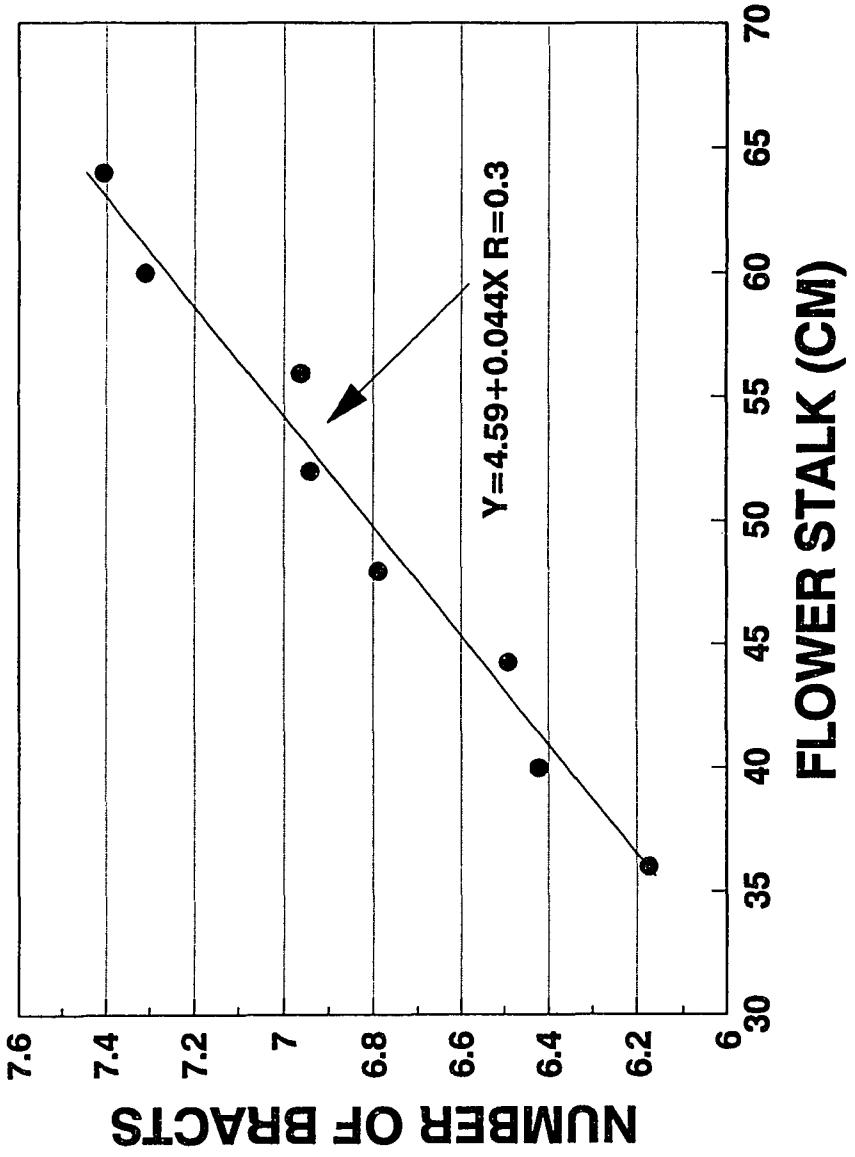

Figure 9. Linear correlation between flower stalk length and number of bracts in H. angusta. The total number of flower stalk was 253.

Table 1. Percentage of reproductive shoot apex after different daylength treatments for H. angusta flower bud initiation in Pope Lab glasshouse.

Duration WKS	Daylength treatment: Natural[y]	12.5	13	13.5	14 hr
5	0 %	0	0	0	0
6	0	0	0	0	0
7	0	0	30.5 A[x]	34.5 A[x]	33.0 A[x]
8	0	0	57.5 B	53.5 A	50.5 A
9	0	0	61.0 B	62.5 B	63.0 B

[x]Mean separation in columns by Duncan's multiple range test.
[y]Natural condition was 11.6-12.4 hr daylength during experiment.

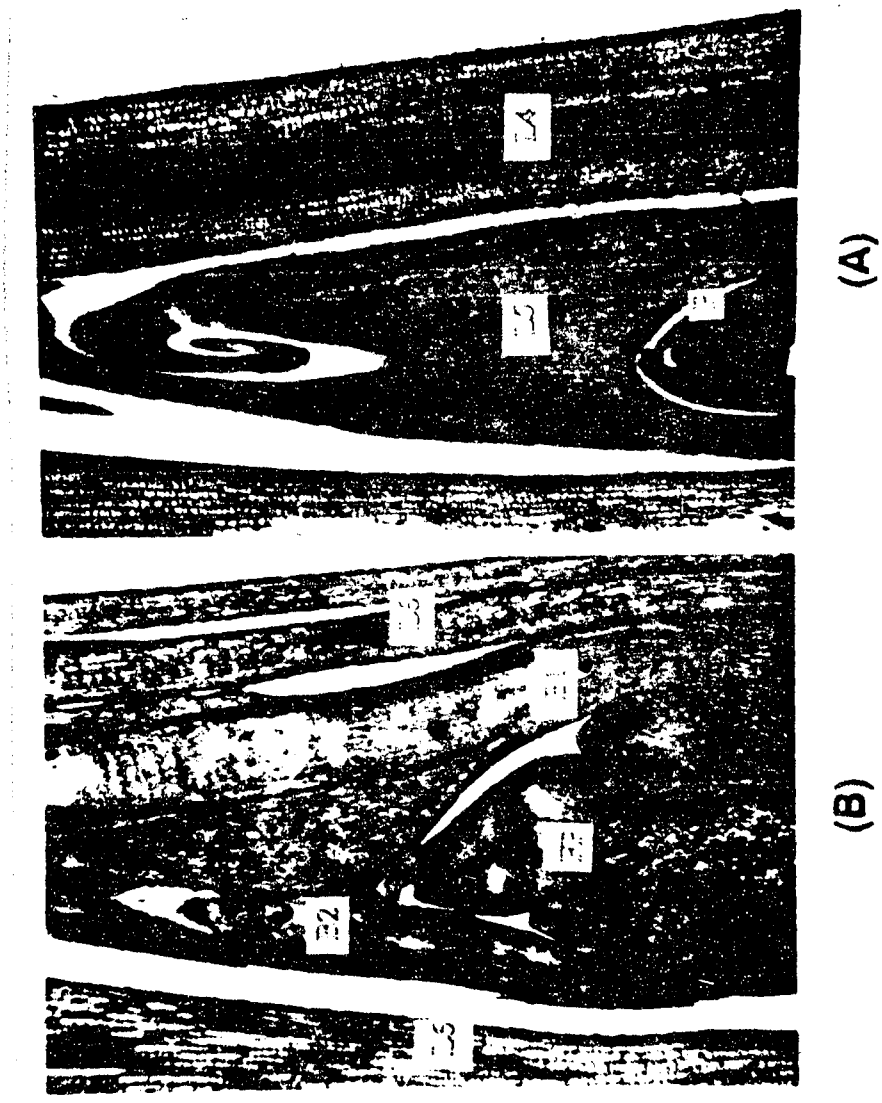

Figure 10. Longitudinal section of H. angusta shoot apex. A is a vegetative state under natural daylength condition (11.6-12.4 hr) and B is a reproductive state after 7 wks in 13 hr daylength. L:leaf number, p:leaf primodia, B:cincinnal bract, FP:flower bud primodia. (Magnification: 320 x)

to develop into flower but under stressful conditions the daughter bulbs received most of ^{14}C assimilates.

Plant growth regulators do not affect the photosynthetic activity or rate of plants but they act on sink capacity. Decreased abscisic acid activity in iris flower buds (Vonk and Ribot, 1982), or increased cytokinin level in shoots with developing flower buds in rose (Van Staden, 1981) increased flower bud development. Cytokinin applied to the flower bud in iris (Elphinstone et al., 1987) appeared to increase sucrose metabolism, thereby increasing the flower sink strength for sucrose.

The increase of flower stalk length in relation to duration of flower bud development (Appendix Table 10) appears to be mainly a result of a great supply of assimilates for a longer period. The inverse linear regression relation between the length of flower stalk and number of initial leaves per stem in H. angusta also indicates that flower quality in terms of length of flower stalk and number of bracts is dependent upon duration of flower bud development.

The minimum number of leaves per stem required for flower initiation was 3. The stems with fewer number leaves take longer time to flower as compared to the stems with more leaves because at later stages there is less competition for assimilates, as well as more assimilates. Thus development can be faster and elongation is less

because the inflorescences compete more successfully. All these results suggest that longer duration of flower development provides more assimilates than shorter duration thus flower quality in terms length of flower stalk and number of bracts because there was a significant positive linear correlation relationship between them enhances. Since it was observed that some long flower stalk had weak stems and the diameter of flower stalks were not measured, the relationship between length and degree of strength of flower stalks should be studied in the future.

There are important practical implications from these results. Since photoperiodic flower bud induction increases metabolic activity at the apical meristem in many species (Kinet et al., 1985), as evidenced by ^{14}C incorporation into flowers (Abou-Haidar et al., 1985), it is a good idea for flower growers to schedule production to initiate flower as soon as possible and allow a longer time for development under stronger sun light intensity to produce good quality of flowers. As for lengthening the daylength, it is good to give artificial supplementary lighting to plants when daylength are shorter than 12.5 hr because there was no experiment done between 12.5 and 13 hr daylength interval, so possibility of flower initiation between 12.5 and 13 hr daylength can not be excluded at all.

CHAPTER 4. THE EFFECT OF DAYLENGTH DURING FLOWER DEVELOPMENT

4.1. Abstract

H. angusta plants were grown in 4 different daylength treatments of 12, 14, 16, 18 hr after 16 wk of 16 hr LD treatment to study the effect of daylength during flower development. There was no significant effect of daylength during flower development on number of flowers per pot, although there was a non-significant trend for a longer time to flower as daylength became longer. In case of length of flower stalk, daylength had significant impact. Among the daylength treatments, a daylength of 18 hr produced the longest flower stalk, while for daylength shorter than 16 hr, the difference in daylength had no significant effect on length of flower stalk.

4.2. Introduction

Some heliconia species such as *H. angusta* and *H. aurantica* show seasonal flowering patterns, while other species such as *H. psittacorum*, or *H. chartacea* show year round flowering. In case of year round flowering species, the production of flowers differs from season to season indicating temperature, light intensity or daylength involvement in controlling flower bud development process.

This experiment was conducted to study the effect of

daylength during flower bud development on number of flowers, time to flower, and length of flower stalk in H. angusta.

4.3. Materials and Methods

This experiment was conducted at the Magoon greenhouse and Pope laboratory glasshouse facilities of the University of Hawaii. H. angusta plants were divided and potted in 16 X 13 cm pots in May, 1990. Eighty pots were used. The potting medium was a mixture of peat moss and perlite in 1:1 ratio (v:v) and amended with dolomite, Micromax (minor elements) and treble superphosphate at the rates of 6.0, 1.0, and 0.6 kg / m^3 respectively. These plants were again divided and potted in 200 16 X 13 cm pots in August 1990, and repotted in 200 25 x 23 cm pots in July 1991. Plants were drip-irrigated automatically with a nutrient solution. The fertilizer ratio in this irrigation was 200N-0P-223K (ppm), at the rate of 1000 ml per pot per day. When these repotted plants rooted and grew well, 32 healthy and uniform pots of H. angusta were selected in September 5, 1991. The pseudostems with more than 3 leaves were cut off, so pseudostems with 1, 2, or 3 leaves could grow under daylength condition shorter than 12.5 hr including morning and evening civil twilight. For the daylength treatments, plants were moved into Pope lab

glasshouse on November 12, 1991, 2 weeks before LD treatment.

All 32 pots were put in one compartment made of cardboard and plastic film which provided a 16 hr daylength for 8 wks duration from November 26, 1991 to January 21, 1992 for flower bud initiation. After the LD treatment, the plants were put in 4 different daylength compartments (170 x 150 x 180 cm) to study the effect of daylength on flower bud development.

Four compartments were used for daylength treatments of 12, 14, 16, and 18 hr following the 16 hr treatment used to stimulate flower initiation. Eight pots were placed in each daylength and in natural condition. The LD was given by supplementing natural daylength with incandescent illumination with 60 W lamps placed 1.6 m above the benches (470 lux). The on and off time settings for the timers were 5:30 AM-5:30 PM for 12 hr, 5:30 AM-7:30 PM for 14 hr, 5:30 AM-9:30 PM for 16 hr, 5:30 AM-11:30 PM for 18 hr of photoperiod. The plants in 12 hr daylength treatment moved daily into Pope lab temperature controlled room (18 °C) from February 10, 1992 until the end of experiment because 12 hr dark condition could not be maintained in Pope glasshouse facilities.

The duration of treatments was 19 weeks from January 21, 1992 to June 1, 1992. Sides of the compartments were raised only during the night when supplementary light was

given. To enable the plants to receive equal amount of supplementary light, plants were moved within each compartment daily. Single pots in each treatment were considered as replications. The maximum air temperature during this experiment was from 38.5 to 26.4 °C with a mean of 28.7 °C, and the minimum air temperature was from 27.6 to 19.5 °C with a mean of 23.9 °C.

The initial number of leaves per stem was recorded at the beginning of LD treatment. Time to flower (emergence of inflorescences), the number of flowers (inflorescences) per pot, and the length of flower stalk (stalk + inflorescence) were recorded. This experiment was terminated on June 1, 1992, 27 weeks after the start of LD treatments.

4.4. Results

All 32 pots showed flowering. Out of total 309 pseudostems with 3 or more initial leaves, 135 pseudostems flowered. The average flowering percentage (number of stems flowered / number of stems with 3 or more initial leaves) was 41.5 % which was comparable to plants grown in 16 x 13 cm pots described in the preceding experiment of Chapter 3.

4.4.1. Effect of daylength on number of flowers

The effect of daylength during flower development on number of flowers per pot is shown in Figure 11. The average number of inflorescence per pot was 4.2. The differences in daylength during flower development had no significant effect on the number of flowers produced per pot (Appendix Table 13).

4.4.2. Effect of daylength on flowering time

The effect of daylength during flower development on time to flower is shown in Figure 12. The average flowering time was 15.2 wks after the beginning of daylength treatments. The differences in daylength during flower development had no significant effect on time to flower at the 5 % level of statistical significance (Appendix Table 14).

4.4.3. Effect of daylength on length of flower stalk

The effect of daylength during flower development on length of flower stalk in Figure 13. The length of flower stalk (53.2 cm) in the 18 hr daylength treatment was significantly greater than those of the other daylength treatments. While the plants in 14 hr daylength treatment had the shortest flower stalks (45.7 cm), the differences among daylength treatments shorter than 16 hr was not significant at 5 % level (Appendix Table 15).

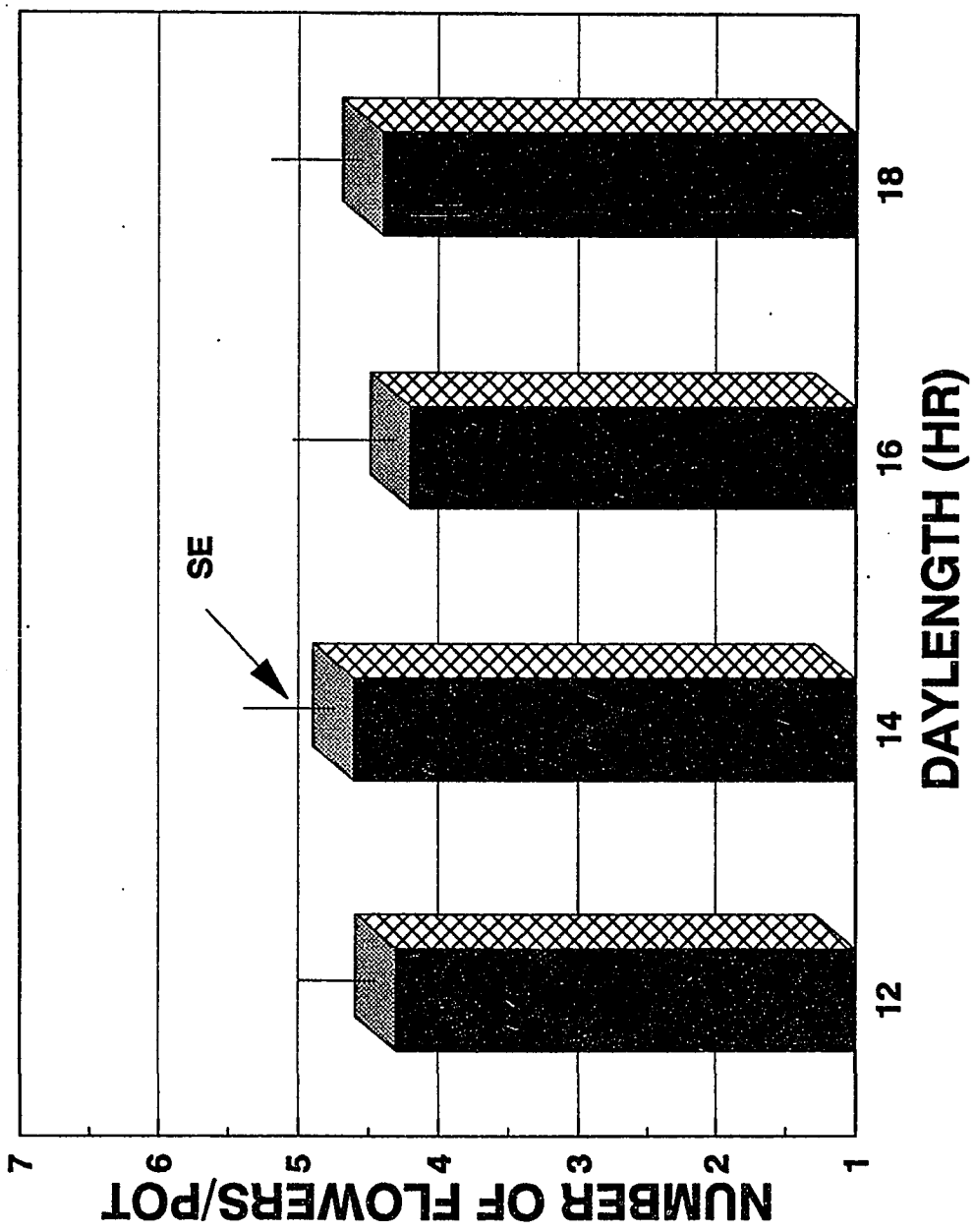

Figure 11. Effect of daylength during flower development (15-19 wks) on number of flowers (inflorescence) per pot in H. angusta.

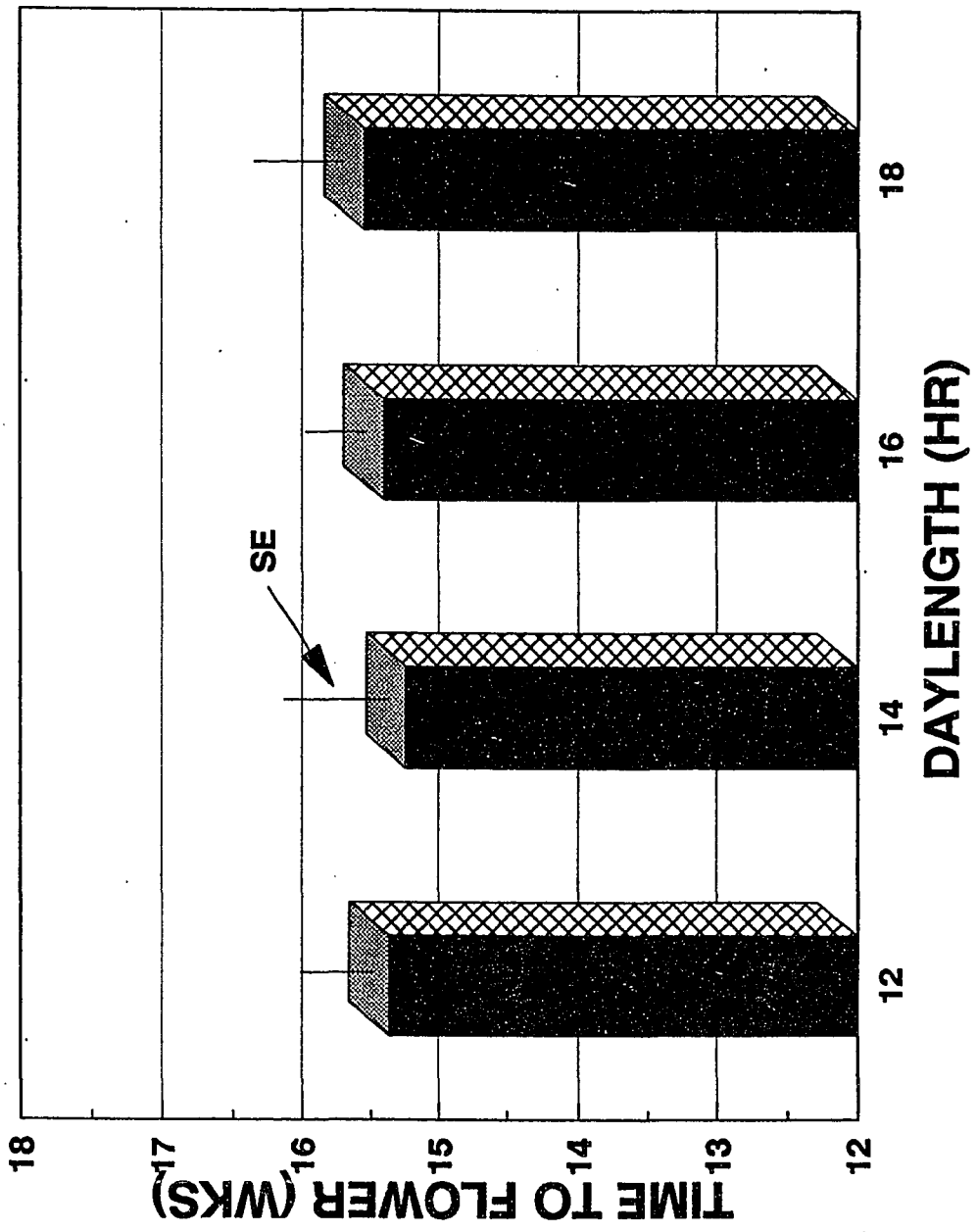

Figure 12. Effect of daylength during flower development on time to flower (emergence of inflorescence) in H. angusta.

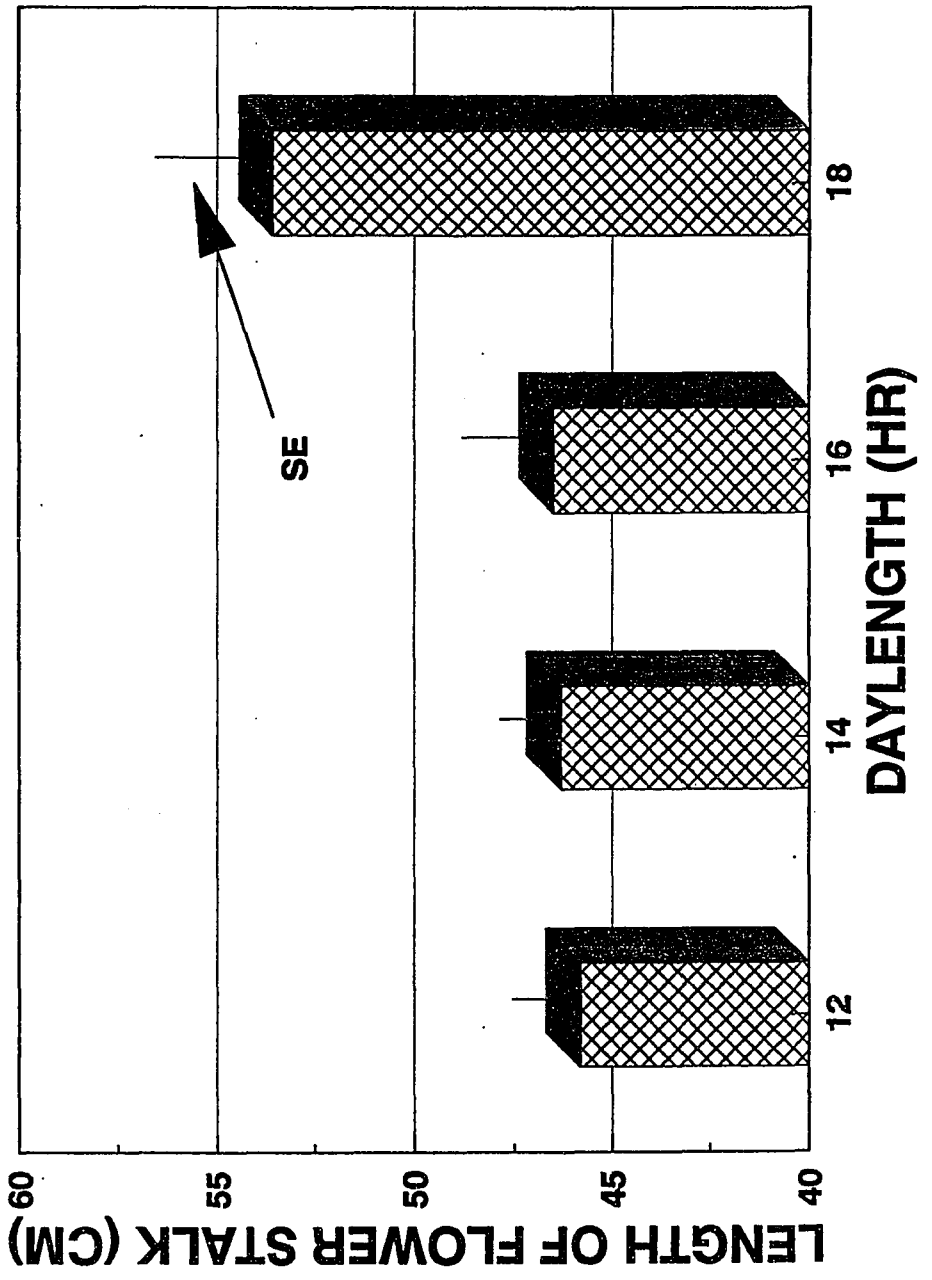

Figure 13. Effect of daylength during flower development on length of flower stalk (total length of peduncle + inflorescence) in H. angusta.

4.4.4. Effect of number of leaves on flowering time

There was no significant effect of daylength on time to flower or number of flowers per pot, but there was an inverse relationship between time to flower and initial number of leaves per stem (Figure 14) as seen in the experiment described in chapter 3. The stems with 3 or more initial leaves started flowering 14 weeks after daylength treatments began. Linear regression of time to flower on the initial number of leaves per stem was significant at the 5 % level (Appendix Table 16). Pseudostems with fewer initial leaves at the start of LD treatment tended to require longer time from the beginning of treatment to flower emergence than those with more initial leaves.

