THE EFFECT OF NIGHT TEMPERATURE AND PHOTOPERIOD ON FLOWERING IN KALANCHOE

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Horticulture

1980

ABSTRACT

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The interaction of photoperiod and night temperature on flowering of 'Mace' and 'Gelbe Melody' kalanchoe was studied. Both cultivars produced the greatest flowering at 25°C night temperature and 9.0 hour daylength. Decreased flowering and delayed response were noted in 'Mace' with night temperatures of 25° and 30°C and 10.5 and 12.0 hour daylength. With 12.0 hour daylength and 25°C night temperature, 'Gelbe Melody' exhibited partial initiation.

The development of the apical meristem of 'Mace' and 'Gelbe Melody' under photoinductive conditions was examined using scanning electron microscopy.

In evaluating kalanchoe cultivars for response to high night temperatures during short day treatment, 'Goddess', 'Rhumba', 'Rotkappchen' and 'Tabasco' were unaffected by night temperatures of 25-30°C. 'Toltec' and 'Montezuma' showed some incomplete flowering at 25-30°C. Flowering time was delayed as compared to 17-20°C night temperature.

TABLE OF CONTENTS

TABLE OF CONTENTS--CONTINUED Page

SECTION III

DEVELOPMENT OF THE INFLORESCENCE OF TWO CULTIVARS OF KALANCHOE USING SCANNING ELECTRON MICROSCOPY

SECTION IV

EFFECTS OF HIGH NIGHT TEMPERATURE ON NINE CULTIVARS OF KALANCHOE

LIST OF TABLES

TABLE Page

SECTION IV

APPENDIX

LIST OF FIGURES

FIGURE Page

SECTION II

SECTION III

INTRODUCTION

Kalanchoe blossfeldiana v. Poellnitz is native to Madagascar and other areas of Africa; it flowers under short day conditions. The unique red flowers and long blooming period of kalanchoe have made it a popular florist crop.

Research has led to precise scheduling for flower production (4,28). Kalanchoe has become a year round container grown crop, by using the lighting and shading sequence developed for chrysanthemum. The introduction of new hybrids has prompted the vegetative propagation of kalanchoe rather than the time-consuming cultivation from seed.

Year round cropping has resulted in problems with flowering. As with most photoperiodic plants, the inductive process is temperature dependent. Temperature extremes disrupt the precise scheduling necessary for commercial flower production. Low temperatures retard the development of the inflorescence and high temperatures result in plants unsuitable for market. High temperature flowering may completely suppress flowering or the number of flowers and cymes may be reduced, while the time to flowering increases.

Daylength and night temperature are two major factors in the flowering process of kalanchoe. The following research was conducted to determine: (1) the effects of high night temperatures and daylength on the floral development, (2) the morphological development of the apical meristem, using scanning electron microscopy; (3) the response of new cultivars of kalanchoe to high night temperatures.

GENERAL LITERATURE REVIEW

Background on Kalanchoe

Botanical description

The genus Kalanchoe includes 125 species, many of which are of horticultural interest (1,19). Kalanchoe belongs to the family Crassulaceae, which includes the genera Crassula, Echeveria, Sedum, and Cotyledon.

Kalanchoes are native to Madagascar, tropical and south Africa, Arabia, India, China and the Malay Peninsula (1,15,19). The genus has been divided into three sections: Bryophyllum, Kalanchoe or Eukalanchoe, and Kitchingia. Formerly separate genera, Bryophyllum and Kitchingia were reclassified as sections in 1907 by Hamet (15). This system was followed by Boiteau and Mannoni in 1947 and Jacobsen in 1954 (1,15,19).

The distinguishing characteristic of the Bryophyllum section is the production of plantlets in the notches of leaf margins and in the inflorescences (1). Commonly known as "Mother-of-Thousands" or the "Pregnant Plant", Kalanchoe daigremontianum and Kalanchoe tubiflora produce great numbers of plantlets along the leaf margins (15). This section also includes an epiphytic species, Kalanchoe uniflora. Most of the plants in this section have pendant flowers, with an inflated tubular calyx (1). Kalanchoe grouped under Kitchingia also have pendant flowers.