4.5. Discussion

Results of daylength treatments during flower development on flowering time show similar trends of the results of the experiment on minimum LD requirement for flower bud initiation described in Chapter 3 and the results of Lekawatana (1986) who reported that there was no significant effect of daylength treatment on flower development in H. angusta whether daylength was short day or long day. Sakai (1990) also reported that flower development could proceed under either LD or short days.

Since nearly 60 % of stalks which could flower did

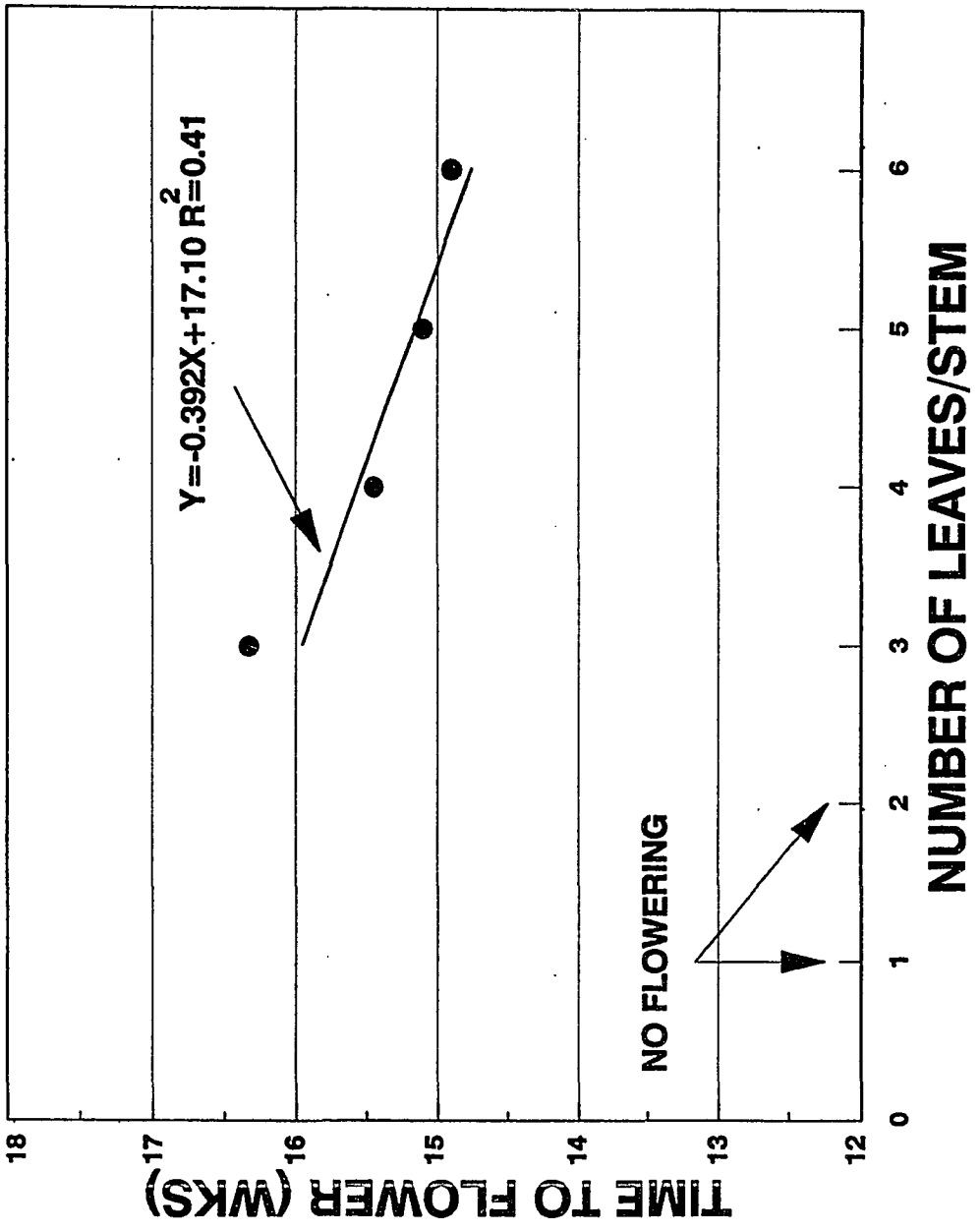

Figure 14. Effect of number of initial leaves per stem at beginning of long day treatment on flowering time (emergence of inflorescence) in H. angusta.

not flower, it can not be ruled out the possible negative effect of daylength on flower development. This possibility can be studied in the future.

The flowering time in chapter 4 experiment was 6.6 days earlier than the flowering time of plants in experiment described in chapter 3. This might be due to different ways of assessing flowering time. The flowering time in experiment in chapter 3 was measured as weeks until flower appearance in the lowest bracts and this flower appearance was usually 5 to 9 days (mean 1 week) after emergence of inflorescences, whereas in this experiment, flowering time was measured as weeks until appearance of inflorescences.

As stems with 4 or more initial leaves flowered earlier than those with fewer leaves, they might have less stem to elongate, whereas stems with fewer leaves needed more time to develop and unfurl the extra leaves and elongate stems. The 18 hr daylength significantly enhanced flower quality in terms of length of flower stalk. The Positive correlation between length of flower stalk and number of bracts (Fig. 9) suggests that longer flower stalks have more count of bract.

The important implication of these results is that once flowers are initiated, the inflorescence seems to continue development whether in shorter than 12 hr or longer photoperiod. Thus a year-round artificial lighting

program would not be disruptive of development because short day period is not required for flower development.

CHAPTER 5. EFFECT OF TEMPERATURE ON FLOWER DEVELOPMENT

5.1. Abstract

H. angusta plants were grown in 3 different night temperature treatments of 14, 18, and 22 °C for 19 weeks after 16 wk of 16 hr LD treatment to study the effect of night temperature on flower development. Daily duration of night (dark) period was 10 hrs.

Increasing night temperature significantly reduced the number of flowers per pot and increased flower stalk length. Linear regression analysis showed a significant relationship between temperature and flower number and length of flower stalk. Differences of flowering time in the range 14 to 22 °C of night temperature were not significant at the 5 % level of significance.

5.2. Introduction

In natural habits, heliconias grow from sea level to 2000 m with the greatest numbers of species occurring at middle elevations from 500 to 1000 m. In Florida, a cool temperature is a major limiting factor in producing heliconias. Growth and number of flowers were decreased as temperature decreased from 21 to 10 °C, and at 10 °C, plant growth and flower production all stop in H. psittacorum. Pseudostems are apt to be injured at

freezing temperature, but rhizomes may survive much colder temperatures than pseudostems.

Commercial flower growers in cool temperature regions have to grow plants in heated greenhouse facilities during winter. The objectives of this experiment were to investigate the effect of night temperature during flower development on number of flowers, time to flower, and length of flower stalk in H. angusta.

5.3. Materials and methods

This experiment was conducted at the Magoon greenhouse and Pope laboratory glasshouse facilities of the University of Hawaii. H. angusta plants were divided and potted in 16 X 13 cm pots in May, 1990. Eighty pots were used. The potting medium was a mixture of peat moss and perlite in 1:1 ratio (v:v) and amended with dolomite, Micromax (minor elements) and treble superphosphate at the rates of 6.0, 1.0, and 0.6 kg / m^3 respectively. These plants were again divided and potted in 200 16 X 13 cm pots in August, 1990, and repotted in 200 25 x 23 cm pots in July, 1991. Plants were drip-irrigated automatically with nutrient solution. The fertilizer ratio in this irrigation was 200N-0P-223K (ppm), at the rate of 1000 ml per pot per day. When these repotted plants rooted and grew well, 27 healthy and uniform pots of H. angusta were selected in September 5, 1991. The pseudostems with more

than 3 leaves were cut off, so pseudostems with 1, 2, or 3 leaves could grow under daylength condition shorter than 12.5 hr including morning and evening civil twilight. For the daylength treatments to initiate flower buds, plants were moved in Pope lab glasshouse on November 12, 1991.

All 27 pots were put in one compartment made of cardboard and plastic film which provided a 16 hr daylength for 8 wks duration from November 26, 1991 to January 21, 1992 for flower bud initiation. Temperature controlled rooms in Pope Lab #104 of 14, 18, and 22 °C were used during development of the inflorescence. In each room, 9 pots were put. The LD was given by supplementing natural daylength with incandescent illumination with two 60 W lamps placed 1.6 m above the benches (940 lux). After LD treatment to initiate flowers, the plants were grown in the Pope glasshouse during the daytime and removed to temperature controlled rooms during the night time from 9:00 pm to 7:00 am next morning. Wheeled carts were used to move these plants daily from January 21, 1992 to June 1, 1992. The maximum air temperature in the glasshouse during this experiment was from 38.5 °C to 26.4 °C with a mean of 28.7 °C, and the minimum air temperature was from 27.6 °C to 19.5 °C with a mean of 23.9 °C.

Number of weeks of time to flower (emergence of inflorescences), number of flowers (number of

inflorescences) per pot, and the length of flower stalk (length of total peduncle + inflorescence) were recorded. The initial number of leaves per stem was recorded at the time of beginning of LD treatment. This experiment was terminated on June 1, 1992, 27 weeks after the start of LD treatment, with the plants subjected to 19 wks of different night temperature treatments.

5.4. Results

Out of 27 pots, 20 pots could be used for data analysis because 1 pot each in 14 °C and 18 °C rooms and 5 pots in 22 °C room were severely damaged unexpectedly by scale infestation. Although these showed one or two flowers, they were excluded from analysis. Out of total 207 pseudostems with 3 or more initial leaves at beginning of LD treatment for flower initiation, 86 pseudostems flowered. The average flowering percentage (number of stems flowered/number of stems with 3 or more initial leaves) was 41.5 % which was comparable to similar plants described in chapter 4, and plants grown in small pot (16 x 13 cm) in the experiment described in chapter 3.

5.4.1. Effect of temperature on number of flowers

The effect of night temperature on flower development in H. angusta is shown in Figure 15. The average number of flowers per pot was 4.5 which was comparable to similar

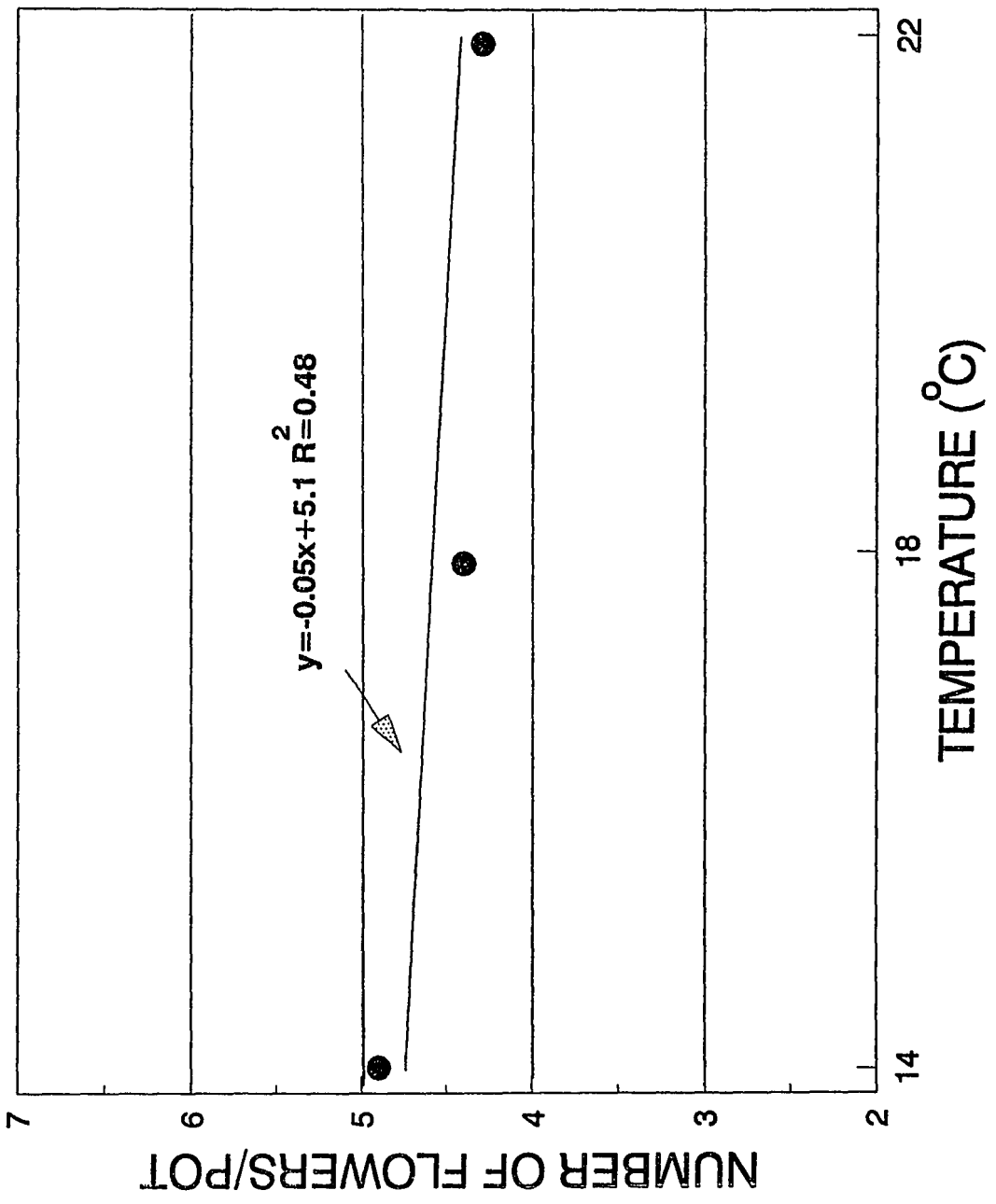

Figure 15. Effect of night temperature during flower development on number of flowers (inflorescence) per pot (25 x 23 cm) in H. angusta.

plants in the previous experiment in chapter 4. The highest number of flowers per pot was obtained in 14 °C treatment, with a tendency to decreasing numbers of flowers per pot as temperature increased. Linear regression analysis showed a significant relationship between night temperature and number of flowers per pot at the 5 % level of significance. (Appendix Table 17).

5.4.2. Effect of temperature on flowering time.

The effect of night temperature on time to flower in H. angusta is shown in Figure 16. The average flowering time in different night temperatures was average 15.4 wks after night temperature treatments began, and this was comparable to similar plants in the previous experiment in chapter 4. The plants grown with 22 °C night temperature showed the latest flowering time of 15.8 weeks. The relationship between temperature and time to flower showed a trend towards earlier flowering as the night temperature became lower. Linear regression analysis showed that there was no difference at the 5 % level of statistical significance among treatment means for time to flower (Appendix Table 18).

5.4.3. Effect of temperature on length of flower stalk

The length of flower stalk was longest in 22 °C treatment (Figure 17). As temperature increased, the

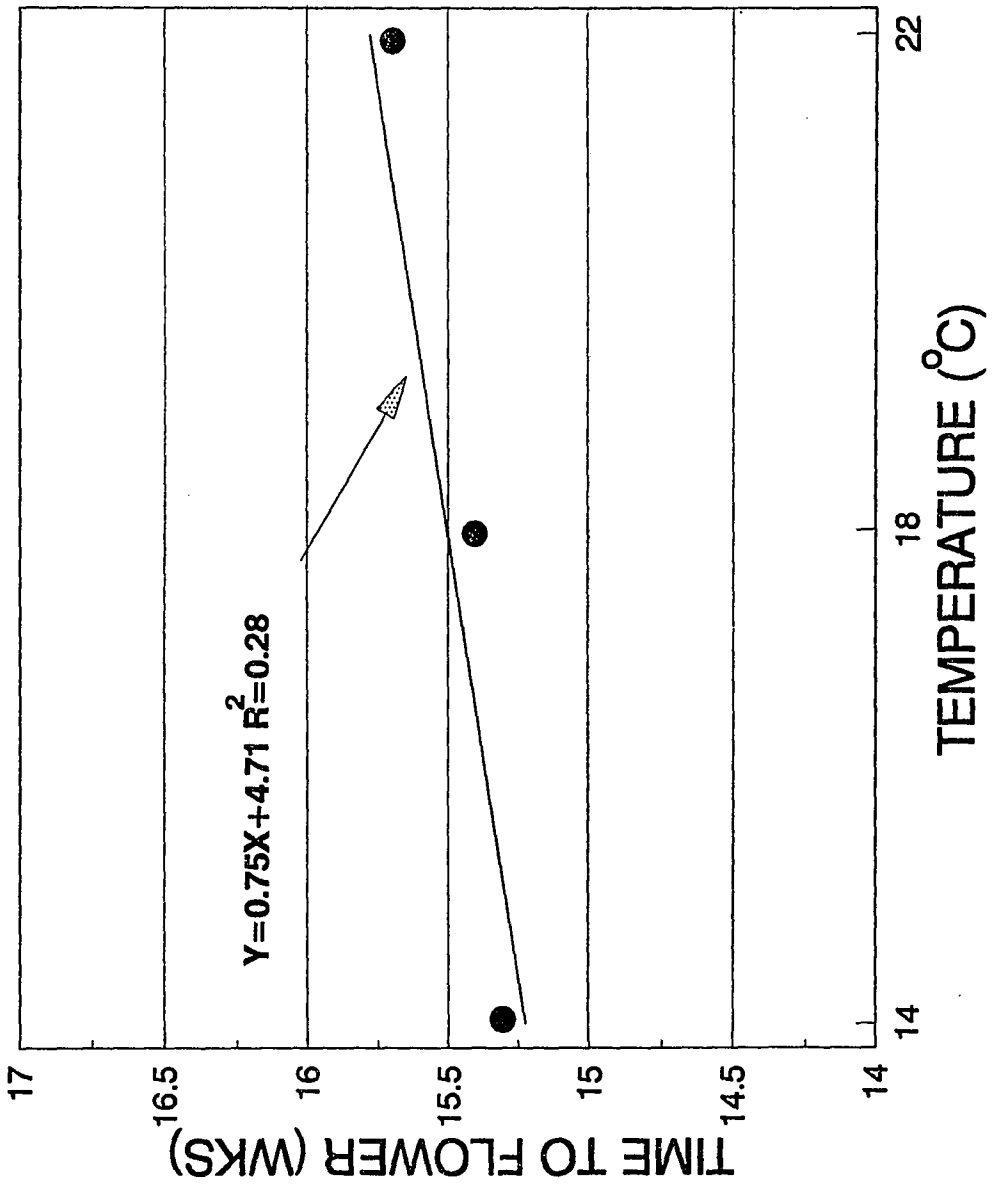

Figure 16. Effect of night temperature during flower development on time to flower (emergence of inflorescence) in H. angusta.

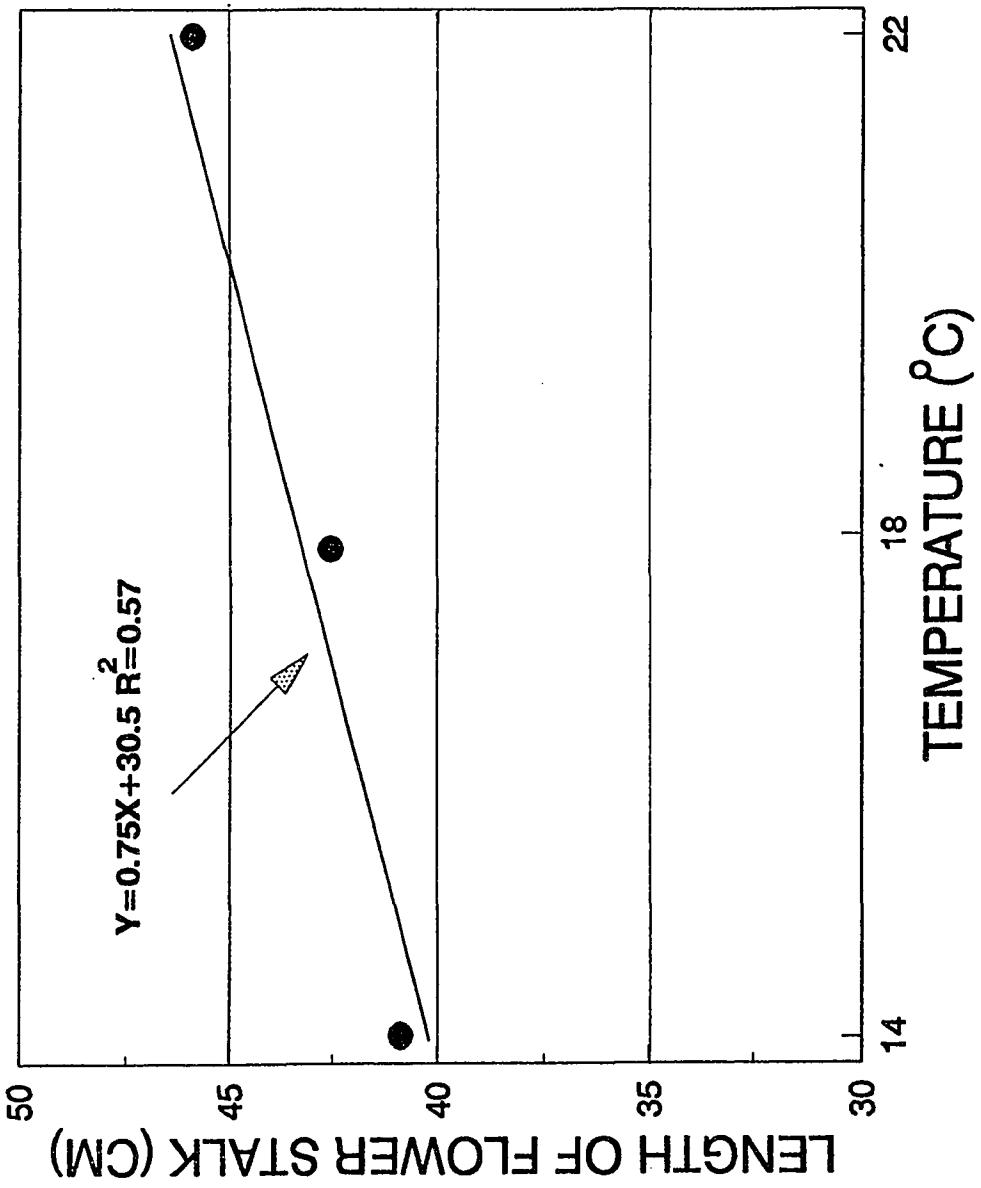

Figure 17. Effect of night temperature during flower development on length of flower stalk (total length of peduncle + inflorescence) in H. angusta.

length of peduncle and inflorescence also lengthened. Elongation rate of flower stalk (flower stalk length/flowering time in weeks) of plants in 22 °C was 2.9 cm/week and that of plants in 14 °C night temperature treatment was 2.7 cm/week. Linear regression analysis showed that this increasing effect of night temperature on the length of flower stalk (peduncle + inflorescence length) was significant at the 5 % level of significance (Appendix Table 19).

5.5. Discussion

There was significant effect of night temperature on number of flowers per pot, or quality of flower in terms of length of flower stalk during flower development in H. angusta. Increasing night temperature significantly decreased the number of flowers per pot at 5 % level of significance. The length of flower stalk was significantly increased with an increase of night temperature at 5 % level of significance. In Denmark, in the case of H. psittacorum, increasing the minimum temperature from 15 to 21 °C improved flower quality and increased stem length (Geertsen, 1989). A similar result was obtained in H. aurantiaca Ghiesbr. ex. Lemaire by Geertsen (1990) who reported that raising the temperature increased the flowering percentage by 20 % and increased the length of flowering stems by 20 cm.

The effect of decreasing night temperature on the number of flowers per pot was different from the published reports of other researchers who used other species. In the case of H. psittacorum, increasing the minimum temperature from 15 to 21 °C produced higher number of stems emerging as well as the number of flowering stems produced per unit area (Geertsen, 1989). But these experiments (Geertsen, 1989 and 1990) were conducted by growing plants in different temperature regimes from the beginning of plant growth, so the effect of temperature only on flower development was not clear.

In general, it is known that increasing daytime temperature indirectly increases flowering percentage due to an increased overall growth rate of plants. Low night temperature might reduce respiration rate of plants. Accumulated carbohydrates might explain the reason for higher flowering percentage (Salisbury and Ross, 1985).

Longer length of flower stalk of H. angusta in high night temperature (Fig. 17) might be a result from a longer duration of flower development (Fig. 16) as seen in the experiment described in chapter 3 (Fig. 8b) rather than a high night temperature effect itself.

CHAPTER 6. EFFECT OF LIGHT INTENSITY ON FLOWER DEVELOPMENT

6.1. Abstract

H. angusta plants were grown in 4 different light intensity treatments of full sun, 30 % shading, 50 % shading, and 30 + 50 % shading (rotation of plants every 2 wk between 30 and 50 % shadings) after 8 wks of 16 hr LD treatment to study the effect of light intensity on flower development. There was no flowering in 100% full sun light intensity, because the plants moved from Pope lab could not acclimate to that condition as evidenced by burn injury on leaves. Light intensity had no effect on time to flower. The plants grown under 30 % shaded compartment produced the highest number of flowers (5.2) per pot. There was a significant positive linear relationship between light intensity and number of flowers only at the intensities lower than full sunlight. Light intensity also had a significant positive linear impact on increasing the length of flower stalk.

6.2. Introduction

In general, more radiation increases plant growth by increasing production of carbohydrates. High light intensity increases flower production in H. psittacorum in Florida and Hawaii. But in the case of container grown H. angusta, a little shading of plants was recommended

because full sun light burns the leaves (Ball, 1987). In some ornamental plants, response of plants to light intensity was different among cultivars even within a same species (Armitage, 1991). The objective of this experiment was to investigate the effect of light intensity during flower development on number of flowers, time to flower, and length of flower stalk in H. angusta.

6.3. Materials and methods

This experiment was conducted at the Magoon greenhouse and Pope laboratory glasshouse facilities of the University of Hawaii. H. angusta plants were divided and potted in 16 X 13 cm pots in May, 1990. Eighty pots were used. The potting medium was a mixture of peat moss and perlite in 1:1 ratio (v:v) and amended with dolomite, Micromax (minor elements) and treble superphosphate at the ratio of 6.0, 1.0, and 0.6 kg per cubic meter, respectively. These plants were again divided and potted in 200 16 X 13 cm pots in August, 1990, and repotted in 200 25 x 23 cm pots in July, 1991. Plants were drip-irrigated automatically with a nutrient solution. The fertilizer ratio in this irrigation was 200N-0P-223K (ppm), at the rate of 1000 ml per pot per day. When these repotted plants rooted and grew well, 32 healthy and uniform pots of H. angusta were selected in August 5, 1991. The pseudostems with more than 3 leaves were cut

off to leave pseudostems with 1, 2, or 3 leaves to grow under daylength condition shorter than 12.5 hr. For the LD treatments to initiate flowers, plants were moved in Pope lab glasshouse on September 17, 1991, 2 weeks before LD treatment.

All 32 pots were put in one compartment (270 x 150 x 180 cm) made of cardboard and plastic film which provided a 16 hr daylength (5 AM to 9 PM) for 8 wks duration from October 1, 1991 to November 26, 1991 for flower bud initiation. The LD was given by supplementing natural daylength with illumination from three 60 W incandescent lamps (1.44 klux) placed 1.6 m above the benches. After LD pretreatment to initiate flowers, the plants were moved back to Magoon for placement on outdoor benches where light intensity treatments were initiated.

To have (assumed) 70 and 50 % of full sun light intensity, two compartments were made with 30 and 50 % shading black polypropylene shade cloths (saran screen), respectively. The size of each compartment was 185 x 150 x 180 cm. Eight pots were placed on open bench and 12 pots in each compartment. 4 pots in each compartment were rotated between 30 and 50 % shaded compartments every two weeks to receive 60 % (assumed) full solar radiation. A Datalogger (Model LI-1000) was used for recording air temperature with 3 LI-1000-16 temperature sensors and solar radiation with 3 LI-200S pyranometers. In each

light intensity treatment, 1 temperature sensor and 1 solar radiation sensor were used. The unit operated on 6 AAA batteries. The interval for data collecting was set to 1 minute and only hourly average temperature and solar radiation were stored in an erasable and programmable read-only memory. The unit was able to store data for 43 days without interruption. The instantaneous reading of the sensors in 1 hour intervals represented the average solar radiation and temperature for the previous 1 hour period. The solar radiation reading was stored as μ mol $s^{-1}m^{-2}$ quantum, and temperature was stored as °C. Both recorded data of temperature and solar radiation were retrieved every month for later analysis.

In addition to temperature and total solar radiation, time to flower in weeks, number of flowers per pot, and the length of flower stalk were recorded. The recording was started on December 5, 1991 and terminated on June 1, 1992.

6.4. Results

During the period of experiment, air temperature in full sun bench was always higher than in the 30 % and 50 % shaded compartments by 0.1 to 0.2 °C during the daytime, whereas, during the night time, both shaded compartments showed temperature 0.1 to 0.2 °C higher than for the open bench. Between shaded compartments, there was no

difference in temperature during night time or day time. Solar radiation was lower in January and February than in the March to June time period (Fig. 18).

Daily average daily radiation calculated from Σ (hourly average solar radiation) / number of days from beginning of light intensity treatments to the end was 6501 μ mol $s^{-1}m^{-2}$ in open bench (100% full sun light). In shaded compartments, daily average solar radiation was 4263 μ mol $s^{-1}m^{-2}$ in 30 % shading, and 2797 μ mol $s^{-1}m^{-2}$ in 50 % shading compartment. As compared to full sun light, these values were 65.5 % and 43 % respectively. But even this varied across the day (Fig. 19).

The difference between shading rates of saran screens and actual light intensities inside these shadings indicated that amount of actual light penetration through the shading screen to the plants did not fall into the categories of shading percentage guaranteed by manufacturer of saran screens. Usually the solar radiation difference among treatments were maintained during clear sky conditions, but when there were clouds in the sky, the difference of this ratio was narrowed. Hourly solar radiation showed that most of the radiation was received between 10:00 AM to 4:00 PM (Fig. 19).

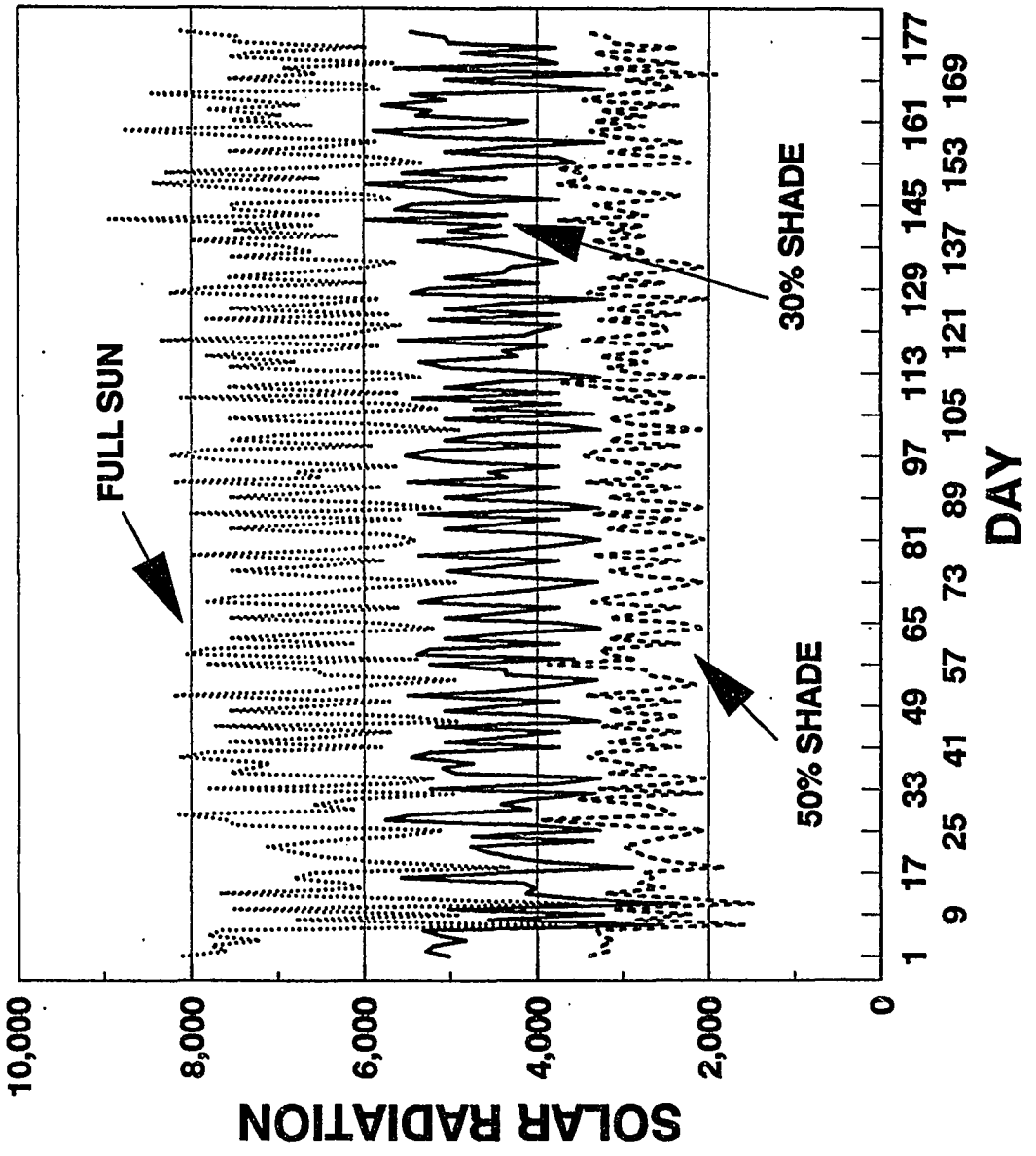

Figure 18. Daily average total solar radiation in Magoon greenhouse from December 5, 1991 to June 1, 1992. Day 1 stands for first day of experiment i.e. December 5, 1991. (Solar radiation unit:μ mol quantum $s^{-1}m^{-2}$)

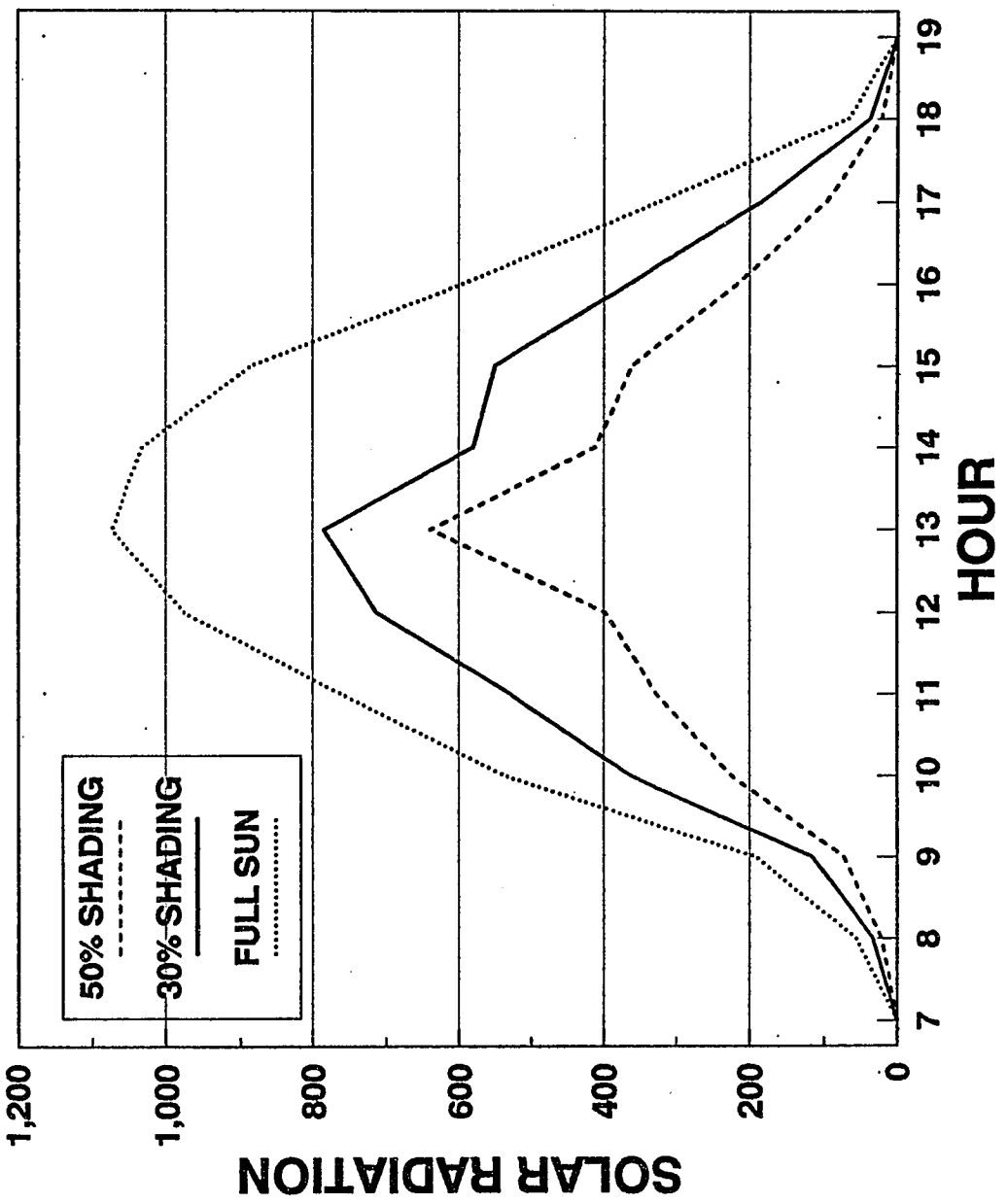

Figure 19. Average hourly total solar radiation in Magoon greenhouse from December 5, 1991 to June 1, 1992. (Solar radiation unit: μ mol quantum $s^{-1}m^{-2}$)

Summations over 19 weeks of daily average solar radiation in two shading compartments and in open bench are shown in Figure 20. The slopes of graph of solar radiation summation of full sun and 70 % shading were almost constant across the days and only 50 % shading showed a little steeper change after March.

6.4.1. Light intensity and number of flowers

The effect of light intensity on number of flowers per pot in H. angusta is shown in Figure 21. Among 251 stems (in shaded compartments) with 3 or more initial leaves at the beginning of LD treatment, 110 stems flowered. The average flowering percentage (number of stems flowered/number of stems with 3 or more initial leaves) was 43.8 % which was comparable to similar plants described in chapter 4 and 5, and plants grown in small pot (16 x 15 cm) in the experiment in chapter 3.

Plants placed in the full sun light treatment did not flower, and most of them showed some of leaf cracking symptoms and drying of the edges, and tip of leaves. In the Pope lab glasshouse where these plants were grown and given LD treatment for flower bud initiation, there was white paint on the glass, and shading screen over the benches to reduce sunlight penetration. Instantaneous reading of light intensity at 2 and 3 PM using Datalogger with Li-200S sensor was 75-85 % of full sun light

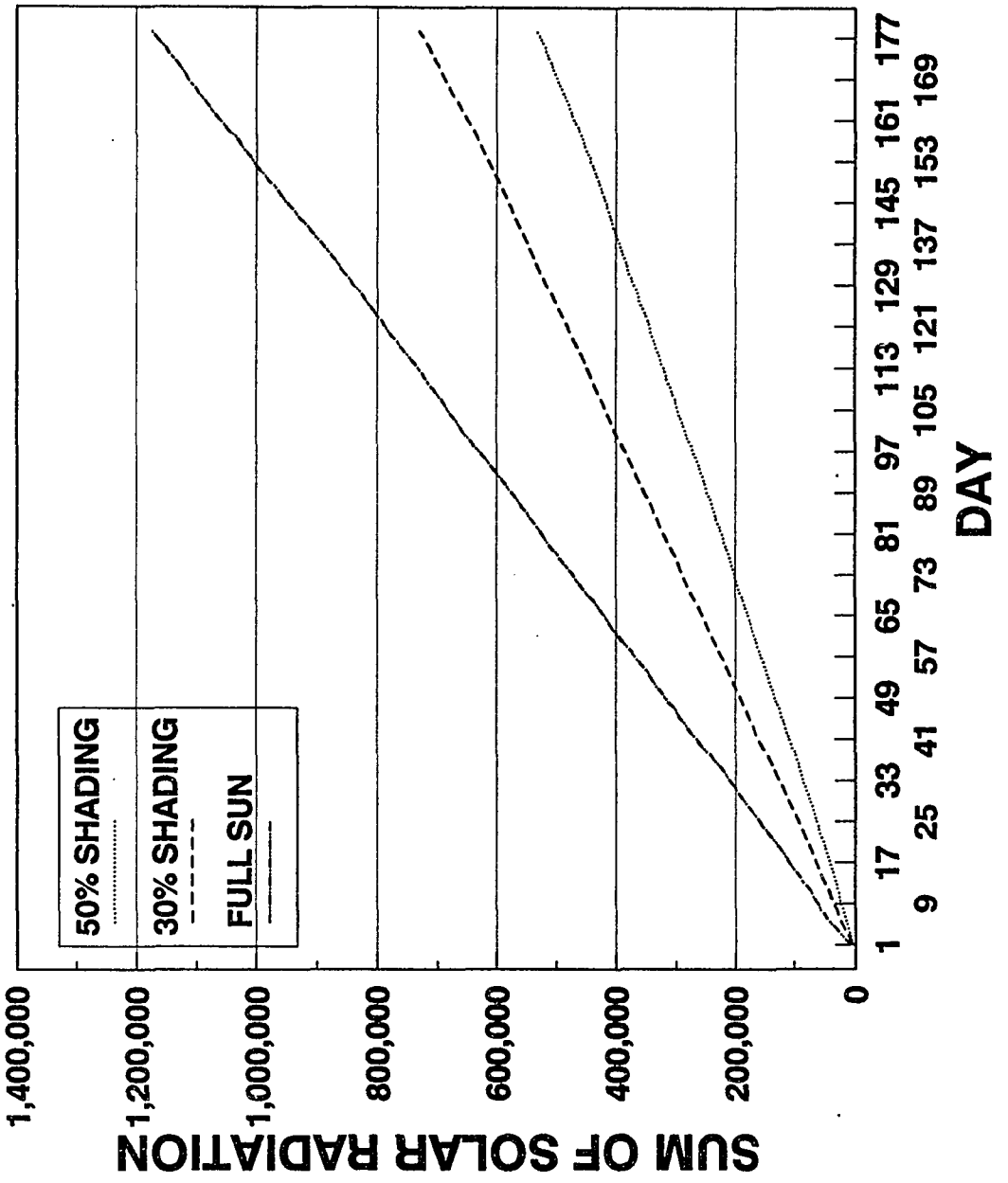

Figure 20. Accumulation of solar radiation in Magoon greenhouse from December 5, 1991 to June 1, 1992. (Solar radiation unit: μ mol quantum $s^{-1}m^{-2}$).

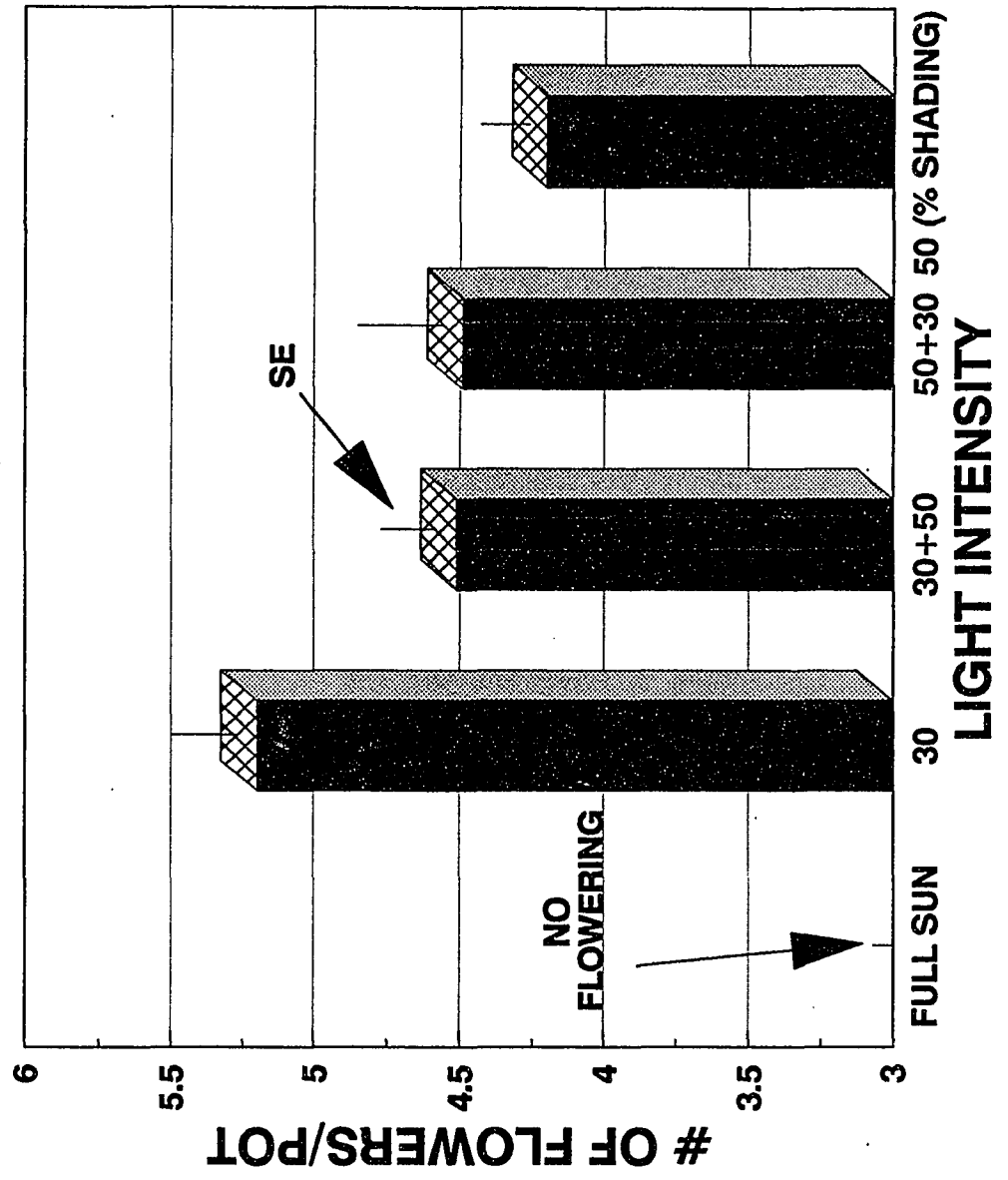

Figure 21. Effect of light intensity during flower development on number of flowers (inflorescence) per pot (25x23cm) in H. angusta. (Shade 30%=4263, 30+50 %=3573, 50+30%=3514, 50 %=2797. Solar radiation unit: μ mol quantum $s^{-1}m^{-2}$).

intensity in Pope glasshouses and 51-62 % of sun light under saran screen in glasshouses in clear sky day. The plants grown in these shaded conditions did not acclimatize to the full sun light condition of open benches.

Out of 24 pots, 110 pseudostems showed flowering beginning 14 weeks after start of treatment. The average number of flowers per pot was 4.6, which was comparable to plants grown in experiments reported in chapter 4 and 5. The treatment of 30 % shading averaged 5.2 flowers per pot, and the treatment of 50 % shading averaged 4.2 flowers per pot. Among the plants grown under shaded compartments, there was a significant regression relationship between number of flowers per pots and light intensity in shaded compartments (Appendix Table 20). The number of flowers per pot increased with the increase of light intensity.

6.4.2. Light intensity and flowering time

The effect of light intensity on time to flower in H. angusta is shown in Figure 22. Time to flower in different light intensities averaged 15.3 weeks after light intensity treatments began. There was no difference at the 5 % level of statistical significance among light intensity treatment means for time to flower (Appendix Table 21).

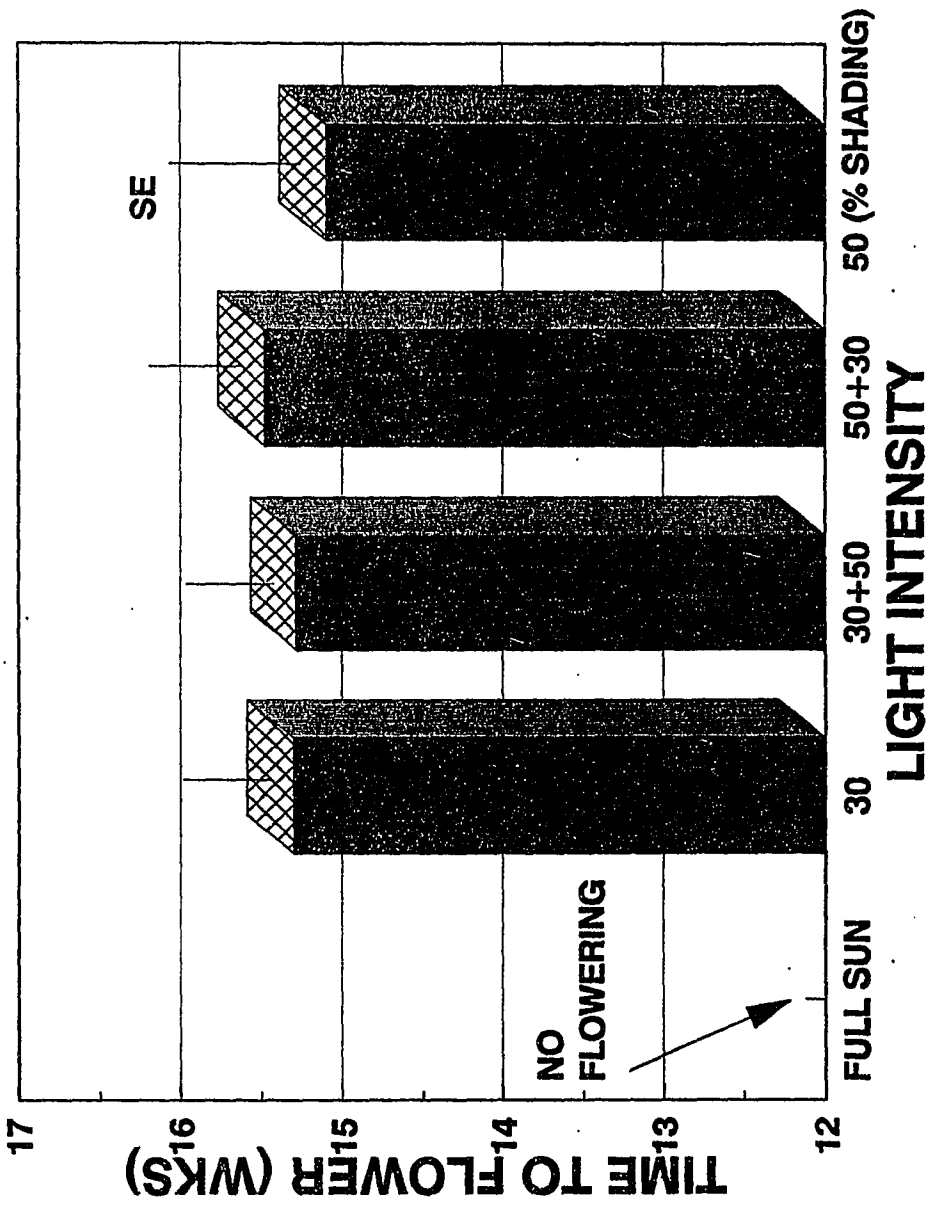

Figure 22. Effect of light intensity during flower development on time to flower (emergence of inflorescence) in H. angusta. (Shade 30%=4263, 30+50 %=3573, 50+30%=3514, 50 %=2797. Solar radiation unit: μ mol quantum $s^{-1}m^{-2}$).

6.4.3. Light intensity and length of flower stalk

The effect of light intensity on length of flower stalk in H. angusta is shown in Figure 23. The average length of peduncle and inflorescence for all treatments was 43.7 cm. Among the treatments, 30 % shading produced longest flower stalk, 47.9 cm, while the shortest length of flower stalk, 41.1 cm, was obtained in 50 % shaded compartment. There was a significant regression relationship between length of flower stalk and light intensity at 5 % level (Appendix Table 22).