In the section Kalanchoe or Eukalanchoe (depending on the translation from the German), flowers are erect with a flask-shaped corolla (1,15). Plantlets are not normally formed on these species. The leaves are mostly opposite with a terminal inflorescence. The sepals and corolla are tubular, with short lobes on the corolla. The flowers have 8 stamens and rarely four. The flowers are 4-merous.

Kalanchoe beharensis (Velvet Leaf), K. marmorata (Pen-wiper's Plant), and K. tomentosa (Panda Plant) are common foliage plants. Hybrids of Kalanchoe blossfeldiana v. Poellnitz (formerly K. globulifera var. coccinea Perr.) are grown as pot flowers (19). This compact perennial is native to Madagascar and Mont Tsaratanana; it was introduced by Robert Blossfeld, a German hybridizer (38). The leaves are glabrous with a thick waxy cuticle and red margins (19). The capitate inflorescence, somewhat corymbose, has been described as a dichasial cyme, ending in cincinni (17). The numerous scarlet flowers are produced under short day (SD) conditions, or January to April in the northern hemisphere (19). The salver-form corolla is subtended by lanceolate sepals. Anthers 8 in number, terminate in a glandular cell; linear nectar glands are also found in the flowers (1).

Horticultural Development

Many cultivars have been developed with unclear parentage. Jacobsen suggested that the cultivar 'Feuerblute' might be a hybrid between K. blossfeldiana and K. flammea (19). The yellow-gold flowers of 'Goldhybriden' also indicate an interspecific hybrid of K. blossfeldiana and another kalanchoe species (19).

Due to appearance and response, 'Mace' has always been included with K. blossfeldiana hybrids. This sterile hybrid is an interspecific cross of two unknown kalanchoe species (9). Many kalanchoe hybrids readily cross with other species of kalanchoe and produce viable seed, making species distinctions difficult (13). While the genetic origins remain unclear, it would be expedient to continue to refer to the commercially available hybrids as K. blossfeldiana cv. hybrida or as K. X'Mace'. As this cultivar remains unpatented further distinction is not possible.

While the cultivars and species involved remain unclear, the direction of breeding efforts has been easier to follow. Early German hybrids were grown from seed, a time-consuming and demanding practice. Early European breeders developed tall cultivars, such as 'Morning Star', more suitable as cut flowers. 'Mace' was developed in the early 1960's by DeWerth and is the basis for further breeding work (23,4). Vegetative propagation of 'Mace' produced a full plant for the florist trade but the inflorescences remained excessively tall.

Irwin (21), working with European cultivars, developed numerous hybrids with compact growth habit and response times of 10 to 12 weeks. The European cultivars were better adapted to northern climates (23). Hybrids developed by Grob (Switzerland), Bull (W. Germany), Hope (Costa Rica) and Mikkelsen (U.S.) were selected for mildew resistance, compact habit and rapid flowering response, especially under low light conditions.

In addition to changes in propagation and growth habit, recent breeding efforts in kalanchoe have been directed towards a broader

range of colors, shorter response time and resistance to 'heat-delay' in the summer (13). Commercially the plant has changed from a limited, winter-flowering crop with a long production time, to a crop with many colors and sizes, grown year-round. The succulent habit and good keeping qualities, make kalanchoe potentially a major floriculture crop.