6.5. Discussion

The plants under full sun light condition mostly burned up and did not flower. Since no anatomical analysis was made on shoot, leaf or rhizome, it was not clear whether failure to flower was due to full sun light intensity, poor climatic adaptation of plants from shading to full sun, abortion of flower bud after initiation, or no flower initiation at all in 16 hr LD treatment, and it was not possible to compare the effects of full sun light and shading on flower development. But among the shading treatments receiving less than 100 % full sun light intensity, a positive effect of light intensity was found on number of flowers (Fig. 21) and the length of flower stalk (Fig. 23). This effect of light intensity on length of flower stalk was also in line with the result (Fig. 13)

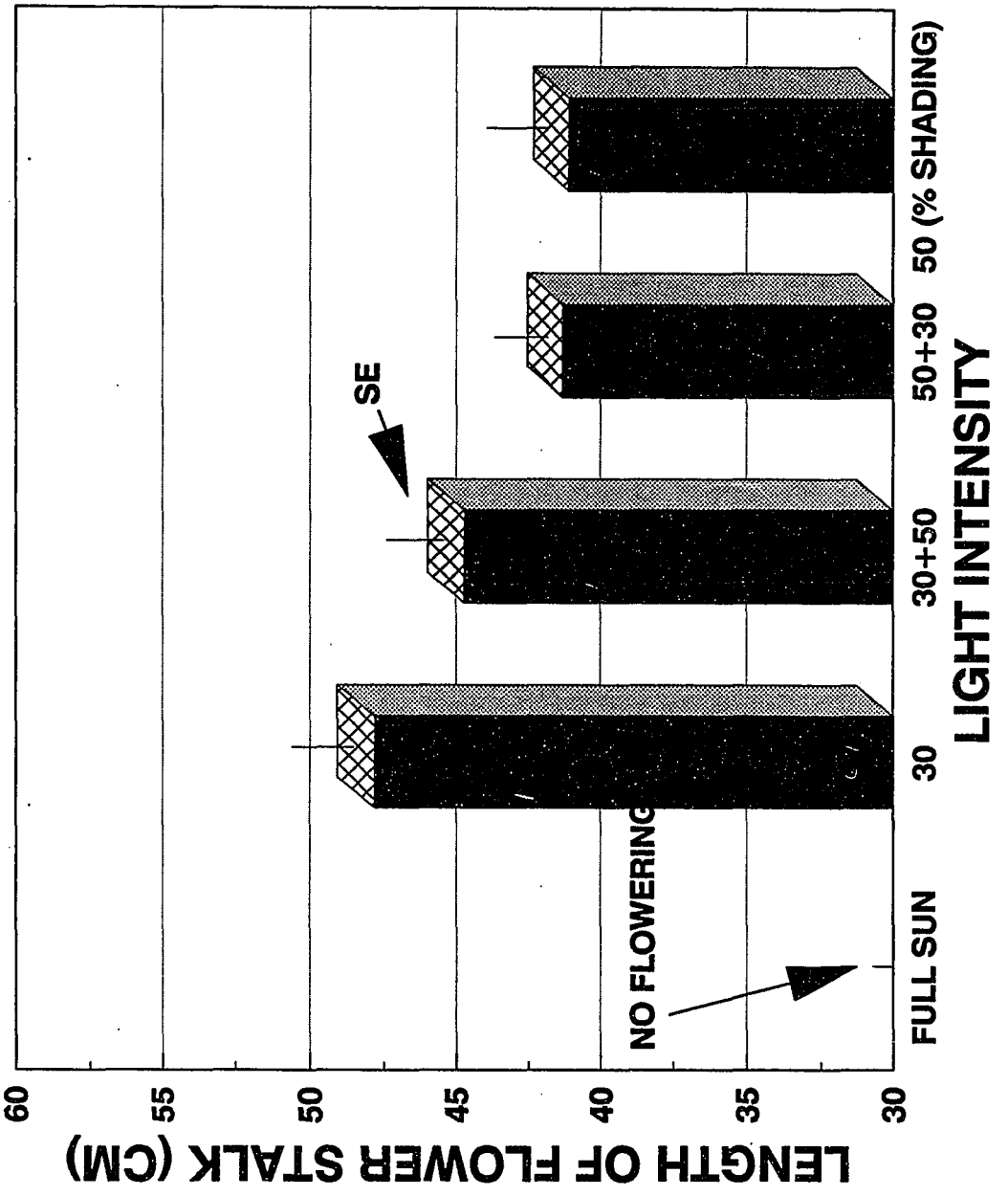

Figure 23. Effect of light intensity during flower development on length of flower stalk (length of peduncle + inflorescence) in H. angusta. (Shade 30%=4263, 30+50 %=3573, 50+30%=3514, 50 %=2797. Solar radiation unit: μ mol quantum $s^{-1}m^{-2}$).

Table 2. Comparison of flowering percentage of H. angusta grown in 2 different pot sizes.

Experiment	Pot size[x]	Flowering percentage[y]	
			%
Long-day treatment for Flower bud initiation (Chapter 3)	small	35.9	A[z]
Daylength during flower development (Chapter 4)	big	41.5	B
Temperature during flower development (Chapter 5)	big	43.6	B
Light intensity during flower development (Chapter 6)	big	43.8	B

[x]Pot size; small= 16 x 13 cm, big = 25 x 23 cm.
[y]Flowering percentage = number of stems flowered /number of stems with 3 or more initial leaves at the beginning long day treatment.
[z]Mean separation in columns by Duncan's multiple range test.

described in chapter 5 in which daylength of 18 hr with artificial supplementary lighting produced longer flower stalk. In contrast to H. angusta, stretching of stem due to crowding and reduced light intensity was observed in H. stricta 'Dwarf Jamaican' plants grown in pots (Lekawatana and Criley, 1989),

Some damaging effect of full sun light on H. angusta was also reported by Ball (1987). It was recommended by him that 30 to 40 % shading be used for container grown H. angusta cv. Holiday because the plants burn under full sun light condition.

A positive effect of light intensity on the number of flowers (Fig. 21) and the length of flower stalk (Fig. 23) was in line with the result of Stiles (1979) who reported that Heliconias in their natural environmental habitat tend to grow best in the high sun light of forest clearings and decrease the number of flowering stalks as light intensity decreases.

In case of H. psittacorum, light intensity is a limiting factor in flower production. H. psittacorum grown in full sun produced three to four times more flower than plants in 63 % shade (Broschat and Donselman, 1983a). In Florida, H. psittacorum grown in heated greenhouses having 80 % light transmittance glass produced fewer flowers than the plants grown under suboptimal colder

outdoor condition because of reduced light intensity (Broschat and Donselman, 1988).

In Hawaii, the reason of the highest production of average shoot and flower production of H. psittacorum X 'Parrot' during the summer (Manarangi et al., 1988) appears to be a result from a factor of greater total sunlight or higher temperature or both factors.

In some cut flower species, similar results of promotion effect of full sun light intensity on flowering also reported in roses (Zieslen and Halevy, 1975; Mor and Halevy, 1979), geranium (Armitage and Weltzstein, 1984), carnation (Bunt, 1973), Centaurea americana, and Eryngium planum (Armitage, 1991).

The effect of light intensity on flower development can be explained in relationship between sink and source concept. In experiments with gladiolus using ^{14}C assimilates (Robinson et al., 1980), the two major sinks, the inflorescences and the new corms compete for assimilates for growth. Once flower buds are initiated, translocation of assimilates to developing flower buds was increased as flower buds developed. However, under stress conditions associated with an inadequate supply of essential assimilates, the young flower bud constitutes a weak sink in comparison with the vegetative apices, developing leaves, fruits or storage organs such as corm, rhizome, and bulb and competed poorly with them for the

available assimilates (Halevy, 1984). This was found to be the case under the conditions of light, temperature or water stress. In plants possessing young flower buds, these environmental stresses promote flower bud abortion, or abscission, while other organs may be only slightly affected.

In case of roses (Mor and Halevy, 1979), a young flower bud tip covered while the rest of plant was held in full sun light, showed promotion of flower bud abortion. As tip of young shoot with flower buds are totally dependent on the translocation of metabolites from mature leaves, this result indicates that light effect directly on the rose flower buds themselves, enhancing their sink activity.

There was a significant difference of flowering percentage between plants grown in two different sizes while differences of flowering percentages of plants grown in 25 x 23 cm pots were not significant (Table 2). Plants grown in 25 x 23 cm pots averaged 28.3 stems per pot (576.8 stems/m^2), while plants grown in 16 x 13 cm pots had average 18.0 stems per pot (895.7 stems/m^2).

In conclusion, high light intensity (only in shaded compartments in this experiment) had a significant effect on increasing number of flowers or/and flower stalk length. Important practical implications of these results are to grow plants in high light intensity, preferably in

open field, and to have a suitable planting density in field in order to avoid severe shading effect by leaves or stems.

CHAPTER 7. ESTIMATION OF LEAF ELONGATION BY HEAT ACCUMULATION MODEL

7.1. Abstract

H. angusta plants were grown under natural condition to build a heat accumulation model (= growing degree day:GDD) and calendar growing day (CGD) to describe the leaf growth (elongation) pattern and to estimate the minimum heat accumulation and growing day requirement for the plants to respond to photoperiod stimulus to initiate flower buds. Comparison between daily maximum and average temperature, base temperature determination, and comparison between linear and non-linear equations were made to build GDD model. For CGD model, only calendar day was used.

A base temperature of 14 °C which had the least coefficient of variance (CV) for GDD across different base temperatures was chosen for GDD calculation of leaf growth pattern. Daily average temperature showed a lower CV value than daily maximum temperature. Out of 3 models - linear, negative exponential curve, and S-curve - for fitting leaf growth on GDD, the S-curve regression model showed the highest F value and regression coefficient. For S-curve fitting, comparison of GDD and CGD model showed a better fit of the GDD model which had a higher regression coefficient. The GDD unit requirement based on daily average temperature with a base temperature at 14 °C

from shoot emergence to leaf 3 was 677-745 (42-54 days) and to leaf 4 was 930-992 (56-72 days). The average elongation rate of leaf 1 to 5 was 0.254 cm/GDD and 3.80 cm/day.

7.2. Introduction

Biological research data are often evaluated by the relationship among several variables (correlation) or the cause and effect among several variables (regression). If this cause (independent variable) and effect (dependent variable) evaluation can be done by linear regression, it has the advantage of being simple to fit to data. However, linear relations seldom occur in nature, so data can be transformed and then a straight line fitted to the data or nonlinear curve fitting has been suggested (Landsberg, 1977). The use of computers in horticulture prompted the response surface analysis, a variation of multiple regression analysis as in the case of predicting time to flower in chrysanthemum 'Bright Golden Anne' (Karlsson and Heins, 1986).

Modelling techniques allows us to predict certain developmental phases of plant growth such as flowering time or harvest time, without destroying the plant materials. In H. angusta, a study of the relationship between the time of pseudostem emergence and flowering showed that only those pseudostems that emerge before

August flowered in the winter. It was suggested that the critical day-length required for initiation of flowering is 13.3 hour (Sakai et al., 1990a).

The objective of this study was to estimate leaf growth pattern based on GDD and CGD models and to compare the fitness between these two models. Questions central to GDD model include:

1. What is the basic growth pattern of leaves?
2. Which temperature should be used for a heat accumulation model- maximum temperature or average temperature?
3. What is the base temperature?

7.3. Materials and Methods

This experiment was conducted in a Magoon greenhouse and Pope lab glasshouse facilities at University of Hawaii. H. angusta plants were divided and potted in 16 X 13 cm pots in May, 1990. Eighty pots were used. The potting medium was a mixture of peat moss and perlite (1:1 v:v) and amended with dolomite, Micromax (minor elements) and treble superphosphate at the ratio of 6.0, 1.0, and 0.6 kg/m^3, respectively. These plants were again divided and potted in 200 16 X 13 cm pots in August, 1990. Plants were drip-irrigated with a nutrient solution of 200N-0P-223K (ppm) at 1000 ml per pot per day. After these repotted plants rooted and grew well, 40 healthy and

uniform potted plants were selected in September, 1990. Pseudostems with more than 3 leaves were cut off to leave pseudostems with 1, 2, or 3 leaves to grow under daylengths shorter than 12.5 hr. All 40 pots were moved into Pope lab on December 18, 1990 and grown under the natural conditions.

Out of a total of 40 pots, 30 pots were used for collecting data for leaf growth. And 10 pots were used to validate the model.

The date of leaf emergence and the length of leaf were recorded from January 1, 1991 to October 10, 1991. The dates of pseudostem emergence and flowering were recorded from August 30, 1991 to April 10, 1992 (later to be used as a validation data set in Chapter 8). Length of leaf (leaf blade + sheath) was measured at 2 day intervals until the growth of the leaf was less than 0.4 cm for 6 days. To record temperature, a strip chart hygrothermograph (Model Belfort 5-594) was used from January 1, 1991 to August 23, 1991 and maximum and minimum temperature thermometer was used from August 24, 1991 to October 10, 1991.

Two methods used to compute GDD were:

Method 1: GDD=Σ(daily mean-base temperature)

where daily mean=(daily maximum+daily minimum air temperature in °C)/2

Method 2: GDD=Σ(daily maximum-base temperature).

Since base temperature was not known, the CV method was used to estimate the base temperature. The base temperature was assigned from 2 to 22 °C in 2 °C intervals for method 1. For method 2, base temperature was assigned 2 to 28 °C in 2 °C intervals. Base temperature was calculated from the data of leaf 1 to leaf 5 as a total. The temperature which gave the lowest CV of GDD (Arnold, 1959) in 5 leaves (leaf 1 to leaf 5) was selected as a base temperature for GDD model building. Only leaves in a vegetative growth phase were used, and the number of leaves sampled at each position was 20. Selection of the best daily maximum or average temperature for GDD modelling was determined by the lowest CV.

Using the growth data of leaf 4 as representative of 5 leaves, regression fitting of leaf growth pattern on GDD was estimated from three methods (Charles-Edwards et al., 1986). The three methods were:

Method 1. linear regression model ($y=a*x+b$)

Method 2. negative exponential growth curve regression model ($y=a(1-e^{-k*x})$)

Method 3. S-curve model ($y=a/(1+e^{-b-k*x})$).

Among these three models, the model which gave the highest F value from the analysis of variance of regression was selected. Non-linear regression analysis to calculate a, b, and k value was done by Secant methods which used fewer parameters for non-linear curve calculation (SAS, 1986 and

1987). Comparison of regression fitting of leaf growth pattern on GDD or CGD was made by plotting the length of leaf on GDD or calendar days respectively, and by F value and/or regression coefficient.

Validation of model was done using a different data set which was described in the experiment in Chapter 6. The number of samples of each leaf position for validation was 10. The observed values from the validation data of each leaf were plotted against the predicted values generated by the model of each leaf and linear correlation analysis was made to check the fitness of model. The slope of correlation, probability, and coefficient of correlation was checked.

7.4. Results

The maximum air temperature during this experiment was from 25.3 to 39.4 °C with a mean of 34.1 °C, and the minimum air temperature was from 18.6 to 31.3 °C with a mean of 23.9 °C. The average daily temperature was 29.0 °C.

7.4.1. Comparison of average and maximum temperature for GDD

The CV of GDD based on daily average and maximum temperature are shown in Figures 24 and 25. CV showed significant quadratic regression relationship with

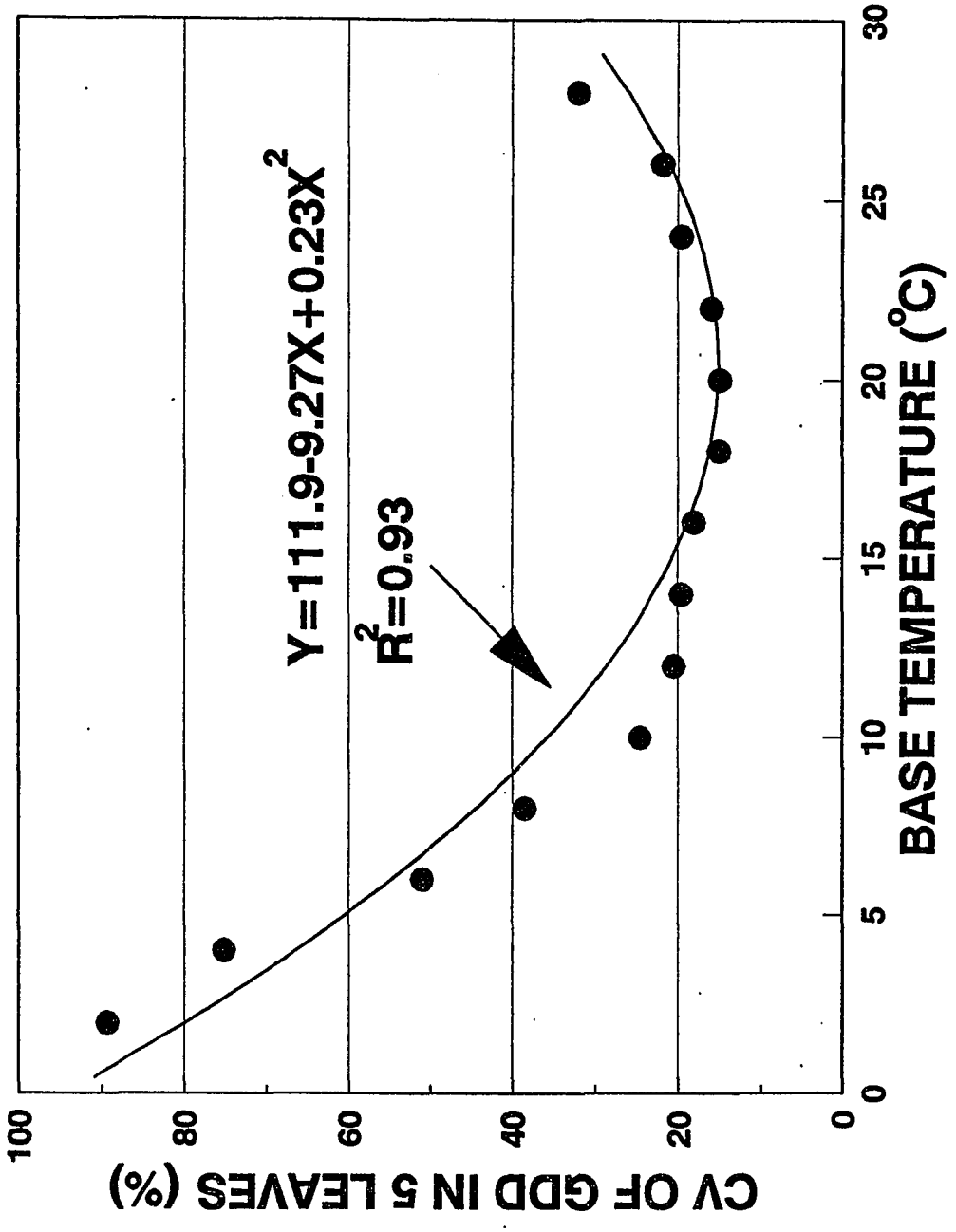

Figure 24. Total coefficient of variance (CV) of GDD based on daily maximum temperature with different base temperatures in leaf 1 to 5 of H. angusta. Number of each leaf was 20.

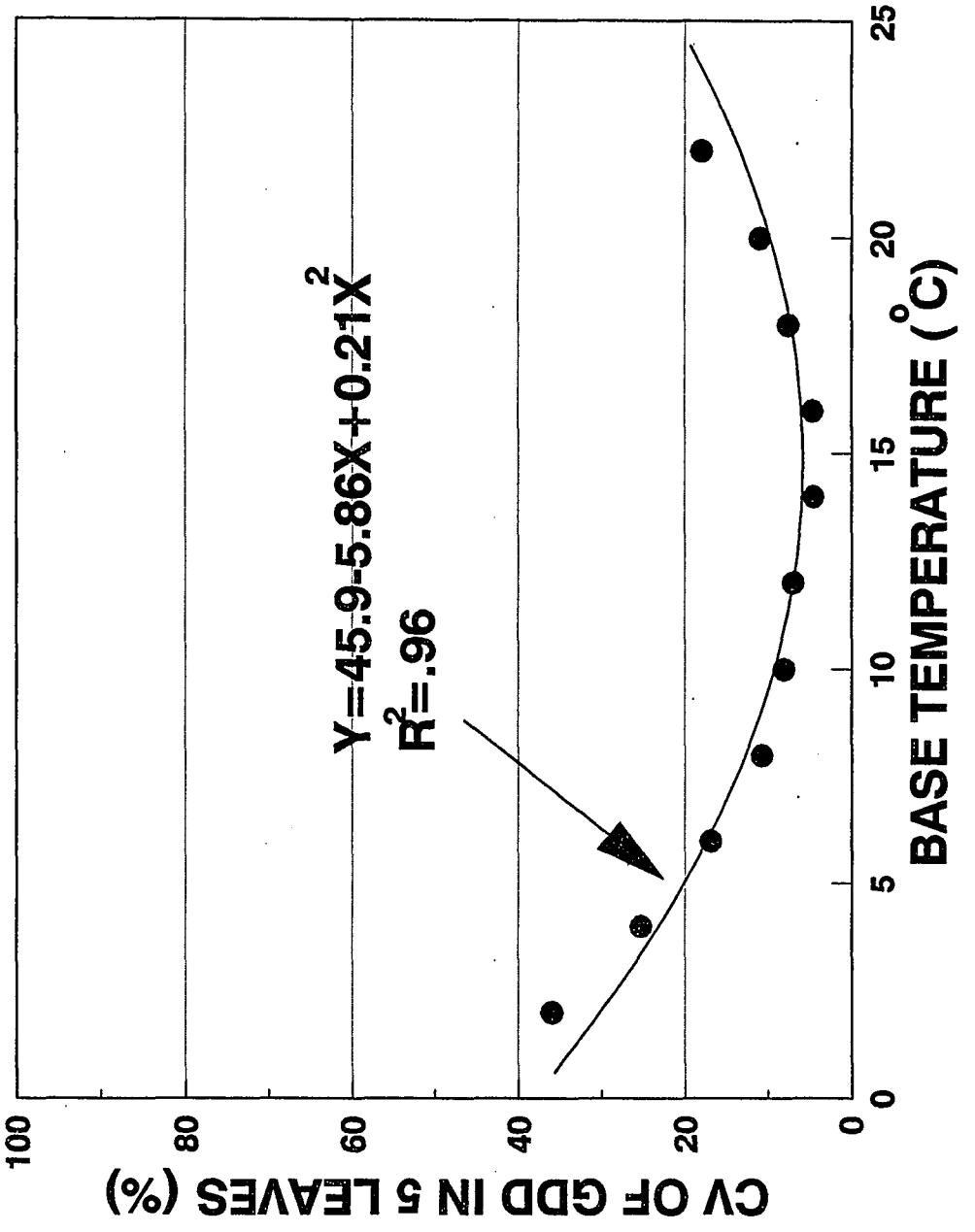

Figure 25. Total coefficient of variance (CV) of GDD based on daily average temperature with different base temperatures in leaf 1 to 5 of H. angusta. Number of each leaf was 20.

different base temperatures at 5 % level of significance (Appendix Table 23 and 24). The CV of GDD based on daily average temperature was lower than the CV of GDD based on daily maximum temperature thus indicating better fitness of GDD modelling. The lowest CV was 4.2 % at 13.96 °C base temperature in GDD based on daily average temperature. Therefore, for the convenience of calculation, base temperature of 14 instead of 13.96 °C was used on average temperature.

7.4.2. Comparison of linear and non-linear regression models

Regression fitting of leaf elongation patterns on based on GDD model with a base temperature at 14 °C are shown in Figure 26 to 28. All 3 models, linear regression (Fig. 26), negative exponential curve (Fig. 27), and S-curve regression (Fig. 28) had significance of fitting at 5 % level (Appendix Table 25-27). Out of these three models, S-curve regression had the highest probability (p value) and regression coefficient (R^2=0.94). Therefore, S-curve fitting model was used for modelling the growth pattern of each leaf.

7.4.3. Comparison of S-curves based on GDD units and calendar day

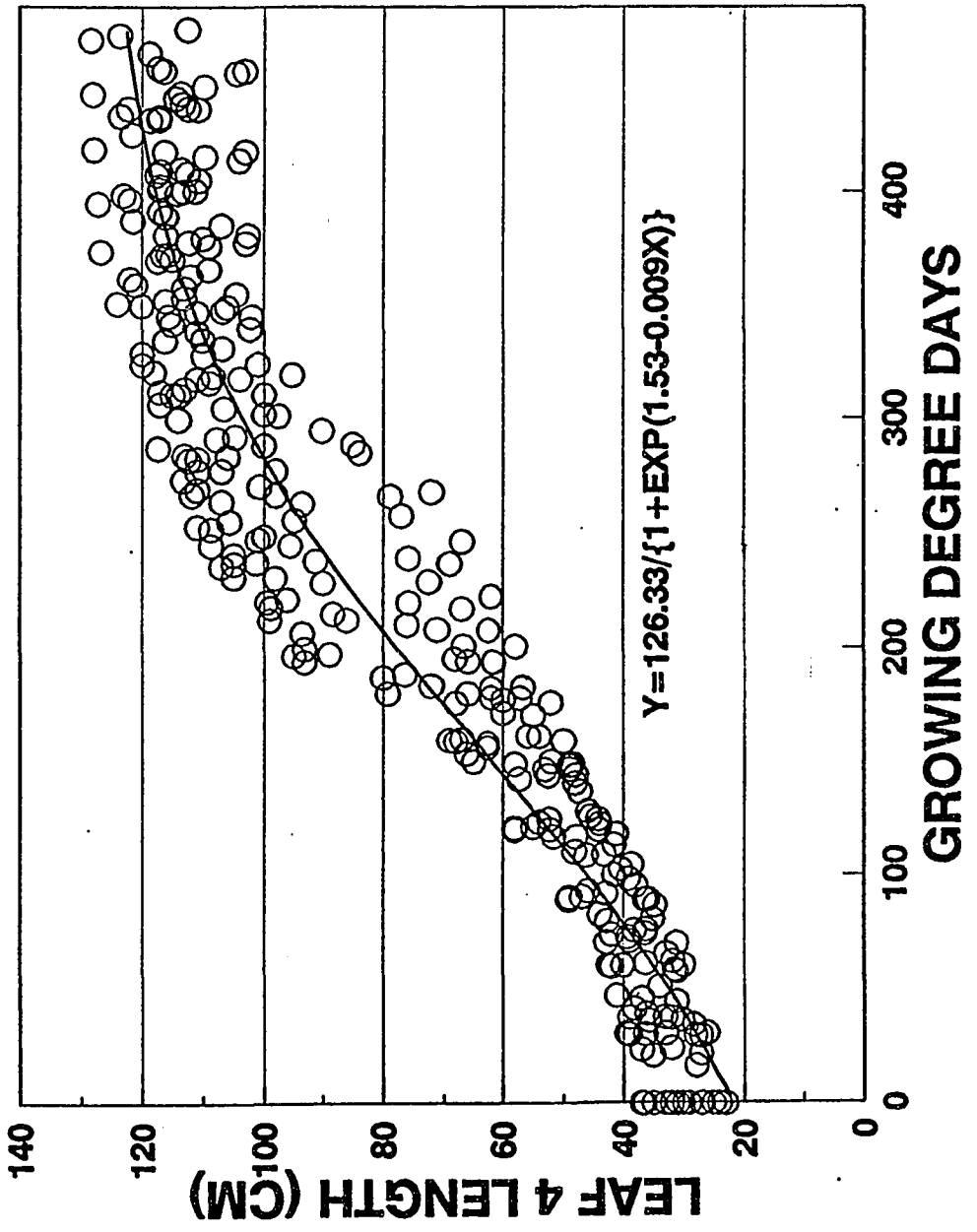

Figure 26. Fitting of leaf 4 elongation pattern by S-curve regression equation of GDD with a base temperature at 14°C in H. angusta. Exp is base of natural log, e.

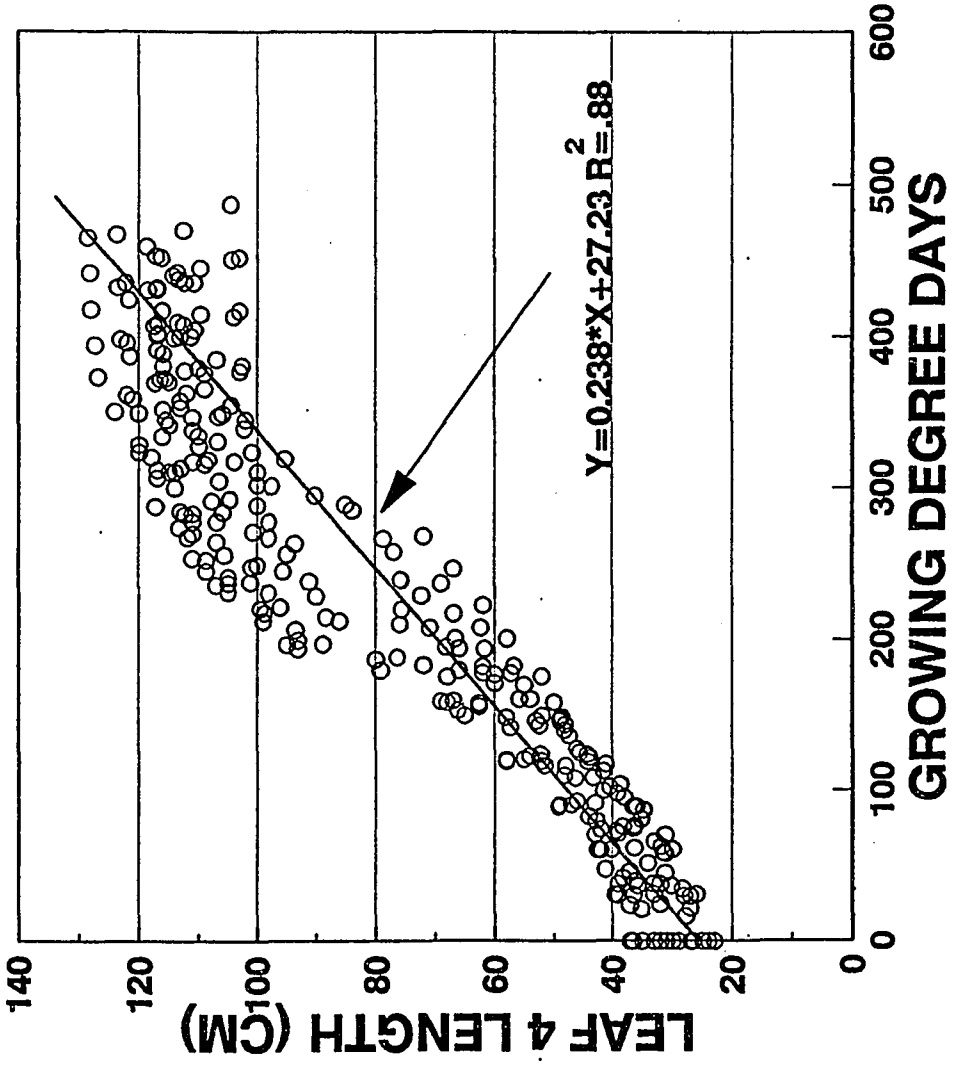

Figure 27. Fitting of leaf 4 elongation pattern by linear regression equation of GDD with a base temperature at 14°C in H. angusta.

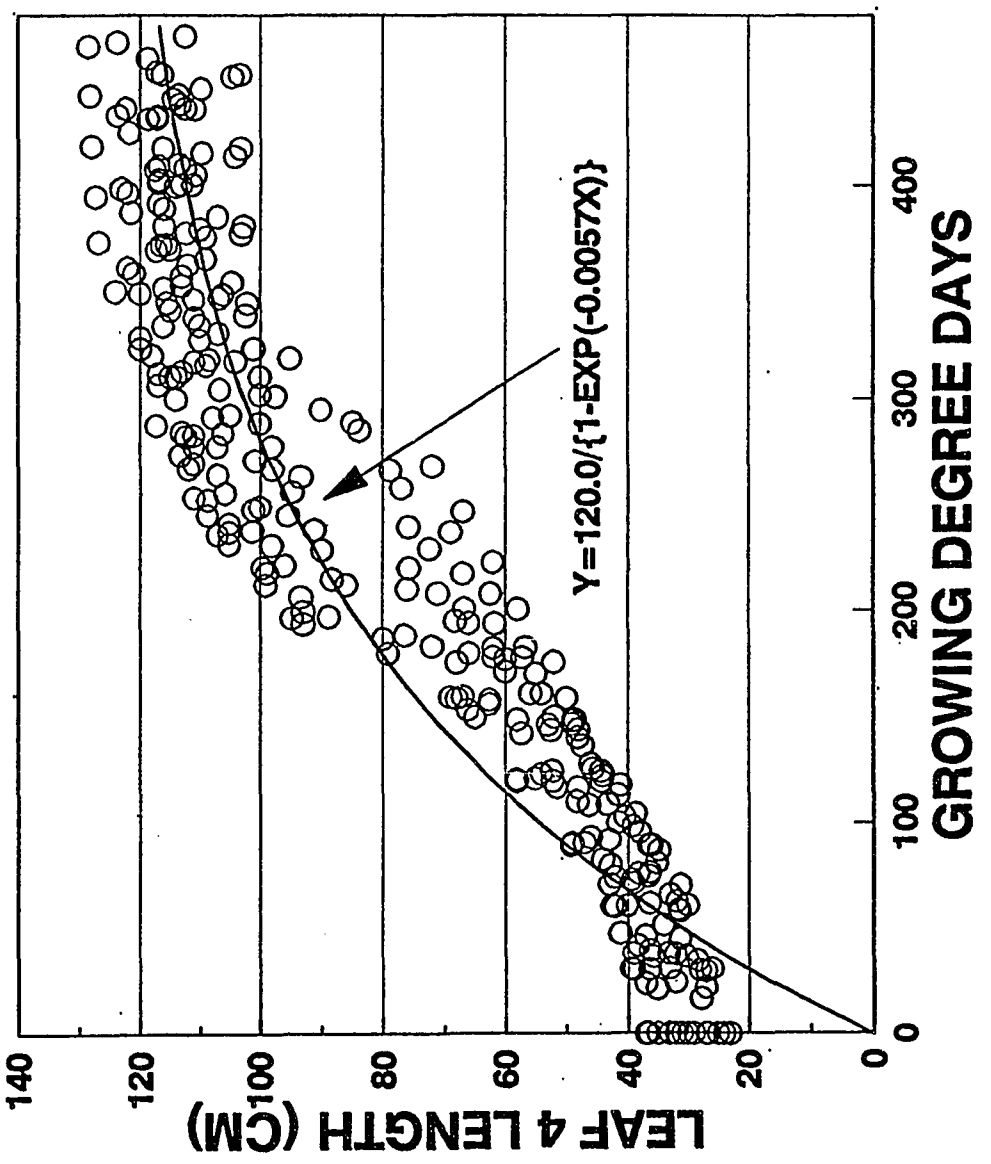

Figure 28. Fitting of leaf 4 elongation pattern by negative exponential equation of GDD with a base temperature at 14°C in H. angusta. Exp is base of natural log, e.

The plots of leaf 4 length on calendar growing day (CGD) model are shown in Figure 29. When compared with the GDD model in Figure 28, both models had significant fitness at 5 % level (Appendix Table 28). Out of 2 models, the plot of leaf length against GDD units showed more concentrated points and had better fitness, and CV values based on GDD were lower than the ones based on calendar days (Table 3).

The regression fittings of leaf growth on GDD by secant non-linear regression analysis method in leaf 1, 2 3, and 5 are shown in Figures 30 and 31. In all leaves, the S-curve regression showed significant fitness at 5 % level (Appendix Tables 29-32).

7.4.4. Validation of models

Validations of model in leaf 4 is shown in Figure 32 and in leaf 1, 2, 3, and 5 is shown in Figure 33. Linear correlation analysis (Appendix Tables 33-37) showed that there was a significant positive correlation between the observed and predicted values thus indicating good prediction capability of models.

7.4.5. Estimation of leaf elongation rate by GDD unit and calendar day

The whole feature of leaf 1 to leaf 7 elongation over time course change is shown in Figure 34. As leaf growth

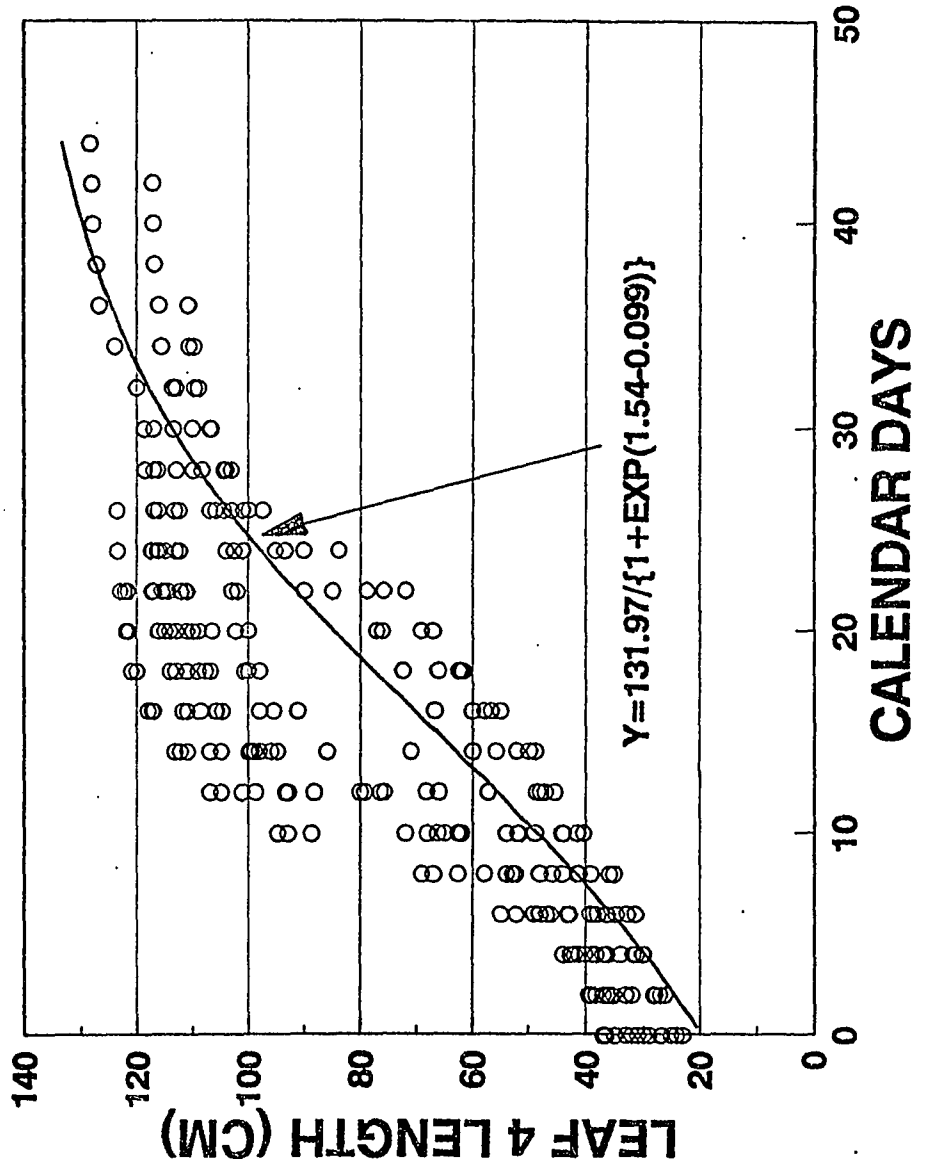

Figure 29. Fitting of leaf 4 elongation pattern by S-curve regression equation of calendar growing days in H. angusta. Exp is base of natural log, e.

Table 3. Comparison of fitness of growing degree model (GDD) based on 14 °C base temperature and calendar growing day (CGD) model for leaf growth in H.angusta.

Leaf	Coefficient of variation (%)[x]	
	GDD model	CGD model
1	5.6	18.8
2	2.4	22.2
3	4.2	22.6
4	4.1	21.8
5	3.6	21.2
6	3.4	15.5
7	6.2	15.8

[x]t-test of coefficient of variation between GDD and CGD models shows significant difference in each leaf.

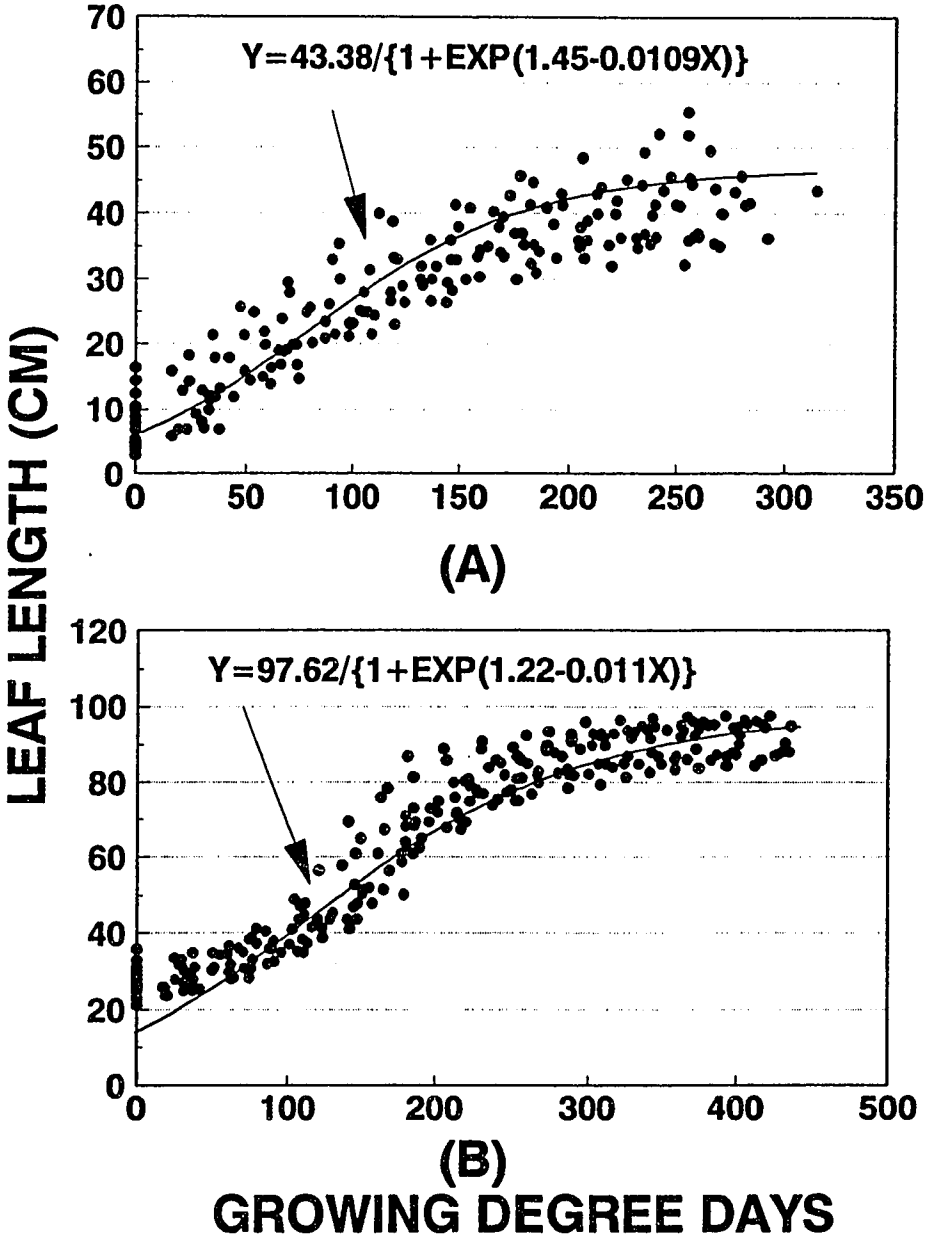

Figure 30. Regression models of GDD of daily average temperature with a base temperature at 14°C for leaf 1(A) and 2(B) elongation patterns in H. angusta. Exp is base of natural log, e.

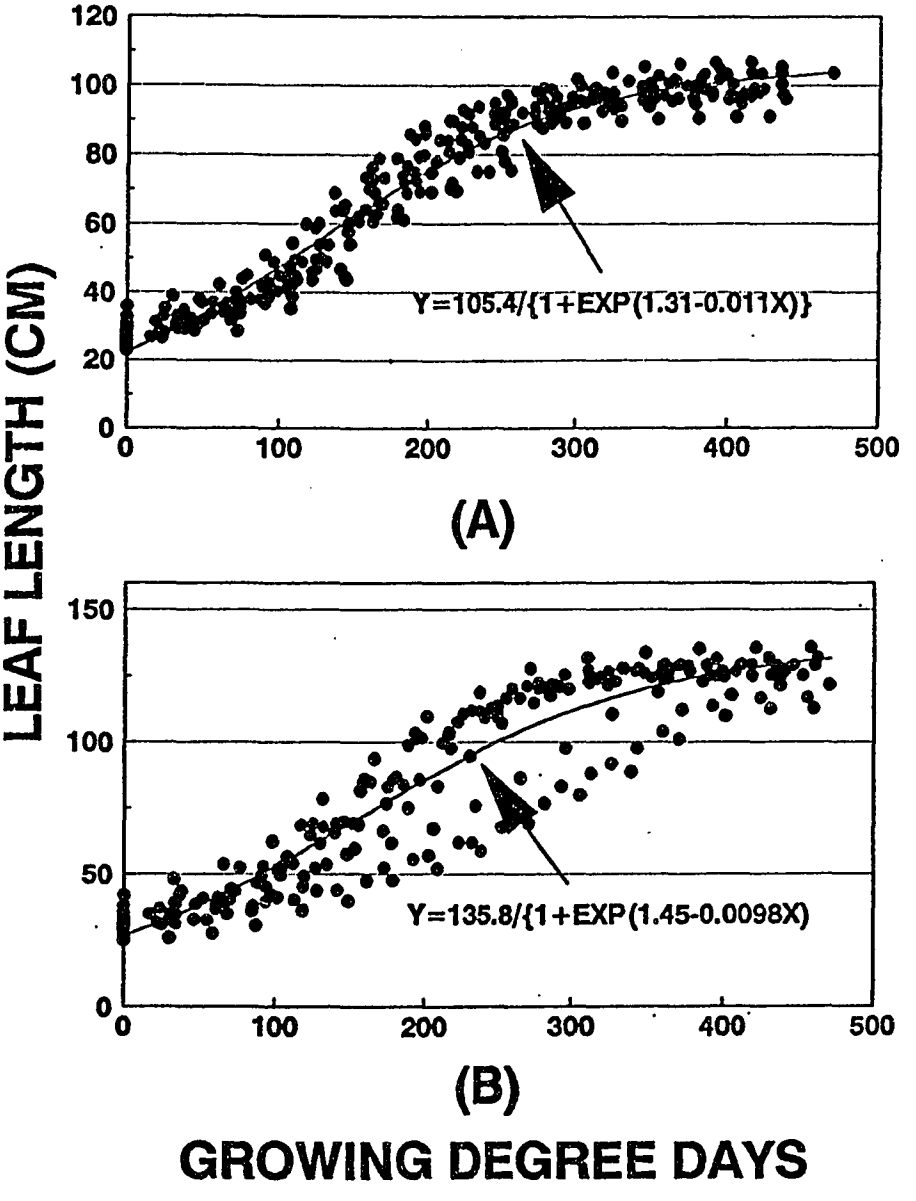

Figure 31. Regression models of GDD of daily average temperature with a base temperature at 14°C for leaf 3(A) and 5(B) elongation patterns in H. angusta. Exp is base of natural log, e.

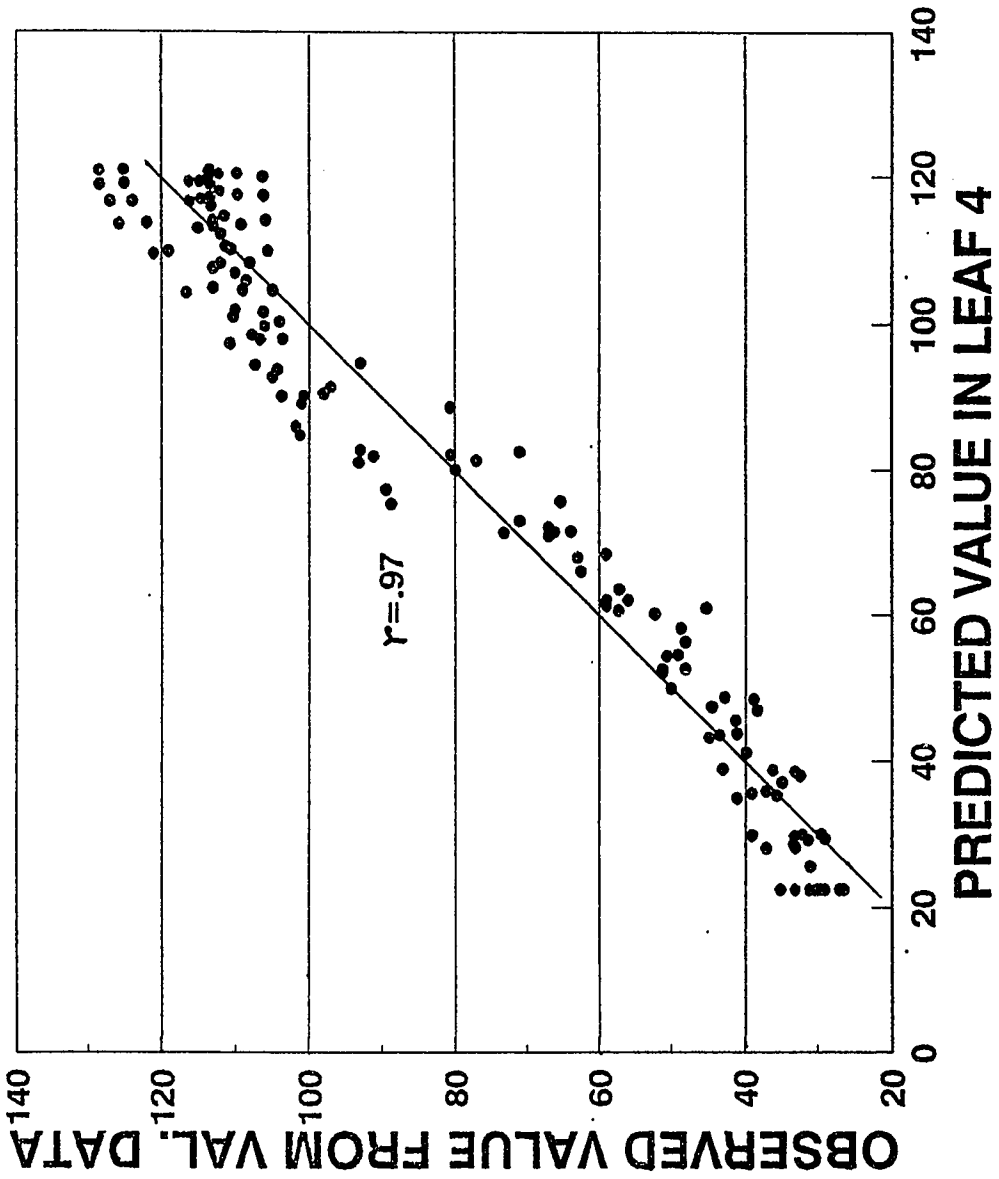

Figure 32. Validation of GDD model for elongation pattern of leaf 4 in H. angusta. Observed lengths from validation data set were plotted against predicted lengths generated from model. Correlation between observed and predicted values was significant.

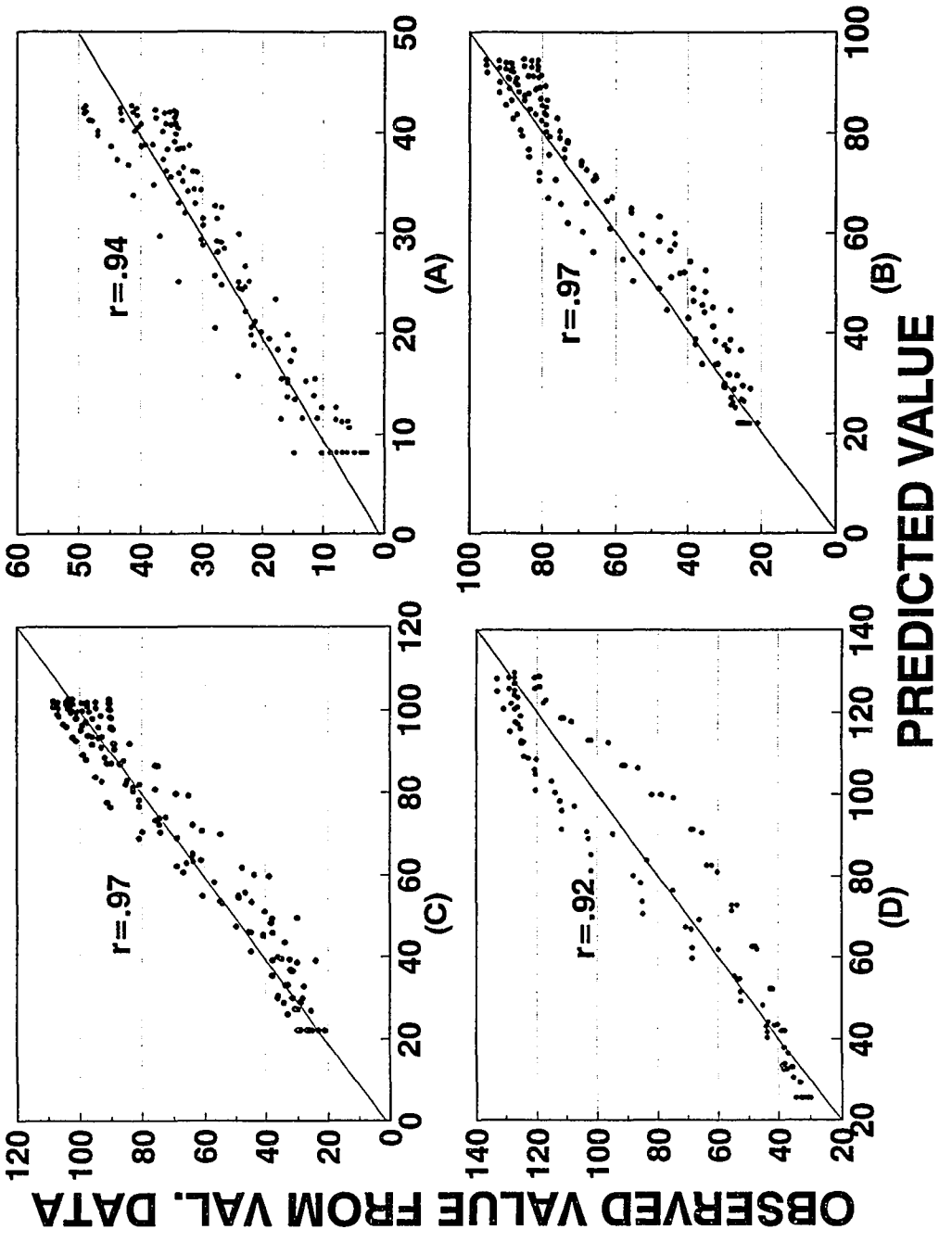

Figure 33. Validation of GDD models for elongation patterns of leaf 1(A), 2(B), 3(C), and 5(D) in H. angusta. Observed lengths from validation data set were plotted against predicted lengths generated from model. Correlation between observed and predicted values was significant.