Physiological Background

Crassulacean Acid Metabolism

A member of the family Crassulaceae, kalanchoe exhibits CO_2 fixation in the dark known as Crassulacean Acid Metabolism (CAM). In order to conserve water in arid regions, this phenomenon is characterized by stomatal opening at night and closing during the day. CO_2 taken up in the dark is fixed by organic acids synthesized from carbohydrates. During the light period, the acids are converted to CO_2 and water. This pathway is 'switched' photoperiodically; the correlation between flower induction and dark fixation of CO_2 has been investigated (3,14,21,25,29,39,41). The change in CO_2 uptake occurs over a period of time close to that for floral induction (25). Both floral induction and CAM have a circadian rhythm. Repeated SD cycles increased CAM enzymatic activity and the floral response (3).

Spear et al. (41) suggested that CO_2 metabolism under SD conditions produced a photo-labile or thermo-labile substance. The interruption of the dark period and high temperatures negate the SD effects in both CO_2 metabolism and floral induction. This is characterized by a brief burst of CO_2 evolved by the plant. However,

no causal relations have been indicated. The dark fixation of CO_2 and floral induction appear to be parallel systems, controlled by photoperiodism (3).

Associated with alternating CO_2 fixation and CAM is a change in leaf succulence and water conservation. 'Tom Thumb' kalanchoe, under 6 weeks of SD, exhibited reduced water uptake compared to plants grown under LD (44). Water loss during light and dark was similar for SD plants. In contrast, plants grown under LD lost 3.5 times the amount of water during the light period as the SD plants. There was a marked difference in water loss during the light and dark periods. Water conservation was correlated with dark fixation of CO_2, stomatal opening in the dark and increased leaf succulence. These characteristics may be viewed as protective adaptations to an arid climate.

Growth Regulators

Growth regulators are widely used for height control, defoliation and flower stimulation. Removal of the terminal either mechanically or chemically has been used for height and flowering control.

Daminozide (succinic acid-2,2-dimethylhydrazide) applied to kalanchoe as a foliar spray reduced plant height but also the number of flowers per plant (26). Terminal removal did not affect plant height or number of flowers however the number of vegetative breaks increased.

Zawawi and Irving (45) applied indole-acetic acid (IAA) and 2,3,5-triiodobenzoic acid (TIBA) to kalanchoe to hasten flowering and to overcome high temperature effects during SD treatment.

Neither compound reversed the high temperature effect although TIBA enhanced flowering under SD. Multiple applications of TIBA resulted in fasciation of the leaves; repeated applications of IAA caused delay and reduction in flowering.

Pertuit (27) tested chlorflurenol (methyl-2-chloro-9-hydroxy-fluorene-9-carboxylate), ancymidol (-cyclopropyl- -(-methoxy-phenyl)-5-pyrimidine methanol), DPX 1840 (3-3a-dihydro-2(-methoxyphenyl)-8H-pyrazolo- 5,1- isoindol-8-one) and ethephon (2-chloroethyl) phosphoric acid on kalanchoe. All compounds reduced plant height except DPX 1840 which produced ring fasciation.

Our work with ancymidol demonstrated reduction in plant height without a decrease in foliage or flowering response (5).

Juvenility

Photoinductive conditions and other factors such as juvenility contribute to the floral response (10).

In juvenile plants or seedlings of kalanchoe, SD treatment did not induce flowering until a minimum number of leaf pairs had formed (35,33). The growth habit was different under SD than under LD conditions. SD conditions produced small, more succulent leaves, shorter internodes and petioles (35).

The duration of the juvenile phase varied with the cultivar (35). Three to 4 leaf pairs were necessary for photoinduction of 'Tom Thumb', 'Vulkan', and 'Alfred Graser'. 'Morgensonne' required 7-8 leaf pairs while 'Ramona', 'Goldrand', and 'Rotglut' required 10-11 leaf pairs.

SD conditions inhibited growth of juvenile plants; subsequent LD treatment was ineffective at promoting growth (33,35).

Supplementary lighting on juvenile kalanchoe under both photoperiods was more effective in promoting growth in plants receiving LD conditions (33).

Photoperiodism and Temperature

Photoinduction

Salisbury (37) summarized the basis of photoperiodic induction as follows:

1. SD plants respond to a daylength shorter than a critical amount; this is more a response to the length of the dark period.