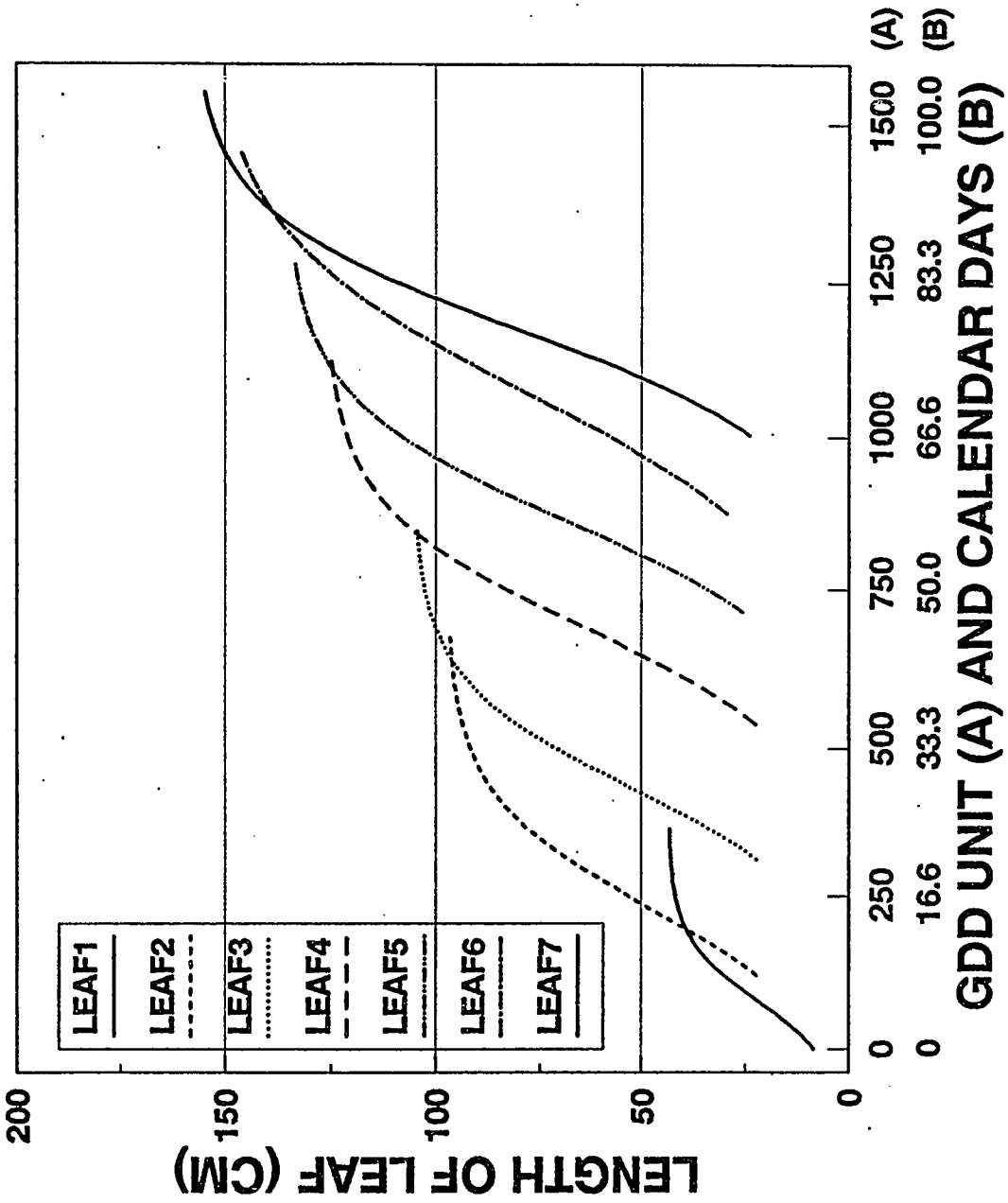

Figure 34. Elongation pattern of leaf 1 to 7 leaves plotted against GDD units and calendar days in H. angusta. GDD 0 and calendar 0 indicateS the day of leaf 1 emergence.

curve model was computed from the day of leaf emergence (leaf blade emergence from sheath) to the end day of leaf growth, all the starting points of models were set to zero. To see the whole feature of leaf growth over time, GDDs requirement for growth of each leaf and regression equations of all leaves, and GDD between shoot emergence and leaf 1 emergence and between leaf 1 emergence and succeeding leaf emergence (Table 4) were taken into consideration. For example, regression equation for leaf 3, $Y=105.43/(1+e^{1.31-0.011X})$ was changed to $Y=105.43/(1+e^{1.31-0.001(X-310)})$ because GDD for interval between shoot emergence to leaf 3 emergence was 310. So this value was used as a starting point for graphical presentation of leaf 3 over time period.

Estimation of leaf elongation rate is shown in Table 5. Leaf 1 has the lowest growth (elongation) rate, whereas, leaf 5 has the highest growth rate among 5 leaves. The average daily growth rate of 5 leaves over GDD unit was 0.254 cm/GDD unit. The average growth rate of 5 leaves over calendar days was 3.80 cm/day. Since average daily temperature during the experiment of leaf growth estimation (January 1 - October 10, 1991) was 29 °C and GDD model was based on a base temperature of 14 °C, average daily heat accumulation was 15 °C/day. Multiplication of leaf growth rate (0.254 cm/GDD) by 15

Table 4. Growing degree day (GDD) units and calendar days from shoot emergence to full length of succeeding leaf and from leaf 1 emergence to next leaf emergence in H. angusta.

Shoot-leaf full growth	GDD units	Calendar days
leaf 1	272-316	18-21
leaf 2	521-587	36-39
leaf 3	677-745	42-54
leaf 4	930-992	66-72
leaf 5	1139-1215	77-82
leaf 6	1279-1371	85-92
leaf 7	1451-1541	96-104

Shoot-leaf emergence	GDD units	Calendar days
leaf 1	21.0	3.1
leaf 2	141.1	9.6
leaf 3	410.0	17.7
leaf 4	516.8	36.8
leaf 5	730.7	48.7
leaf 6	893.3	59.6
leaf 7	1067.9	68.3

Table 5. Estimation of growth rate of leaf 1 to leaf 5 by GDD units and calendar days in H. angusta.

Leaf[x]	Length[y] (cm)(Y)	GDD unit(A)	Calendar days(B)	Y/A (cm/GDD)	Y/B (cm/day)
1	43.3	273.8	19.4	.18	2.23
2	97.6	418.0	28.8	.25	3.39
3	105.4	421.9	28.8	.26	3.66
4	126.3	446.0	28.7	.28	4.40
5	135.9	447.0	28.3	.30	4.80
Average				.254	3.80

[x]Number of each leaf was 20.
[y]Leaf length was length of total leaf blade + sheath.

was 3.80 cm/day which was the same value derived from average daily growth rate.

7.5. Discussion

Modelling is only one of the many techniques that are available to us in our quest to understand the mechanism underlying plant development and growth. Like all other techniques the level of detail employed in any particular study is primarily determined by the objectives of the model (Charles-Edwards, 1979a and 1983). If the mechanism determining the rate and/or extent of leaf growth is the main interest a detailed, mechanistic model will be more appropriate to study leaf growth mechanism (Charles-Edwards, 1979a).

To predict certain time or study the relationship, an empirical model such as GDD models is used (Dennett et al., 1978). GDD models are used in various ways to understand certain developmental stage of development or growth process over time because interpretation of development process over calendar time is not accurate to due to unequal temperature or light irradiation year round. In heliconia, the GDD requirement for leaf growth has a practical implication in calculating the potential shoot emergence period that permits flowering.

Plant growth is often analyzed in terms of the influence of environmental factors on leaf length or area.

Temperature affects growth more than other factors because plant growth involves numerous enzyme-catalyzed biosynthetic chemical reactions, each of which is rate-controlled by temperature (Terry et al., 1983).

In grasses, leaf growth proceeds by cell division and cell expansion at the base of leaf. In the studies of Zea mays, it was found temperature at the base of leaf had a more pronounced role than ambient temperature (Watts, 1972a). In the field, the effect of large diurnal variations of air temperature was negligible if soil temperature at the base of leaves were kept constant (Watts, 1972b). Similar results were reported in rye (Peacock, 1975) and pearl millet (Ong and Baker, 1985). It might be more accurate to study leaf growth of H. angusta with soil temperature or leaf temperature as seen in bird of paradise (Kawabata, 1986). In practice, since prediction of soil temperature (Albright et al., 1989), or media temperature in container (Martin and Ingram, 1992) based on air temperature is available, modelling leaf growth pattern with air temperature is more convenient than with soil temperature because measurement of air temperature is more standard and data are readily accessed from nearby weather stations.

The best fitted S-curve equation can be applied to predict leaf growth in any location if temperature data in that particular location is available. The important

practical implication of GDD units 677-745 is the minimum GDD units requirement of vegetative growth of plants to initiate flower because leaf 3 is the earliest stage of H. angusta to respond to photoperiod stimulus.

The important role of temperature and light playing in leaf growth can not be, but carbon dioxide supply, water and salt stress, and mineral nutrient supply are also involved in leaf growth. If a more detailed model of leaf growth is required or sufficient time and resources were given, it might be more appropriate to include all these factors in model building.

CHAPTER 8. ESTIMATION OF THE LATEST SHOOT EMERGENCE TIME FOR FLOWERING

8.1. Abstract

H. angusta plants were grown under natural condition to estimate the potential flower initiation, flower development, flowering (inflorescence emergence) period, and the latest shoot emergence day for flowering in Honolulu. Daily average temperatures of 30 years from January 1, 1962 to December 31, 1991 and daily daylength including morning and evening civil twilight in Honolulu were used for this estimation. Out of 79 flowered stems, 76 (96.2 %) stems initiated flowers under the daylength 13 hr or longer and only 3 (3.8 %) stems initiated flowers under the daylength between 13 and 12.5 hr. In Honolulu temperature and daylength conditions, a potential flower initiation period was from March 28 to July 30, a potential flower development period was from May 16 to December 5, and a potential flowering period was from August 30 to January 7. Monthly harvest data from a commercial heliconia grower showed that the peak harvest times fitted the models with 99.6 % of the yield falling within predicted dates. The latest shoot emergence which 2could initiate a flower under 13 hr or longer daylengths was from June 16 to 28 indicating that it is almost

impossible for the shoots which emerge after June 29 to initiate and develop.

8.2. Introduction

Climate is one of the factors that affect growth rate and flower production of H. angusta. In Oahu, there is no significant difference in monthly rainfall, average monthly temperature, or average monthly light intensity, but photoperiod was suggested as an influence on flower bud initiation (Criley, 1985). Flower bud initiation of H. angusta under LD photoperiod was reported (Lekawatana, 1986). A critical daylength of 13.3 hr for flower bud initiation was proposed because pseudostems which emerged after August failed to flower (Sakai et al., 1990a).

The problem in H. angusta production is that H. angusta blooms over too short a period, and growers want to extend the flowering period. The objectives of this experiment were:

1. To determine the potential flower initiation, flower development, and flowering periods in Honolulu.
2. To determine the latest shoot emergence dates which permit flowering.

The results derived from this experiment might help commercial heliconia growers who want to expand the flowering period of H. angusta to produce flowers off-

season and plan their production schedule depending on the demand in the flower markets.

8.3. Materials and methods.

8.3.1. Weather data collection

Local climatological data, Honolulu (collected at Honolulu International Airport), Hawaii Monthly Summary (USDT, 1962-1991) was used for temperature. The daily average temperature was chosen since daily average temperature, as seen in Chapter 7, was better for modelling leaf growth than daily maximum temperature. The period of data collection was 30 years from January 1, 1962 to December 31, 1991. From these 30 year temperature data, 5 % level confidence limits for daily average temperature and GDD based on 14 °C base temperature were computed.

8.3.2. Daylength data collection

Daily daylength at Honolulu was calculated from the table of morning civil twilight and evening civil twilight (NAO, 1992). As location of Honolulu is N21°20′ W157°48′, interpolation equation for morning civil twilight (MCT) was MCT of N20°+/-{(21°20′-20°)/(30°-20°)} depending on MCT at N 20° and N30°. When MCT at N30° occurred later than MCT at N20° during the winter time, the sign in equation

was +(positive) and vice versa. The evening civil twilight time (ECT) was calculated in the same way.

Based on this daily daylength including civil twilight, a critical range for flower bud initiation was calculated. As the duration of flower bud initiation was between 7 and 8 weeks, the days for the plant to have enough time to respond to LD photoperiods longer than 13 hr was July 26 to August 2 for pseudostems. From these dates, the latest day for shoot emergence which enables the plants to grow fully before the potential last day for flower bud initiation was calculated by applying GDD estimate requirements for 3 and 4 leaf growth. As seen in Chapter 7, GDD requirement from shoot emergence to leaf 3 full expansion was 667-745 and 870-973 GDD from shoot emergence to leaf 4 full expansion, so the potential latest shoot emergence day for shoots with 3 leaves to respond to photoperiods of 13 hr or longer was calculated by equation: (September 2)- (7 to 8 weeks for flower bud initiation)- (Number of days which meet GDD 667-745 requirement from 30 year temperature data set in Honolulu and Pope lab temperature data set for shoots with 3 leaves). The potential latest shoot emergence day for shoots with 4 leaves to respond to photoperiods of 13 hr or longer was calculated in the same way from 30 year temperature data.

8.3.3. Validation of model

Two sets of data were used for validation. Monthly production data of H. angusta obtained from a commercial heliconia grower and the data of shoot emergence and flowering date obtained from the experiment described in chapter 7 were used.

8.4. Results

8.4.1. Estimation of potential flower initiation, development, and flowering period by daylength model

The daylength including morning and evening civil twilight in Honolulu was in range of 11.8 to 14.2 hr (Fig. 35). The longest daylength was around June 21 and the shortest one was around December 21. The period between March 2 to October 10 had daylengths longer than 12.5 hr and the period between March 28 to September 20 had daylengths longer than 13.0 hr in Honolulu.

The minimum daylength requirement for H. angusta flower bud initiation was shown to be 13 hr. Although no flowers developed in pseudostems treated under 12.5 hr daylength (Fig. 1), the possibility of flower bud initiation between 13 and 12.5 hr daylengths could not be totally excluded. In this model, the critical daylength for flower bud initiation was set at 13 hr.

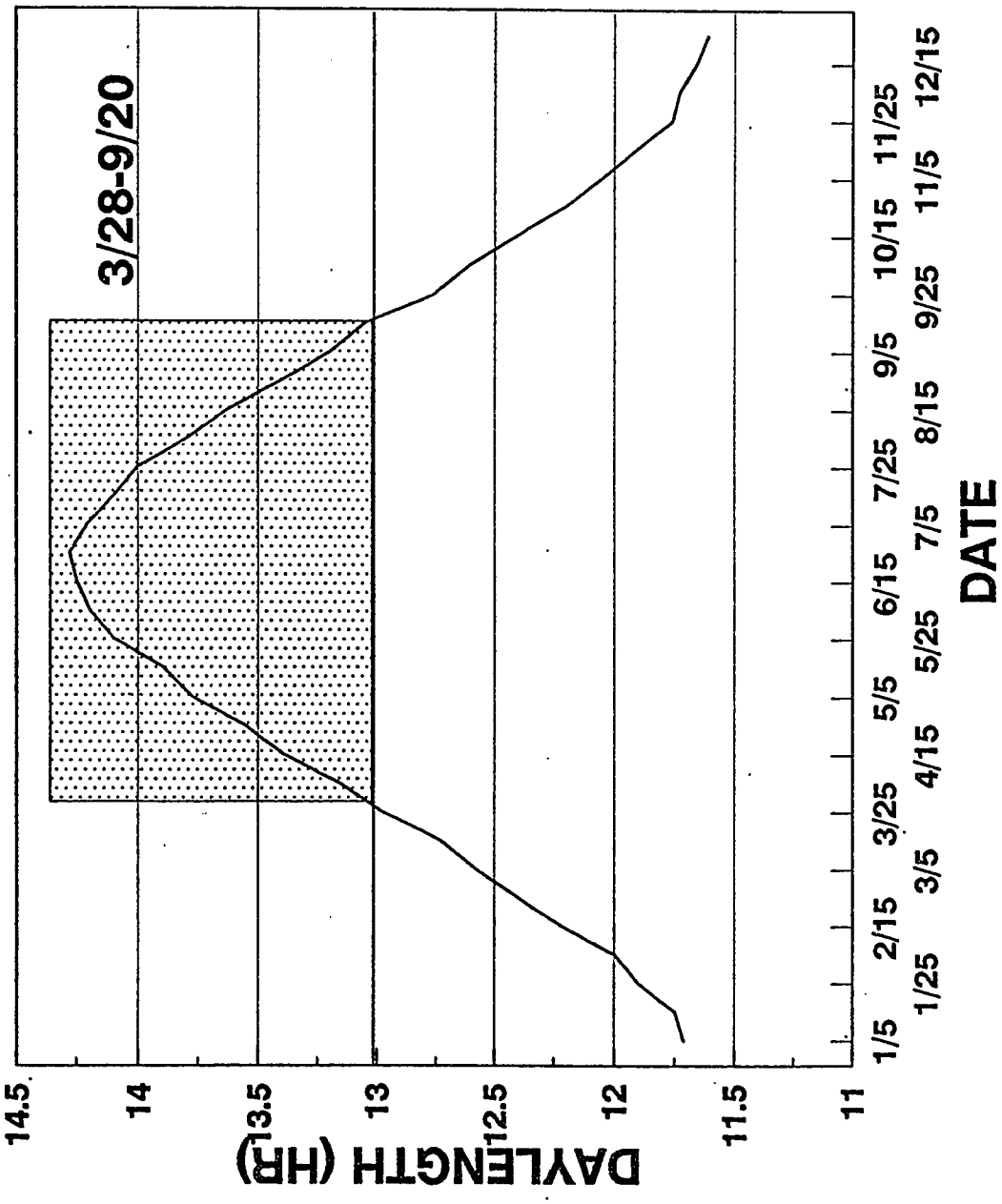

Figure 35. Daylength including morning and evening civil twilight in Honolulu (N 21°20′ W157°48′at International Airport), Hawaii. (Nautical Almanac Office, 1992). Box denotes 13 hr photoperiod.

The daylength model which combined daylength data and 13 hr critical daylength requirement for flower initiation proposed potential flower bud initiation and flowering periods (Fig. 36). The potential flower bud initiation period was from March 28 to July 30 (+/- 3 days) under daylength of 13 hr or longer. Since flower bud development required 15 to 17 weeks after long day treatment, the potential flowering time could be calculated, and it was from August 30 to January 7 next year.

The validation of this daylength model was made using production data obtained from a commercial heliconia grower. Monthly harvest data (Fig. 37) of H. angusta from a commercial heliconia grower showed that the peak harvest times fit the model proposed in Fig. 36 with 99.6 % (5619 out of 5642 stems) of the yield falling within predicted dates indicating that model was adequate to explain the seasonal flowering period of heliconia.

8.4.2. Estimation of potential flower initiation, development, and flowering period by GDD model

The latest shoot emergence period which allowed flower bud initiation was June 5-16 for pseudostems which will develop 4 leaves and June 16-28 for pseudostems which will develop 3 leaves prior to initiation when the minimum day length requirement was set to 13 hr.

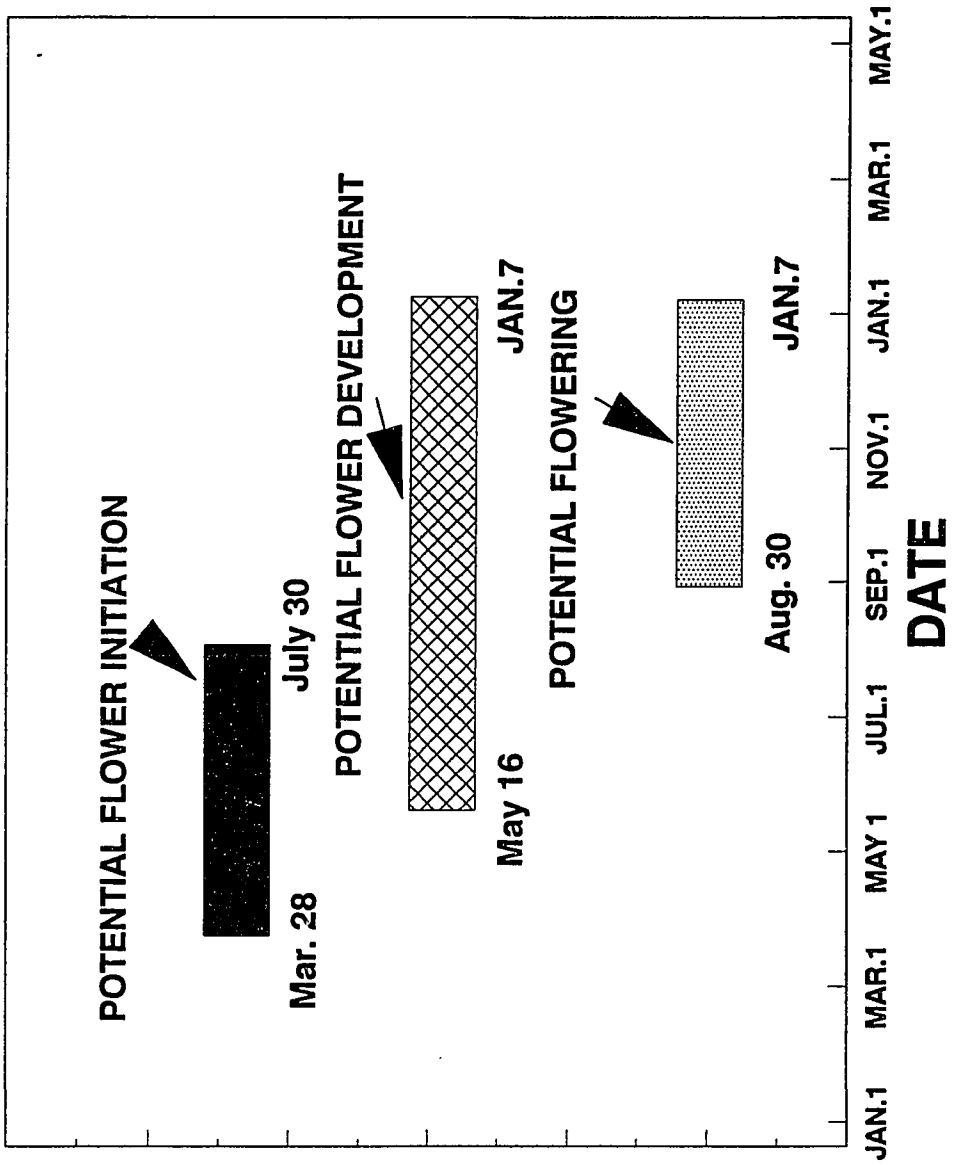

Figure 36. Model of potential flower initiation, flower development,and flowering time (emergence of inflorescence) for stems with 3 leaves based on Honolulu daylength and minimum long-day requirement for flower initiation in H. angusta. Assumption of shortest initiation time of 7wks and shortest development time of 15 wks for the earliest flowers.

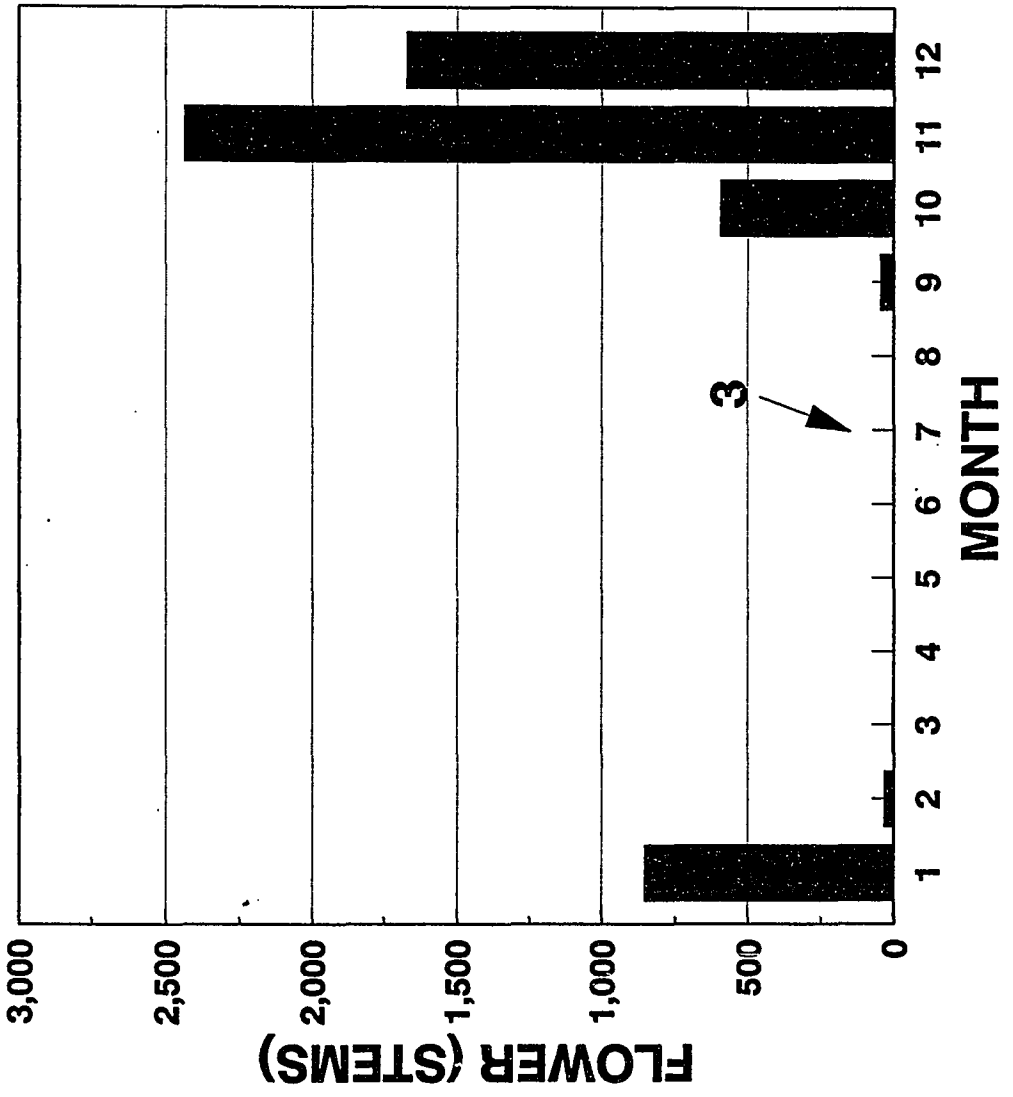

Figure 37. Monthly harvests of H. angusta from a commercial heliconia grower. The peak harvest times fit the model generated in Fig. 36 with 99.9% of the yield falling within predicted dates. 3 stems in July does not fall within predicted dates.