2. LD plants respond to a daylength greater than the critical amount.

3. Light interruptions of the dark period both inhibit SD plants and promote flowering in SD plants.

4. The action spectrum for light interruption is centered around orange-red or 620-665 nm; it is reversed by far-red or 710-740 nm.

5. A flowering hormone (florigen), formed in the leaves and moves to the apical meristem, has been postulated, but not isolated.

6. Continuous inductive conditions are not necessary for continuation of the flowering process.

7. Photoperiodic response may involve other factors, such as temperature, nutrition, sequence of LD and SD combinations and light.

Doorenbos and Wellensiek (10) defined floral induction as the "chain of processes proceding and leading to flower initiation". Factors such as high intensity light before the photoperiodic conditions and the length of the photoperiods before inductive treatment

were emphasized. With 12 SD cycles, kalanchoe was induced to flower; when the 12 SD cycles were alternated with LD cycles, floral initiation was blocked (38).

Grafting and the floral stimulus

Flower induction in a vegetative plant by grafting an induced leaf has indicated the possibility of a 'floral stimulus'. Vegetative kalanchoe plants flowered after grafting of induced bryophyllum leaves (46). The reverse combination produced a weak flowering response. Differences in response were also noted in early and late flowering cultivars of kalanchoe. The late flowering kalanchoe needed longer contact with the induced donor than early flowering strains.

While the transfer of a floral stimulus has been successful in different response types, there is no conclusive evidence for a single floral stimulus. Carr and Evans (46) postulated two separate substances: a primary photoperiodic stimulus, produced in the donor plant, transmissible across the graft union and in receptor plants, a secondary stimulus which produced a flowering response in plants of a different response group from the donor.

Photoperiodism and Floriculture Crops

Cathey (6) investigated the effect of temperature on critical photoperiod for the initiation and development of flowers in Chrysanthemum morifolium. Cultivars requiring extended natural SD conditions, required a shorter photoperiod. Lower temperatures decreased the critical photoperiod for both initiation and development. Generally, a shorter daylength was necessary for flower development than for initiation. However, there was no difference at low

temperatures (50°F).

Poinsettia, is also dependent on temperature for floral induction (20,43). Shorter daylengths were required for floral initiation and development as temperatures were increased. In addition to cultivar response, the critical photoperiod differed for initiation and organogenesis. A poinsettia 'flower' of 22 cyathia and 27 bracts required 45-55 SD. Fewer SD reduced cyathium development.

In dahlia, temperature affected the rate of flower development but not flower initiation (24). Of 18 cultivars evaluated, 12 cultivars were regulated by daylength (24). At least 14 SD cycles were required for initiation, followed by LD or continuous light. Continuous SD reduced the number of ray florets.

Temperature Effects on Floral Induction of Kalanchoe

Low temperatures (8-10°C) inhibit the inductive influence of SD conditions on kalanchoe (16,28,31,32,34,36). Harder and Witsch (16) observed a reduction in the number of flowers as dark temperatures decreased from 24° to 8°C. At 8°C, flowering was suppressed. Decreasing temperatures produced phyllody of the inflorescence, with a decrease in flower number and dichasia, and the appearance of larger leaf-like bracts. This condition was accompanied by a decrease in leaf succulence, which is enhanced by SD conditions (17).

The induction of kalanchoe was retarded at reduced temperatures, requiring extended inductive conditions (28,34). In 9 cultivars given 15°C and 30 SD cycles, all flowered, while 5 flowered with 20 SD and only 2 with 10 SD (28,34). 'Mace' required 2 weeks of SD treatment at 10, 16 and 21°C night temperature, but exhibited a lower percentage of flowering at 10°C and 2-3 weeks of inductive

(SD) conditions (28). At 20-25°C, the critical photoperiod of the nine cultivars was 10 3/4 to 12½ hr (34). For most cultivars, the greatest degree of flowering and largest number of florets were produced in this temperature range (28,31,32,33,34). The number of inductive cycles necessary was reduced in this temperature range.

Temperatures of 30°C during the inductive period inhibited the flowering response (31,30). 'Tom Thumb' produced limited florets with increased phyllody under 30°C night temperature. Most cultivars did not flower or exhibited reduced flowering response at 30°C (34). The cultivars 'Morgensonne' and 'Goldrand' required inductive periods of 30 SD cycles with flowering responses limited in degree and number at 30°C. 'Red Glow', at night temperatures greater than 23°C, did not flower after 5 months of SD conditions (45).

Using a 12 hour photoperiod and 20°C temperature, Schwemmle (39) found that 3 hours of 30°C at the beginning of the dark period promoted flowering, while the last three hours of 30°C at the end of the 12 hour dark period, completely inhibited flowering.

Flowering in 'Amethyst' was delayed at 10°C (34,36). Flowering occurred with 10 inductive cycles at 20 and 30°C. However, at 5, 10 and 15°C, flower initiation took place under either SD or LD. All plants flowered with a 10 hour photoperiod at 15, 20 and 25°C.

Reproductive Development of Kalanchoe

Apical Meristem Development

Stein and Stein (42) studied changes in the shoot apex of Kalanchoe cv. Brilliant Star during the transition from the vegetative to the reproductive state. The plants were grown under 8 hr light and 16 hr dark in either a greenhouse or controlled environment chamber.

The apical meristem remained flat and rectangular in the vegetative phase. After 10 days of inductive photoperiodic conditions, the apical dome increased in height; embryonic internodes lengthened after 12 days.

The shoot apex changed from rectangular to elliptical and increased in area after 18 days of SD treatment. Axillary bud development, at 20 days, indicated the initiation of the dichasium. The last two leaf pairs formed after 25 days of inductive conditions and were small and bract-like. By 34 days, the terminal floret was formed, with the development of four sepals and petal primordia. Stamens appeared after 46 days. The anther primordia occurred in two sets: 4 adnate to the midrib and 4 in the petal junction.

The Inflorescence and Fractional Induction

The inflorescence of Kalanchoe blossfeldiana consists of a dichasial cyme, ending in cincinni or scorpioid cymes (17). The main axis terminates with a single floret, subtended by two small bracts. Lateral shoots develop in the axils of each bract; these also end with a single floret. This pattern continues until three to four bifurcations or forkings are formed, which end in cincinni.

Partial initiation or induction is characterized by modifications in the inflorescence. They form a continuum ranging from a well-branched cyme with hundreds of florets (complete initiation) to a leafy branched structure, with only one floret (very limited induction) (16,17). Phyllody of the bracts is the change in size and shape of the bracts until they resemble leaves. As the scorpioid cymes disappear, branches with well-developed bracts are evident. Harder (16) noted an inverse relationship between the number of flowers and the size of bracts in plants that were given partial inductive treatment. The number of dichasial bifurcations also decreases.

Harder (17) related the changes in the structure of the inflorescence to the amount of stimulus received, and the amount of flowering hormone present. Fractional induction is dependent on the number of SD cycles and the duration of the light period. Temperature interacts with photoperiod and light interruptions of the dark period. Low CO_2 levels and certain anaesthetics can block the complete flower induction.

Scanning Electron Microscopy: Techniques and Applications

The scanning electron microscope (SEM) and its related technology has refined the study of surface features (22,30). Electrons with a wavelength of 0.04 to 0.007nm, focused into a beam results in improved resolution over light microscopy (LM) (30).

The range of magnification with the SEM is 20 X to 50,000 X (30). In comparison to light microscopy (LM), the long working distance allows for viewing whole organisms or larger structures than was previously possible.

The SEM has been used in studies of pollen grains (22), development and regeneration of leaf waxes (7), root morphology (22), and the developmental stages in the organogenesis of apical meristems (2, 8,11,12,40).