Shoot emergence time and flowering time fit the model proposed in Figure 36. Out of 79 flowered stems, 76 (96.2 %) stems occurred within predicted dates. Shoots which emerged before June 28 could initiate flower under a daylengths 13 hr or longer while only three (3.8 %) stems that emerged after July 1 could initiate flower under the daylength between 13 and 12.5 hr in Pope lab glasshouse condition (Table 6). The stems initiated within the potential shoot emergence days showed 38.8 to 43.7 % flowering percentage (number of flowered stems per total number of stems) and the stems whose emergence did not fall within the potential shoot emergence time showed 21.4 % flowering percentage.

The days for emergence of a pseudostem (July 14) which was capable of flowering later was after GDD requirement for full leaf expansion of leaf 3 or leaf 4. GDD from July 14 to July 30 was 323 which was far below the normal GDD requirement for leaf 3 (667-745: 42-54 days) and leaf 4 (930-992: 66-72 days). 323 GDD units means only 46 to 61 % length of full leaf 3. There are some possible explanations about this. One explanation is that minimum LD photoperiod for flower bud initiation might be shorter than 13 hr thus allowing sufficient time to complete initiation. The other explanation proposes an ability of a pseudostem to respond to photoperiod stimulus with 46 to 61 % of fully grown leaf 3 length.

Table 6. Flowering percentage of H. angusta in relation to shoot emergence day in Pope lab condition.

Shoot emergence day	Number of Shoots (X)	Number[y] of Flowers(Y)	Y/X(%)	
Jan. 1---May 31	147	62	42.2	A[z]
Jun. 1---Jun. 15	16	7	43.7	A
Jun. 15--Jun. 30	18	7	38.8	A
Jul. 1---Jul. 11	11	2	18.2	B
Jul. 12--Jul. 15	5	1	20.0	B
Jul. 15--Jul. 31	17	NO FLOWERING		

[y]Number of flowers was number of stems that showed flower stalk.
[z]Mean separation in column by Duncan's multiple range test.

As pseudostems emerging after July 15 did not flower, the minimum photoperiod for plants to initiate flower buds could not be 12.5 hr and should be longer than 12.5 hr daylength. The combination of results of pseudostem emergence and flowering capability based on critical daylength of 13 hr indicated that minimum daylength for flower bud initiation was between 13 and 12.5 hr if only a fully expanded leaf had capability of responding to photoperiodic stimulus.

Daily average temperatures were collected from 30 years data (Fig. 38) in Honolulu (measured at international airport). Accumulation of GDD units based on this daily average temperature with a 14 °C base temperature (Fig. 39), daily daylength in Honolulu (Fig. 35) were combined together to determine the shoot emergence days that permits for flower bud initiation in H. angusta (Fig. 40).

When minimum daylength for flower bud initiation was set at 13 hr, the latest shoot emergence day for the stems with 3 leaves to respond to photoperiodic stimulus was June 16 to June 28. When minimum daylength for flower bud initiation was set at 12.5 hr, the late shoot emergence days for the stems with 3 leaves to respond to photoperiodic stimulus was June 23 to July 11. It is obvious that plants can initiate flower buds if shoots emerge before June 16. In contrast to this, plants can

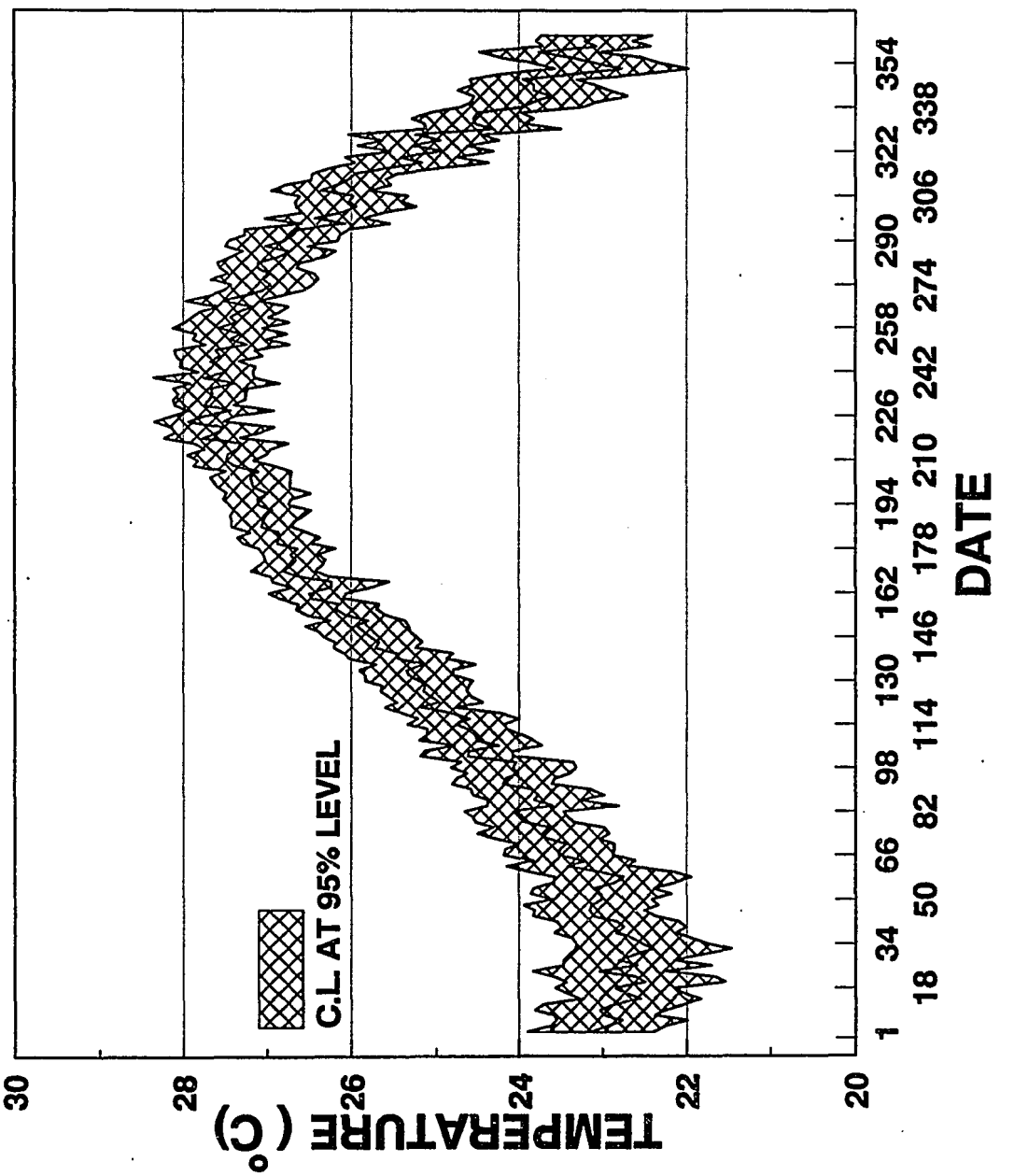

Figure 38. Average daily temperature measured at Honolulu international airport, Hawaii, during January 1, 1962 to December 31, 1991. Date 1 is January 1. (From USDC, 1962-1991)

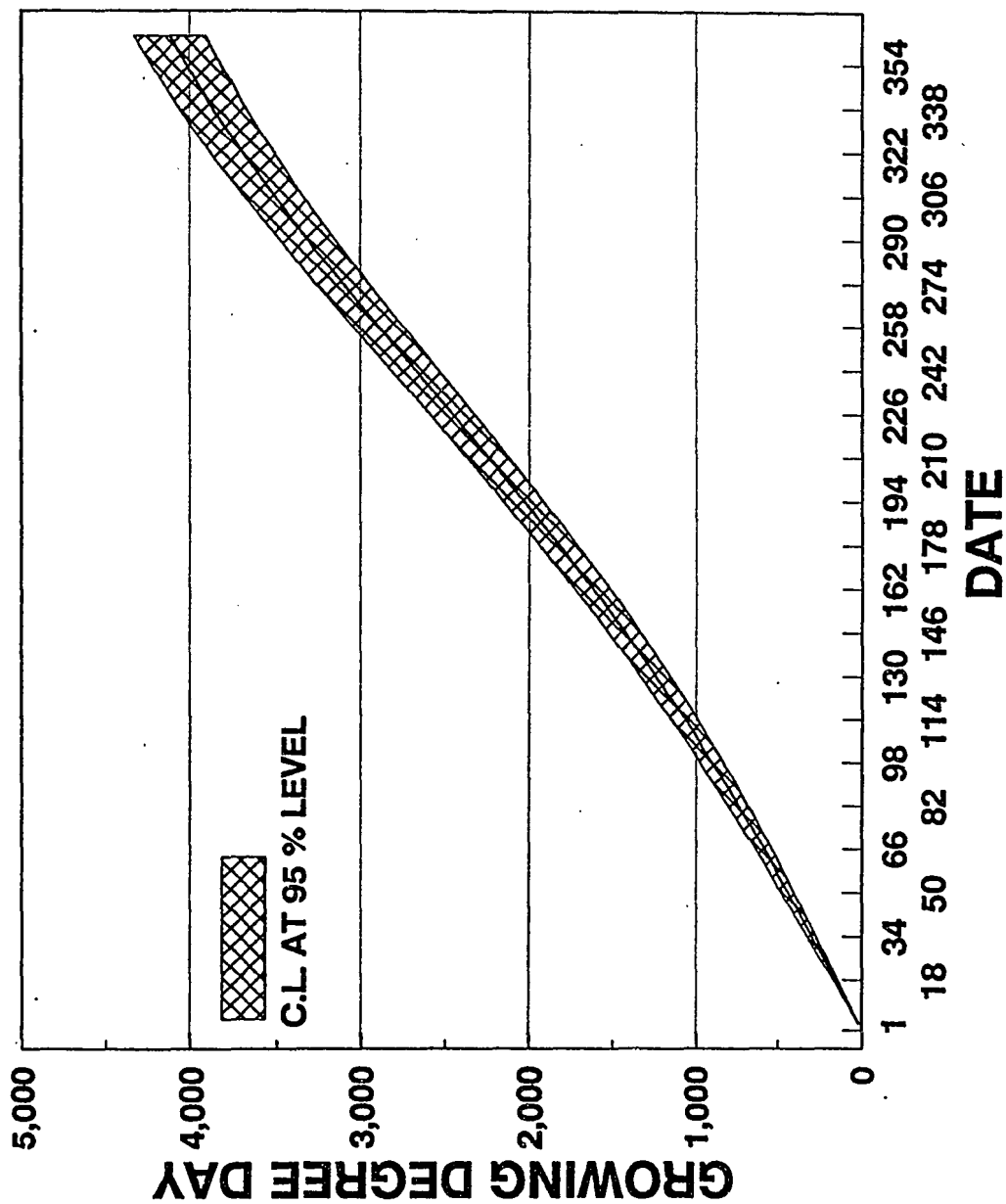

Figure 39. Accumulated GDD units based on average daily temperature from 30 year temperature data of Fig. 38 with a base temperature at 14°C in Honolulu. CL is confidence limit.

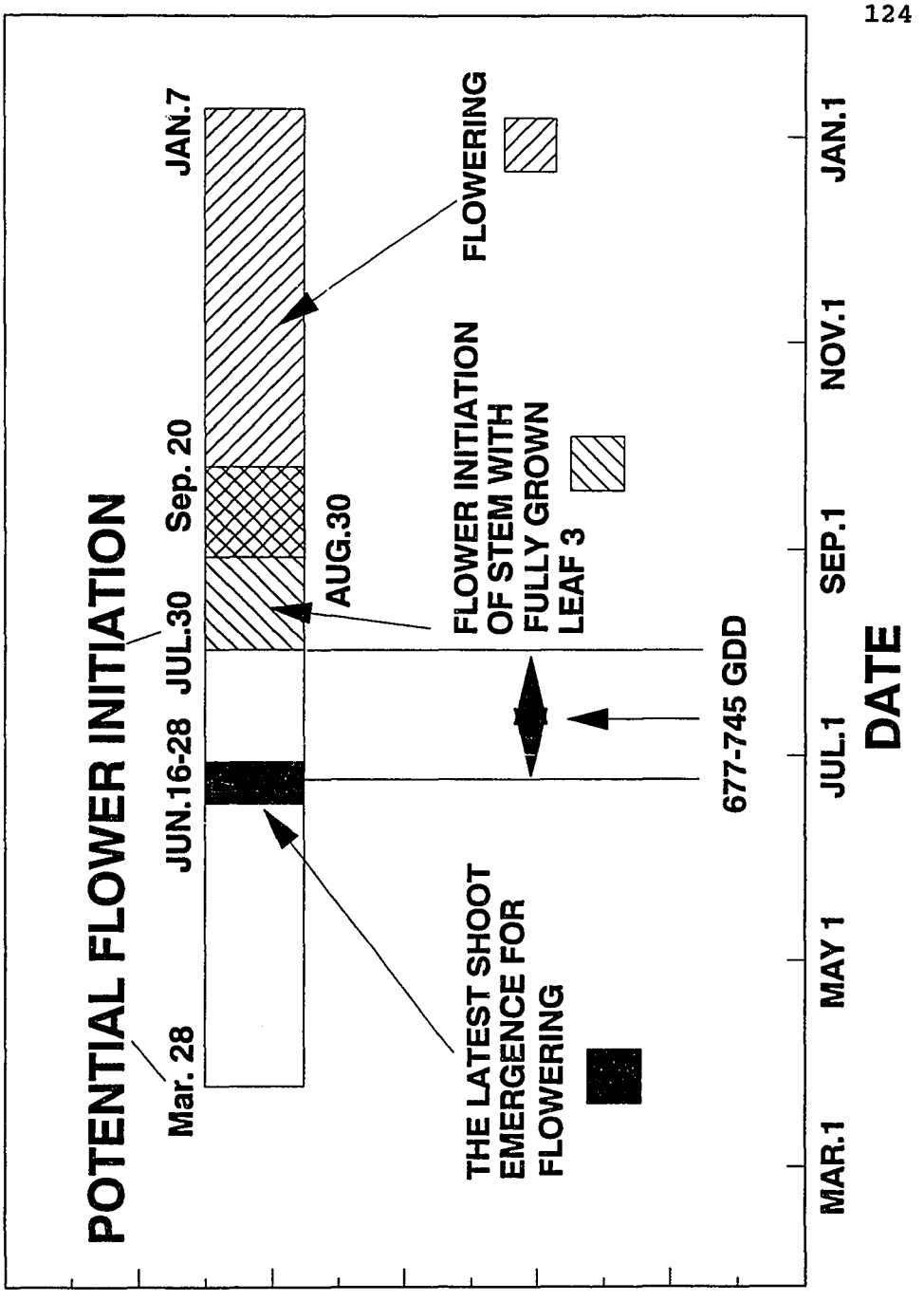

Figure 40. Model of the latest shoot emergence for H. angusta to initiate flower under daylengths of 13 hr or longer in Honolulu. GDD unit requirement from shoot emergence to leaf 3 expansion is 677-745.

not initiate flower buds if shoots emerge after July 11 because the daylength condition after July 11 is shorter than 12.5 hr.

8.5. Discussion

The result of the flower bud initiation experiment described in chapter 3 showed no flowering in the shoots treated under 12.5 hr daylength condition. Production data from a commercial heliconia grower showed that out of 5642 flowered shoots, 23 did not fall within predicted dates, because conditions in Koolau were different enough from Honolulu to permit 'escapes' to flower. In the Chapter 6 experiment, 3 shoots (3.6 %) emerged after July 1 (Table 6) which initiated under daylength condition shorter than 13 hr. This implied that there are some other factors in addition to daylength involved in the process of flowering in H. angusta. So this suggests the necessity to study those other factors in the future.

There are important practical implications of relationship between shoot emergence date and flowering possibility. In case of floriculture, prices of most flowers are higher in off-season than in the main production season so commercial flower growers attempt to produce flowers off-season (MAFF, 1987). It is well known that flowering can be manipulated by controlling temperature, daylength, light intensity, pruning,

fertilization, or application of plant growth regulators. By knowing potential flower initiation, development, and flowering periods, and the latest shoot emergence day which permits flowering, farmers can manipulate the shoot emergence dates or decide when to give long day condition with supplementary light. It is recommended that the best starting day to extend daylength to be after September 20 because natural daylength becomes shorter than 13 hr. From the view point of farmers for flower production management, supplemental lighting cost has to be considered. The best way may be to compare the lighting cost with the expected price of flowers when farmers sell those flowers in off-season market.

CHAPTER 9. CONCLUSION

Observance of seasonal flowering pattern of H. angusta led to Criley (1985) to suggest a possible photoresponse. Previous studies by Lekawatana (1986) and Sakai et al. (1990b) reported that flower bud initiation in H. angusta occurred under long day condition.

The minimum LD flower bud initiation was 13 hr for 7 wks. In daylength shorter than 13 hr, there was no initiation. In daylength longer than 13 hr, the difference in daylengths had no significant effect on time to flower which was 16 wks after the end of LD treatment. When flower initiation period and flower development duration were combined, the total duration from start of LD treatment to flowering had no significant difference, even though duration of LD treatments for initiation was had significant. The minimum number of leaves for flower bud initiation was three.

There was significant inverse relationship between number of pseudostems per pot and flowers produced indicating a effect of shoot density. Plants grown in 25 x 23 cm pots described in the experiment in chapter 4, 5, and 6 produced more flowers than the plants grown 16 x 13 cm pots described in chapter 3. Crop yield in field plantings generally has a positive linear relationship with planting density (MAFF, 1991), but above a certain

optimal planting density, crop yield decreases with increased planting density. Since flowers are the final product for heliconia growers, suitable density in field should be determined.

Longer durations of flower development produced longer flower stalk as compared to the shorter durations. In rice and soybean, later varieties which require longer seed development period yielded more than earlier varieties from the same planting date (ORD, 1991).

Night temperature during flower bud development showed significant effect on number of flowers and quality of flowers but not on flowering time. A similar results was obtained by Lekawatana (1986) who reported that there was a trend with increased temperature to fewer flowers, delayed flowering, longer stems and increased flower bud abortion (Lekawatana, 1986). Daylength had no effect on flower development similar to night temperature, but the 18 hr daylength treatment significantly enhanced the length of flower stalk. There was a positive correlation between length of flower stalk and the number of bracts as seen Chapter 3, so it was assumed that longer flower stalk produced more bracts.

Optimum light intensity increased flower production and quality. These results imply that higher solar radiation is a cause for a greater supply of assimilates for flower development following increase of

photosynthesis (Halevy, 1984). No flower production in 100 % full sun light condition was in agreement with the result of container grown H. angusta plants (Ball, 1987). In order to study the effect of full sun light, it is recommended that plants be grown under 100 % sun condition and be placed under different degree of shading conditions for the future study.

Leaf growth (elongation) patterns were fitted to S-curve non-linear regression models. The fitness of growing degree day models for leaf elongation patterns based on daily average temperature with 14 °C as a base temperature in order to describe was better than those using daily maximum temperature or calendar days.

The GDD requirement from shoot emergence to full expansion of leaf 3 under daylengths of 13 hr or longer was 677-745 (42-54 calendar days). And it was 930-992 (56-72 calendar days) from shoot emergence to leaf 4. The average elongation rate of leaf 1 to 5 was 2.54 mm/GDD unit and in calendar days, it was 3.8 cm/day.

In Honolulu daylength condition, potential flower bud initiation period under daylengths 13 hr or longer was March 28-July 30, flower development was May 16-December 5, and flowering was August 30-January 7. Validation with monthly harvest data from a commercial grower showed that 99.6 % of flowers was within the predicted flowering period. Based on Honolulu daylength and accumulation of

GDD units calculated from 30 year weather data (from January 1, 1962 to December 31, 1991), the potential latest shoot emergence for stems with full expanded leaf 3 to initiate flower bud under daylengths of 13 hr longer was June 16-28.

The practical implication of these results is that stimulating plants to initiate the flower bud earlier and develop flower over longer duration produces a better quality of flowers. High light intensity lamps might be useful in LD treatment for flower bud initiation. Shoots with 3 or 4 leaves at the start of LD treatments for flower bud initiation produced a better flower quality than the shoots with 5 or 6 initial leaves at the start of LD treatment because shoots with 3 or 4 leaves took longer time for flower development, but shoots with 3 initial leaves also showed the lowest flowering percentage. Therefore, compensation between these two parameters should be kept in grower's mind in his decision making. It might be considered in field management to enhance nutrition and do cutback practice in such a way to produce 3 to 4 leaf stems earlier in the year which would be receptive to LD stimulus.

For the future studies, although effects of environmental factors on flower development have been studied in such a way of the effect of one factor on flowering process, it is needed in the future to study

these effects in factorial design or response surface analysis to understand interaction of many factors if resources are enough to carry out this kind of experiment (Hopper and Hammer, 1991).

APPENDIX

Table 1. ANOVA of effect of daylength for flower bud initiation on number of flowers per pot in H. angusta.

Source	DF	SS	F Value	Pr > F
Daylength	2	0.666	0.32	0.7304
Error	60	63.333		

Table 2. ANOVA of effect of duration of daylength for flower bud initiation on number of flowers per pot in H. angusta.

Source	DF	SS	F Value	Pr > F
Duration	2	10.2777	25.35	0.0021
Error	250	125.3611		

Table 3. ANOVA of effect of daylength for flower bud initiation on time to flower in H. angusta.

Source	DF	SS	F Value	Pr > F
Daylength	2	0.2777	0.15	0.8651
Error	250	239.3270		

Table 4. ANOVA of regressing flowering time on duration of daylength for flower bud initiation in H. angusta.

Dependent variable: flowering time				
Source	DF	SS	F Value	Pr > F
Duration	1	38.878	48.62	0.0001
Error	251	200.725		

Table 5. ANOVA of regressing time to flower on number of leaves per stem in H. angusta.

Dependent Variable: Flowering time				
Source	DF	SS	F Value	Pr > F
Leaf number	1	31.1980	37.57	0.0001
Error	251	208.4066		

Table 6. ANOVA of effect of leaves per stem on flowering percentage in H. angusta.

Source	DF	SS	F Value	Pr > F
Leaf number	3	22.078	39.15	0.0001
Error	781	146.831		

Table 7. ANOVA of regressing number of flowers per pot on number of stems per pot in H. angusta.

Dependent Variable: Number of flowers per pot				
Source	DF	SS	F Value	Pr > F
Stems/pot	1	7.530	8.14	0.0059
Error	61	56.469		

Table 8. ANOVA of effect of daylength for flower initiation on length of flower stalk in H. angusta.

Dependent Variable: Flower stalk length				
Source	DF	SS	F Value	Pr > F
Daylength	2	369.35	2.83	0.0609
Error	250	16318.04	65.27	

Table 9. Linear correlation analysis of length of flower stalk on daylength duration for flower initiation in H. angusta.

Dependent Variable: Flower stalk length				
Source	DF	SS	F Value	Pr > F
Duration	1	515.268	7.35	0.0072
Error	251	17597.343		

Table 10. ANOVA of regressing length of flower stalk on time to flower in H. angusta.

Dependent variable: Flower stalk length				
Source	DF	SS	F Value	Pr > F
Flowering time	1	5981.75	140.25	0.0001
Error	251	10705.64		

Table 11. ANOVA of regressing length of flower stalk on initial number of leaves at flower initiation in H. angusta.

Dependent variable: Flower stalk length

Source	DF	SS	F Value	Pr > F
Leaf number	1	1736.86	29.16	0.0001
Error	251	14950.53		

Table 12. Linear correlation analysis of number of bracts on length of flower stalk in H. angusta.

Dependent variable: Number of bracts

Source	DF	SS	F Value	Pr > F
Correlation line	1	31.83	20.96	0.0001
Error	125	381.25		

Table 13. ANOVA of effect of daylength for flower bud development on number of flowers per pot in H. angusta.

Source	DF	SS	F Value	Pr > F
Daylength	3	0.176	0.22	0.8810
Error	27	7.178		

Table 14. ANOVA of effect of daylength during flower development on time to flower in H. angusta.

Source	DF	SS	F Value	Pr > F
Daylength	3	1.413	0.52	0.66
Error	131	118.779		

Table 15. ANOVA of effect of daylength during flower development on length of flower stalk in H. angusta.

Source	DF	SS	F Value	Pr > F
Daylength	3	265.75	1.68	0.1751
Error	131	6919.77		

Table 16. ANOVA of effect of initial number of leaves on time to flower in H. angusta.

Source	DF	SS	F Value	Pr > F
Leaf numbers	3	39.23	21.16	0.0001
Error	131	80.96		

Table 17. ANOVA of regressing number of flowers on night temperature during flower development in H. angusta.

Source	DF	SS	F Value	Pr > F
# of flowers	1	16.07	95.91	0.028
Error	16	2.68		

Table 18. ANOVA of regressing of flowering time on night temperature during flower development in H. angusta.

Source	DF	SS	F Value	Pr > F
Flowering time	2	6.61	1.36	0.079
Error	83	81.21		

Table 19. ANOVA of regressing length of flower stalk on night temperature during flower development in H. angusta.

Source	DF	SS	F Value	Pr > F
Flower stalk	2	171.23	4.06	0.018
Error	83	3501.11		

Table 20. ANOVA for regressing number of flowers per pot on light intensity during flower development in H. angusta.

Source	DF	SS	F Value	Pr > F
Light intensity	1	2.55	10.65	0.0036
Error	22	5.27		

Table 21. ANOVA for regressing time to flower on light intensity during flower development in H. angusta.

Dependent variable: Flowering time

Source	DF	SS	F Value	Pr > F
Regression	1	0.820	1.53	0.2186
Error	108	57.870		

Table 22. ANOVA for regressing length of flower stalk on light intensity during flower development in H. angusta.