Because of the nature of the electron beam and the detection mechanism, material for viewing requires special preparation (22). The procedure must retain morphological detail of the specimen and eliminate charging and beam distortion (30).

The use of fresh-frozen samples requires a cold stage and then some distortion of the sample may result from this process.

Dehydration techniques overcome many problems but can alter the original features. Materials such as wood or pollen grains can be air-dried together with cuticle waxes on leaf surfaces which would be destroyed by some dehydration techniques. Fresh leaf or petal tissue requires fixation to stabilize the sample.

Critical point drying reduces the surface distortion associated with air-drying by eliminating surface tension (18). At the critical temperature and critical pressure for a given material (the critical point), the surface tension equals zero; there is no distinction between the vapor and liquid phases. This is accomplished by heating a liquid, usually CO_2, in equilibrium with its vapor, within a confined space. Above the critical temperature, additional pressure increases the vapor density until it equals the density of the liquid phase (critical pressure). At this point, the gas can be released while maintaining the temperature, and vapor condensation will not occur.

Since the critical point of water is too high for this application,

it must be replaced by ethanol or amyl acetate (18). Liquid nitrous oxide and fluorocarbon fluids have been used, eliminating the need for ethanol dehydration in the latter (18).

Since dried samples are non-conductive a conductive coating must be applied to the specimen to prevent "charging". To observe morphological detail, the tissue is coated with a thin layer of metal and/or carbon. This can be applied in a vacuum evaporator or cold cathode sputter coater.

Einert et al. (11) prepared apical meristems of Lilium longiflorum cv. Ace by quench freezing in liquid N_2 and freeze drying. The specimens were carbon coated to improve conductivity. Samples were studied with SEM and LM to compare techniques and determine floral initiation. The greater depth of field in the SEM provided details of the changes in the topography of the apices. Even though the dried and coated samples appeared more definitive than fresh material, the LM did not have sufficient depth of field to illustrate the features as clearly as the SEM.

Fresh shoot apices of Dianthus caryophyllus were studied by Emino and Rasmussen (12). Samples were mounted with a carbon adhesive; time sequence micrographs were taken to determine the changes in tissue while on the viewing stage of the SEM. In previous LM studies, the appearance of individual cells on the surface of the apex caused a "cobblestone" effect, a characteristic of the morphology of the apex. After 4 minutes, individual cells were visible but became smooth after 5 minutes. Wrinkling and desiccation occurred after 10 minutes, the result of ballooning and collapse of the cuticle.

Shoub and DeHertogh (40) studied the organogenesis in Tulipa gesneriana cv. Paul Richter. The development of the tulip apical meristem was followed with pictures of longitudinal sections and SEM micrographs of whole apices. The tissue was prepared by standard critical point drying. The samples were coated with carbon and gold/palladium (20nm each). The SEM micrographs illustrate the centripetal development of the floral organs of the entire shoot apex.

Several methods of sample prepation were used to study morphological changes in the apical meristems of Easter lilies (8). Freeze-dried samples were frozen in liquid N_2 and dried in a lyophilizer. Another method utilized a fixation process with FAA, ethanol series dehydration and critical point drying with liquid CO_2. All dried meristems were coated with carbon and gold/palladium (20nm). Uncoated fresh meristems were also viewed. While both freeze-drying and critical point drying provide acceptable specimens, the critical point drying technique provided the most reliable results. With this plant tissue, freeze-drying produced artifacts and distorted the meristematic mantle.

A similar critical point drying procedure was followed by Barrett and DeHertogh (2), in the development of the inflorescence of dahlia. The complexity of this composite was clearly illustrated by the SEM micrographs. Fresh apices and a binocular light microscope were used to determine the stage of development during forcing.

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The Effect of Night Temperature and Photoperiod on Flowering in Kalanchoe

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Abstract: The interaction of photoperiod and temperature on flowering of 'Mace' and 'Gelbe Melody' kalanchoe was studied, using controlled environment chambers. Both cultivars produced the greatest flowering response at 25°C night temperature and 9.0 hour daylength. The number of cymes per plant was not significantly different at 20°C and 9.0 hour daylength.

Decreased flowering and an increase in days to flowering was noted in 'Mace' with night temperatures of 25° and 30°C, and photoperiod of 10.5 hours and 12.0 hours. There was no flowering response at 30°C and 12.0 hour daylength for either cultivar. With 12.0 hour daylength and 25°C night temperature, 'Gelbe Melody' exhibited partial initiation in individual plants.

INTRODUCTION

Kalanchoe is similar to other photoperiodic floriculture crops, in that the daylength response is temperature dependent (1,2,3,5,10). In chrysanthemum, the critical photoperiod decreased with lower temperatures (3). Conversely, as temperature increased, poinsettia required shorter daylengths for floral induction (5).

Pertuit (6) determined that low temperatures (10°C) during the inductive period necessitated a greater number of photoperiodic cycles for flowering in kalanchoe. Temperatures of 8-10°C suppressed the inductive effects of SD in some cultivars of kalanchoe (7,8).

The flowering response of 'Tom Thumb' kalanchoe was inhibited and greatly altered at high temperatures (7,8). Limited florets were produced with increased bract size or phyllody. After 5 months of SD treatment, 'Red Glow' kalanchoe did not flower with night temperatures above 23°C (11).

Cultivar differences were evident in the photoperiodic requirements of nine cultivars of kalanchoe at 20-25°C (9). Depending on the cultivar, the critical photoperiod ranged from 10 3/4 to 12½ hours. However, little work has been done on photoperiodic response over a wide temperature range.

This study was undertaken to determine the effect of temperature and photoperiod on the floral induction of two cultivars of kalanchoe.

MATERIALS AND METHODS

The cultivars 'Mace' and 'Gelbe Melody' were chosen for their rapid response to inductive treatment: both required 14 SD cycles at 17°C night temperature for floral induction (Carlson et al., 1978). In a preliminary study, 'Mace' appeared more resistant to 'heat delay' than 'Gelbe Melody'. At high temperatures, 'Gelbe Melody' exhibited easily recognized signs of insufficient stimulus, i.e. few florets and cymes, enlargment of bracts or phyllody and

delayed response.

Commercially rooted vegetative cuttings of both cultivars were received at several dates from January to May 1978. On arrival, they were potted in 7.5 cm square plastic containers in a pasteurized mix of peat/loam/perlite (1:1:1 by volume). The soil was amended with superphosphate (0-20-0) at a rate of 1 kg/m^3; the pH of the soil was approximately 6.2. The plants were fertilized with 25-0-25 to 200 ppm N and K_2) on a constant liquid feed system; after 4-5 weeks, the fertilizer was changed to 20-20-20 which provided 200 ppm N, P_2O_5 and K_2O. To avoid excessive salts, the soil was leached weekly.

The plants were maintained under LD conditions until they were moved to controlled environment chambers for temperature and photoperiod treatments. Artificial LD conditions were provided by incandescent light at $100W/m^2$ for 4 hours (11:00 PM to 3:00 AM).

In growth chambers, plants received equal light intensity (approximately 1000 fc.) at the level of the plants. Temperatures were maintained at $\pm$ 2°C and daylengths were within 10 minutes of the desired length.

Factorial treatments of three night temperatures by three photoperiods consisted of 20, 25, 30°C and 9.0, 10.5, 12.0 hour daylengths. The day temperature for all treatments was 30°C. Treatments were applied for 4 weeks in the growth chambers after which the plants were transferred to LD conditions in the greenhouse for 11 additional weeks. Plants were in a randomized complete block design, with three blocks per treatment and two observations per block.