Dependent variable: Length of flower stalk

Source	DF	SS	F Value	Pr > F
Regression	1	491.91	6.19	0.0143
Error	108	8576.45		

Table 23. ANOVA for regressing CV of GDD by daily maximum temperature on different base temperatures in H. angusta.

Dependent variable: Coefficient of variation

Source	DF	SS	F Value	Pr > F
Regression	1	3168.55	126.30	0.0001
Error	1338	33567.15		

Table 24. ANOVA for regressing CV of GDD by daily average temperature on different base temperatures in H. angusta.

Dependent variable: Coefficient of variation

Source	DF	SS	F Value	Pr > F
Regression	1	5156.16	187.50	0.0001
Error	1338	36795.67		

Table 25. ANOVA for regressing length of leaf 4 on linear equation based on GDD in H. angusta.

Dependent variable: Leaf length

Source	DF	SS	F Value	Pr > F
Linear regression	1	293421.80	2327.10	0.0001
Error	290	36565.75		

Table 26. ANOVA for regressing length of leaf 4 on negative exponential equation based on GDD in H. angusta.

Dependent variable: leaf length

Source	DF	SS	F Value
Exponential regression	1	2040428.11	1036.56
Error	291	57279.70	

Table 27. ANOVA for regressing length of leaf 4 on GDD model in H. angusta.

Dependent Variable : Length of leaf 4

Source	DF	SS	F Value
Regression	1	691038.06	8125.89
Error	289	24577.16	

Table 28. ANOVA for regressing length of leaf 4 on calendar growing day model in H. angusta.

Dependent Variable : Length of leaf 4

Source	DF	SS	F Value
Regression	1	100048.88	1176.47
Error	289	24577.16	

Table 29. ANOVA for regressing length of leaf 1 on GDD model in H. angusta

Dependent Variable : Length of leaf 1

Source	DF	SS	F Value
Regression	1	59670.25	1702.14
Error	181	6345.14	

Table 30. ANOVA for regressing length of leaf 2 on GDD model in H. angusta.

Dependent Variable : Length of leaf 2

Source	DF	SS	F Value
Regression	1	419459.03	7810.87
Error	255	13694.05	

Table 31. ANOVA for regressing length of leaf 3 on GDD model in H. angusta.

Dependent Variable : Length of leaf 3			
Source	DF	SS	F Value
Regression	1	523925.93	16176.27
Error	275	8907.72	

Table 32. ANOVA for regressing length of leaf on S-curve growth model of leaf 5 in H. angusta.

Dependent Variable : Length of leaf 5			
Source	DF	SS	F Value
Regression	3	633011.76	3665.75
Error	227	39207.75	

Table 33. Linear correlation analysis of validation data of leaf 1 on predicted value by GDD model in H. angusta.

Dependent variable: Observed length of leaf 1				
Source	DF	SS	F Value	Pr > F
Correlation line	1	16949.47	1013.84	0.0001
Error	125	2089.76		

Table 34. Linear correlation analysis of validation data of leaf 2 on predicted value by GDD model in H. angusta.

Dependent variable: Observed length of leaf 2				
Source	DF	SS	F Value	Pr > F
Correlation line	1	83186.90	2281.40	0.0001
Error	147	5360.07		

Table 35. Linear correlation analysis of validation data of leaf 3 on predicted value by GDD model in H. angusta.

Dependent variable: Observed length of leaf 3				
Source	DF	SS	F Value	Pr > F
Correlation line	1	130204.82	3126.89	0.0001
Error	173	7203.77		

Table 36. Linear correlation analysis of validation data of leaf 4 on predicted value by GDD model in H. angusta.

Dependent variable: Observed length of leaf 4

Source	DF	SS	F Value	Pr > F
Correlation line	1	148297.10	2867.57	0.0001
Error	134	6929.83		

Table 37. Linear correlation analysis of validation data of leaf 5 on predicted value by GDD model in H. angusta.

Dependent variable: Observed length of leaf 5

Source	DF	SS	F Value	Pr > F
Correlation line	1	145373.22	1234.06	0.0001
Error	121	14253.95		

REFERENCES

Abou-Haidar, S.S., E. Miginiac, and R.M. Sachs. 1985. ^{14}C-assimilate partitioning in photoperiodically induced seedlings of Pharbitis nil. The effects of benzyladenine. Physiol. Plant. 64:265-270.

Acock, B. 1988. Crop modelling in USA. Acta Hort. 248:365-371.

Albright, L.D., D. Wolfe and S. Novak. 1989. Modelling row cover effects on microclimate and yield: II. Thermal model and simulations. J. Amer. Soc. Hort. Sci. 114:569-578.

Alvim, P.de T. 1960. Moisture stress as a requirement for flowering of coffee. Science. 132:354.

Amer, F.A. and W.T. Williams. 1957. Leaf-area growth in Pelargonium zonale. Ann. Bot. 31:339-342.

Armitage, A.M. 1991. Shade affects yield and stem length of filed-grown cut-flower species. Hortscience. 26(9):1174-1176.

Armitage, A.M., N.G. Seager, I.J. Warrington, and D.H. Greer. 1990. Response of Oxypetalum caeruleum to irradiance, temperature and photoperiod. J. Amer. Soc. Hort. Sci. 115:910-914.

Armitage, A.M. and H.Y. Weltzstein. 1984. Influence of light intensity on flower initiation and differentiation in hybrid geranium. HortScience. 19:114-116.

Armitage, A.M., W.H. Carlson, and C.E. Cress. 1981a. Determination of flowering time and vegetative habit of Tagetes patula through response surface techniques. J. Amer. Soc. Hort. Sci. 106:632-638.

Armitage, A.M., W.H. Carlson, and J.A. Flore. 1981b. The effect of temperature and quantum flux density on the morphology, physiology, and flowering of hybrid geranium. J. Amer. Soc. Hort. Sci. 106:643-647.

Arnold, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Amer. Soc. Hort. Sci. 74:430-445.

Aspiazu, C. and R.H. Shaw. 1972. Comparison of several methods of growing-degree-unit calculations for corn (Zea mays L.). Iowa State J. Sci. 46:435-442.

Ball, D. 1987. Container culture for Heliconia angusta cv 'Holiday'. Bul. Heliconia. Soc. Intl. 2(1):2.

Ball, D. 1986. Viruses on heliconias. Bul. Heliconia Soc. Intl. 1(3):7.

Berlyn, G.P. and J.P. Miksche. 1976. Botanical microtechnique and cytochemistry. The Iowa State University Press. Iowa.

Berry, F. and W.J. Kress. 1991. Heliconia: An Identification Guide. Smithsonian Institution Press, Washington.

Blom, T.J. and B.D. Piott. 1990. Constant soil temperature influences flowering of alstroemerias. HortScience. 25:189-191.

Broschat, T.K., H.M. Donselman., and A.A. Will 1984. 'Andromeda' and 'Golden Torch' heliconias. HortScience. 19:736-737.

Broschat, T.K. and H.M. Donselman. 1983a. Production and postharvest culture of Heliconia psittacorum flowers in South Florida. Proc. Fla. State Hort. Soc. 96:272-273.

Broschat, T.K. and H.M. Donselman. 1983b. Heliconias: A promising new cut flower crop. HortScience. 18:1-2.

Broschat, T.K. and H.M. Donselman. 1988. University of Florida research update #1. Bul. Heliconia Soc. Intl. 2:5-6.

Bronstein, J.L. 1988. The origin of bract liquid in a neotropical Heliconia species. Biotropica. 18:111-114.

Bunt, A.C. 1973. Effect of season on the carnation (Dianthus caryophyllus) II.Flower production. J. Hort. Sci. 48:315-325.

Cain, J. 1971. Effects of mechanical pruning apple hedgerows with a slotting saw on light penetration and fruiting. J. Amer. Soc. Hort. Sci. 96:664-667.

Carle, A.W. 1990. Heliconias by seed. Bul. Heliconia Soc. Intl. 4:6.

Causton, D. and J. Venus. 1981. The biometry of plant growth. London.

Charles-Edwards, D.A. 1979. A model for leaf growth. Annals of Botany. 44:525-535.

Charles-Edwards, D.A. 1983. Modelling leaf growth and function. p.489-497. In the growth and functioning of leaves. Ed J.E. Dale and F.L.Milthorpe. Cambridge. Cambridge University Press.

Charles-Edwards, D.A., D. Doley., and G.M. Rimmington. 1986. Modelling plant growth and development. Academic Press. N.Y. pp:6-7.

Clough, B.F. and F.L. Milthorpe. 1975. Effect of water deficit on leaf development in tobacco. Aust. J. Plant Physiol. 2:292-300.

Constable, G.A. and H.M. Rawson. 1980. Carbon production and utilization in cotton: inferences from a carbon budget. Aust. J. Plant Physiol. 7:539-553.

Criley, R.A. 1985. Heliconias. pp.125-129. In: Handbook of flowering. A.H. Halevy (Ed). CRC Press Inc. Florida.

Criley, R.A. 1988. Propagation of tropical cut flowers : Strelitzia, Alpinia, and Heliconia. Acta Hort. 226:247-258.

Criley, R.A. 1989. Development of Heliconia and Alpinia in Hawaii: Cultivar selection and culture. Acta Hort. 246:247-258.

Criley, R.A. 1990. Production of heliconia as cut flower and their potential as new potted plants. Hort. Digest. University of Hawaii. 92:1-7.

Criley, R.A. and O. Kawabata. 1986. Evidence for a short-day flowering response in Heliconia Stricta 'Dwarf Jamaican'. HortScience. 21:506-507.

Criley, R.A. and S. Lekawatana, 1990a. Environment influences seasonality in flowering of Heliconia. XXIII Intl. Hort. Congr. Abstr. Vol.1:376, abstr no.1824.

Criley, R.A. and S. Lekawatana, 1990b. Phenology of flowering in cultivated Heliconia chartacea. HortScience. 25(9):138, abstr. no.530

Criley, R.A. and S. Lekawatana. 1991. A temperature-based model for growth and yield of Heliconia chartacea cv. Sexy Pink. Twelfth annual plant physiology in Hawaii symposium: program and abstract, University of Hawaii. Page:5.

Criley, R.A., P.E. Parvin, and S.Lekawatana. 1990. flower development in Leucospermum cordifolium cv. Vlam. Acta Hort. 264:61-70.

Croat, T.B. 1969. Seasonal flowering behavior in central Panama. Ann. Mo. Bot. Gard. 56:295-307. (Cited from Criley, 1985).

Dennett, M.D., B.A. Auld, and J. Elston. 1978. A description of leaf growth in Vicia faba L. Ann. Bot. 42:223-232.

Dennett, M.D., J.R. Milford, J. Elston. 1978. The effect of temperature on the relative leaf growth rate of crops of Vicia fava L. Agri. Meteorol. 19:505-514.

Donselman, H.M., and T.K. Broschat. 1986. Production of Heliconia psittacorum for cut flower in South Florida. Bul. Heliconia Soc. Intl. 1(4):4-6.

Donselman, H.M. and T.K. Broschat. 1987. Commercial heliconia production in South Florida. Nuseryman's Digest. 21(1):48-52.

Dufault, R.J., D.R. Decoteau, J.T. Garrett, R.T. Nagata, K.D. Batal, W.J. McLaurin, D.M. Granberry, K.B. Perry, and D. Sanders. 1989. Determination of heat unit requirement for collard harvest in the southeastern United States. J. Amer. Soc. Hort. Sci.114:898-903.

Eisensmith, S.P., A.L. Jones, E.D. Goodman, and J.A. Flore. 1982. Predicting leaf emergence of 'Montmorency' sour cherry from degree-day accumulations. J. Amer. Soc. Hort. Sci. 107(5):717-722.

Elphinstone, E.D. and A.R. Rees. 1987. Flower development in the bulbous iris. p.393-405. In: Manipulation of flowering. Atherton, J.C (Ed). Butterworths. London

Erickson, R.O.and F.J. Michelini. 1957. The plastochron index. Amer. J. Bot. 44:297-306.

Ferreira, S. 1990. Bacterial wilt on heliconia: Hawaii's experience. Bul. Heliconia Soc. Intl. 5(1):9-11.

Gagnon, S. and B. Dansereau. 1992. Temperature and duration of pretreatment effects on growth and development of geraniums. HortScience. 27:216-217.

Geertsen, V. 1989. Effect of photoperiod and temperature on the growth and flower production of Heliconia psittacorum 'Tay'. Acta Hort. 252:117-122.

Geertsen, V. 1990. Influence of photoperiod and temperature on the growth and flowering of Heliconia aurantiaca. HortScience. 25:646-648.

Halevy, A.H. 1984. Light and autonomous induction. pp.65-73. In: Light and the flowering process. D.Vince-Prue, B. Thomas, and K.E. Cockshull (Eds). Academic Press, New York.

Halevy, A.H. 1987. Assimilate allocation and flower development. pp.363-378 . In: Manipulation of flowering. Atherton, J.G (Eds). Butterworths. London.

Hammer, P.A. and R.W. Langhans. 1978. Modeling of plant growth in Horticulture. HortScience. 13(4):456-458.

Hansen, J.D., E. Tanoue, and R. Peckenpaugh. 1990. Flower cleaning and handling for export shipment. Bul. Heliconia Soc. Intl. 5(1):6 (Abstr.).

Hawaii Department of Agriculture. Agricultural Statistics Service. 1991. Statistics of Hawaiian Agriculture 1990. Honolulu, Hawaii.

Healy, W.E. and H.F. Wilkins. 1986. Relationship between rhizome temperature and shoot temperatures for floral initiation and cut flower production of Alstroemeria 'Regina'. J. Amer. Soc. Hort. Sci. 111:94-97.

Healy, W.E., H.F. Wilkins, and M. Celusta. 1982. Role of light quality, photoperiod, and high intensity supplemental lighting on flowering of Alstroemeria 'Regina' J. Amer. Soc. Hort. Sci. 107:1046-1049.

Hickleton, P.R. 1984. Response of pot chrysanthemum to supplemental irradiation during rooting, long day and short day production stages. J. Amer. Soc. Hort. Sci. 109:468-472.

Hickleton, P.R. 1985. Influence of different levels and timing of supplemental irradiation of pot chrysanthemum production. HortScience. 20:374-376.

Hirano, R.T. 1989. Some observations of Heliconia 'Richmond Red' in relation to H. caribaea and H. bihai. Bul. Heliconia Soc. Intl. 4:4-5, 9.

Hopper, D.A., and P.A. Hammer. 1991. Regression models describing Rosa hybrida response top day/night temperature and photosynthetic photon flux. J. Amer. Soc. Hort. Sci. 116:609-617.

Hussey, G. 1963. Growth and development in the young tomato. II. The effect of defoliation on the development of the shoot apex. J. Exp. Bot. 14:325-333.

Jacob, F. 1977. Objectives and organization of the work. Science. 196:1161-1166.

Jacobs. G. 1983. Flower initiation and development in Leucospermum cv. Red Sunset. J. Amer. Soc. Hort. Sci. 108:32-35.

Jacobs, G. and H.R. Minnar. 1980. Light intensity and flower development of Leucospermum cordifolium. HortScience. 15:644-645.

Jacobs, G., D.N. Napier, and D.G. Malan. 1986. Prospect of delaying flowering time of Leucospermum. Acta Hort. 185:61-65.

Johansen, D. 1940. Plant microtechnique. McGraw Hill. N.Y.

Ka-ipo, R., W.S. Sakai, S.C. Furutani, and M. Collins. 1989. Effect of postharvest treatment with antitranspirants on the shelf-life of H.psittacorum cv. Parakeet cut flowers. Bul. Heliconia Soc. Intl. 4(3):13-14.

Karlsson, M.G. and R.D. Heins. 1986. Response surface analysis of flowering in chrysanthemum cv. 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253-259.

Katz, Y. H. 1952. The relationship between heat unit accumulation and the planting and harvesting of canning peas. Agro. J. 44(2):74-78.

Kawabata, O. 1989. The seasonal fluctuation of flowering production of Bird of Paradise as affected by leaf

cooling practice in Hawaii. Ph D Dissertation. University of Hawaii.

Keil-Gunderson, L.S., K.L. Goldsberry, and P.L. Chapman. 1989. Air and substrate temperature for 'Atlas' and 'Monika' Alstroemeria. HortScience 24:613-616.

Kinet, J.M., R.M. Sachs, and G. Bernier. 1985a. The physiology of flowering. Vol.II. Transition to reproductive growth. CRC Press Inc. Florida.

Kinet, J.M., R.M. Sachs, and G. Bernier. 1985b. The physiology of flowering. Vol.III. The development of flowers. CRC Press Inc. Florida.

Kraszewski, R.A., and D.P. Ormond. 1986. Utilization of a response surface technique to study light acclimation of indoor flowering plants. J. Amer. Soc. Hort. Sci. 111:47-55.

Kress, W.J. 1985. Bat pollination of an old world Heliconia. Biotropica. 17:302-308.

Kress, W.J. 1990. Pollination and potentials in breeding heliconias. Bul. Heliconia Soc. Intl. 5(1):1-2. (Abstr.).

Lana, E.P. and E.S. Harber. 1952. Seasonal variability as indicated by cumulative degree hours with sweet corn. Proc. Amer. Soc. Hort. Sci. 59:389-392.

Landsberg, J.J. 1977. Some useful equations for biological studies. Expl. Agri. 13:273-286.

Larsen, R. 1988. A prediction model for floral development of Senecio x Hybridus Hyl. "Moll's Stam". Swedish J. Agric. Res. 18:99-103.

Lekawatana, S. 1986. Growth and flowering of Heliconia sticta Huber and Heliconia angusta Vell. MSc Thesis. University of Hawaii.

Lekawatana, S. and R.A. Criley. 1989. Pot culture of Heliconia stricta 'Dwarf Jamaican'. Acta Hort. 252:123-128.

Lin, W.C. 1985. Influence of soil cooling and high light intensity lighting on the growth and flowering of Altroemeria cv. 'Regina'. HortScience. 20:378-380.

Logan, S.H. and P.B. Boyland. 1983. Calculating heat units via a sine function. J. Amer. Soc. Hort. Sci. 108:977-980.

Madariaga, F.J. and J.E. Knott. 1951. Temperature summations in relation to lettuce growth. Proc. Amer. Soc. Hort. Sci. 58:147-152.

Manarangi, A.W., W.S. Sakai, C. Gerkin, M. Crowell, G. Nielson, and R. Short. 1988. Growth and flowering of Heliconia psittacorum cv. Parrot in Hawaii. J. Hawaiian and Pacific Agric. 1(1):1-3.

Martin, C.A. and D.L. Ingram. 1992. Simulation modeling of temperatures in root container media. J. Amer. Soc. Hort. Sci. 117:571-577.

Ministry of Agriculture, Fisheries, and Forestry (MAFF). Republic of Korea. 1987. Report of study tour on flower marketing system in the Netherlands, Italy, Israel, and Japan.

Ministry of Agriculture, Fisheries, and Forestry (MAFF). Republic of Korea. 1991. The yearbook.

Mor, Y. and A.H. Halevy. 1979. Translocation of ^{14}C-assimilates in roses I. The effect of the age of the shoot and the location of the source leaf. Physiol. Plant. 35:177-182.

Morris, D.A. and A.J. Newell. 1987. The regulation of assimilate partition and inflorescence development in the tomato. pp.379-405. In: Manipulation of flowering. Atherton, J.G (Eds). Butterworths. London.

Napier, D.R. and G. Jacobs. 1989. Growth regulators and shading reduce flowering of Leucospermum cv. Red Sunset. HortScience. 24:966-968.

Nau, J. 1991. Heliconia. p.575. In: Ball redbook. Vic Ball(Ed). Geo. J. Ball Publishing.

Nautical Almanac Office. 1992. The astronomical almanac. US Government Printing Office. Washington.

Office of Rural Development (ORD). Republic of Korea. 1991. List of varieties in major crops.

Ong, C.K. and C.K. Baker. 1985. Temperature and leaf growth pp.175-200. : In Control of leaf growth.

N.R.Baker, W.J.Davies and C.K.Ong (Eds). Cambridge University Press. London.

Opler, P.A., G.W. Frankie, and H.G. Parker. 1976. Rainfall as a factor in the synchronization, release and timing of anthesis by tropical trees and shrubs. J. Biogeogr. 3:231-236.

Parton, W.J. and J.A. Logan. 1981. A model for diurnal variation in soil and air temperature. Agri. Meteorol. 23:205-216.

Peacock, J.M. 1975. Temperature and leaf growth in Lolium perenne. II. The site of temperature perception. J. Appl. Ecol. 12:115-123.

Perry, K.B., T.C. Wehner, and G.L. Johnson. 1986. Comparison of 14 methods to determine heat unit requirements for cucumber harvest. HortScience. 21:419-423.

Pierik, R.K.M. 1967. Effect of light and temperature on flowering Cardamine pratensis L. Z. Pflanzenphysiol. Bd. 56:141-152.

Reath, A.N. and S.H. Wittwer. 1952. The effects of temperature and photoperiod on the development of pea varieties. Proc. Amer. Soc. Hort. Sci. 60:301-310.

Richardson, E.A., S.D. Seely, and D.R. Walker. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. HortSceince. 9:331-332.

Robinson, N., T. Harav, A.H. Halevy, and Z. Plaut. 1980. Distribution of assimilates from various source leaves during the development of Gladiolus grandiflorus. Ann. Bot. 45:113-122.

Sachs, R.M. 1987. Roles of photosynthesis and assimilate partitioning in flower initiation. PP:317-340. In: Manipulation of Flowering. J.G. Atherton (ED). Butterworth. London.

Sakai, W.S. 1990. Long-day flowering in Heliconia angusta cv.'Holiday': Possibility for year-round flower production. The Hawaii tropical cut flower industry conference. University of Hawaii. HITAHR. Res-Ext. Ser. 124:173-177.

Sakai, W.S., A. Manarangi, R. Short, G. Nielson, and M.D. Crowell. 1990a. Evidence of long-day flower

initiation in Heliconia angusta cv.Holiday--- Relationship between time of shoot emergence and flowering. Bul. Heliconia Soc. Intl. 4(4):1-3.

Sakai, W.S., G. Nielson, S. Short, R. Ka-ipo, A. Umemoto, and K. Inada. 1990b. Forcing off-season flower production in Heliconia angusta cv. Holiday with artificial long-days. Bul. Heliconia Soc. Intl. 4(4):10-11.

Salisbury, F.B. and C.W. Ross. 1985. Plant physiology. Wadsworth Publishing Company. CA.

SAS Institute. 1986. SAS system for regression. SAS Inst. Cary, N.C.

SAS Institute, 1987. SAS/STAT Guide for personal computers. Version 6 edition. SAS Inst. Cary, N.C.

Shillo, R. and A.H. Halevy, 1976. The effect of various environmental factors on flowering of gladiolus I. Light intensity. Scientia Hort. 4:131-137.

Smith, R.R. 1977. Heliconia in Nicaragua. Phytologia. 36:252-261.

Stiles, F.G. 1979. Notes on some natural history of Heliconia (Musaceae) in Costa Rica. Brenesia. 15:151-180.

Summerfield, R.J. and E.H. Roberts. 1987. Effect of illuminance of flowering in long and short-day grain legumes: a reappraisal and unifying model. pp:203-223. In: Manipulation of Flowering. J.G. Atherton (Ed). Butterworth. London.

Terry, N., L.J. Waldron, and S.E. Taylor. 1983. Environmental influences on leaf expansion. p:179-204. In: The growth and functioning of leaves. J.E. Dale and F.L. Milthorpe (Eds). Cambridge University Press. Cambridge.

Tjia, B. 1985. Longevity and postharvest studies of various Heliconia psittacorum bracts. Bul. Heliconia Soc. Intl. 1(1):6.

Tjia, B. and T.J. Sheehan. 1984. Preserving profits and beauty: Longevity, quality studies help prolong life of Heliconia. Greenhouse manager. 2(11):94-100.

Tomlinson, P.B. 1969. Anatomy of the monocotyledons. Vol.3. Oxford University Press. London.

U.S. Department of Commerce (USDC). 1962-9991. Local climatological data, Honolulu (collected at Honolulu International Airport), Hawaii monthly summary.

Van Staden, J., Zieslen, N., Spiegelstein, H. and A.H. Halevy. 1981. The effect of light on cytokinin content of developing rose shoots. Ann. Bot. 47:155-157.

Vlahos, J.C. 1991a. Daylength influences growth and development of Achimenes cultivars. HortScience. 25:1595-1596.

Vlahos, J.C. 1991b. Temperature and irradiance influence growth and development of three cultivars of Achimenes. HortScience. 25:1597-1598.

Vonk, C.R. and S.A. Ribot. 1982. Assimilate distribution and the role of abscisic acid and zeatin in relation to flower-bud blasting, induced by lack of light, in iris cv.Ideal. Pl. Growth Regul. 1:93-105.

Wann, M.D., D.Yen., and H.J. Gold. 1985. Evaluation and calibration of three models for daily cycle of air temperature. Agri. & For. Meteorol. 34:121-128.

Warnock, S.J. 1973. Tomato development in California in relation to heat unit accumulation. HortScience. 8:487-488.

Watson, J.B. 1986. Heliconias: a new challenge for landscape design. Fairchild Trop. Gardens Bull. 41(1):6-19.

Watts, W.R. 1972a. Leaf extension in Zea mays. II. Field measurements of leaf extension in response to temperature an leaf water potential. J. Expt. B. 25:1085-96.

Watts, W.R. 1972b. Leaf extension in Zea mays. II. Leaf extension in response to independent variation of the temperature of the apical meristem, of the air temperature around the leaves, and the root zone. J. Expt. Bot. 23:713-21.

Weiss, A. 1981. Computer techniques and meteorological data applied to problem of agriculture and forestry: A workshop. Ameri. Meteoro. Soc. PP.184-193.

White, J.W. and I.J. Warrington. 1984. Growth and development response of geranium to temperature,

light integral, CO_2, and chlormequat. J. Amer. Soc. Hort. Sci. 109:728-735.

White, J.W. and I.J. Warrington. 1988. Temperature and light integral effects on growth and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 113:354-359.

Whitton, B. and W.E. Healy. 1990. Flowering of aeschynanthus 'Koral' at fluctuating and constant temperatures. J. Amer. Soc. Hort. Sci. 115:906-909.

Wilson, W.T. and W.W. Barnett. 1983. Degree-days: An aid in crop and pest management. Calif. Agri. 37(1):4-7.

Wootton, J.T. and I-F. Sun. 1990. Bract liquid as a herbivore defense mechanism for Heliconia wagneriana inflorescences. Biotropica. 22(2):155-159.

Yandell, B.S., A. Najar., R. Wheeler, and T.W. Tibbitts. 1988. Modelling the effects of light, carbon dioxide, and temperature on the growth of potato. Crop Sci. 28:811-818.

Zieslin, N. and A.H. Halevy. 1975. Flower bud atrophy in 'Baccara' roses. II. The effect of environmental factors. Scientia Hort. 3:383-391.