Data were recorded when all plants in a treatment were fully flowered or 15 weeks after the start of SD treatment. Data included

number of florets, number of cymes and number of days to first open floret, with 150 days assigned to plants which did not produce florets. Flowering response was measured by number of cymes and number of florets. The terminal cyme was defined as the inflorescence above the last pair of true leaves; lateral cymes occurred below this pair of leaves, or in the axils of leaf pairs.

RESULTS AND DISCUSSION

Cyme production was greatest with 9.0 hour daylength and 20° and 25°C night temperature for 'Mace' and 'Gelbe Melody' kalanchoe (Fig. 1,2). ('Gelbe Melody' grown at 20°C night temperature and 10.5 hour photoperiod did not conform to the trend; mechanical failure of the environmental chambers or a light interruption is suspected.) 'Mace' produced an average of 9.0 and 8.8 cymes at 20° and 25°C respectively while 'Gelbe Melody' had 6.5 and 5.3 cymes at those temperatures and daylength. 'Mace' followed a general trend of decreased cymes with increased night temperature and increased daylength. While the number of cymes for 'Gelbe Melody' does not follow this pattern at 25°C night temperature, the means of 5.3, 3.7 and 5.2 at 9.0 , 10.5 and 12.0 hour daylength are not significantly different ($HSD_{.01}$=3.96). No cymes were produced at 30°C night temperature; in addition, 'Mace' had no cymes when grown at 10.2 hour photoperiod.

'Mace' and 'Gelbe Melody' produced the greatest number of florets at 25°C night temperature and 9.0 hour photoperiod, an average of 1415.5 and 613.8 respectively (Fig. 3,4). With all photoperiods, there was an increase in the number of florets at

25°C in comparison with 20°C night temperature. At 30°C night temperature, neither cultivar flowered or exhibited any reproductive growth. With an increase in daylength, 'Mace' produced fewer florets at 20° and 25°C night temperature. 'Gelbe Melody' also showed an increase in average florets with a decrease in daylength at 25°C night temperature (350.0, 404.3 and 613.8 florets at 12.0, 10.5 and 9.0 hour photoperiods).

'Gelbe Melody' was slightly delayed in days to first open floret at 25°C with a 12.0 hour photoperiod (Fig. 5). This delay was the result of incomplete development of the terminal cyme in 1/3 of the plants in this treatment; the earliest floret usually opens on the terminal cyme. The apparent delay of 'Mace' at 10.5 hour photoperiod was due to one plant in each treatment failing to flower (Fig. 6). Both of these delays indicate conditions marginal for induction. None of the 'Mace' kalanchoe grown under 12.0 hour photoperiods or 30°C night temperature responded to SD conditions. 'Gelbe Melody' did not respond at 30°C night temperature.

'Mace' appeared more sensitive to temperature and daylength variations than 'Gelbe Melody'; complete floral initiation was limited to conditions of 9.0 hour photoperiod and a narrow range of temperatures (20-25°C). 'Gelbe Melody' responded to all photoperiods at 20° and 25°C, with partial initiation in some plants at 25°C and 12.0 hour daylength. While most of these plants would be commercially acceptable, the most floriferous and therefore most desirable plants were produced at 25°C night temperature with a 9.0 hour photoperiod.

Commercial production of kalanchoe requires a fully initiated plant, with a maximum number of flowers and a predictable flowering

time. If the required inductive conditions of daylength, number of cycles and temperature are given, kalanchoe initiates full inflorescences.

Modifications of the factors influencing induction resulted in incomplete initiation. In 'Gelbe Melody', the terminal cyme was lacking, fewer florets were formed and cymes with large leaf-like bracts appeared. This deformation of the inflorescence was described by Harder (4) as the result of insufficient inductive stimulus.

'Mace' exhibited a different pattern; ideal inductive conditions produced maximum cymes and florets while marginal conditions reduced their numbers. Modified cymes were not apparent in this study; all cymes of 'Mace' were floriferous with bracts of normal shape and size.

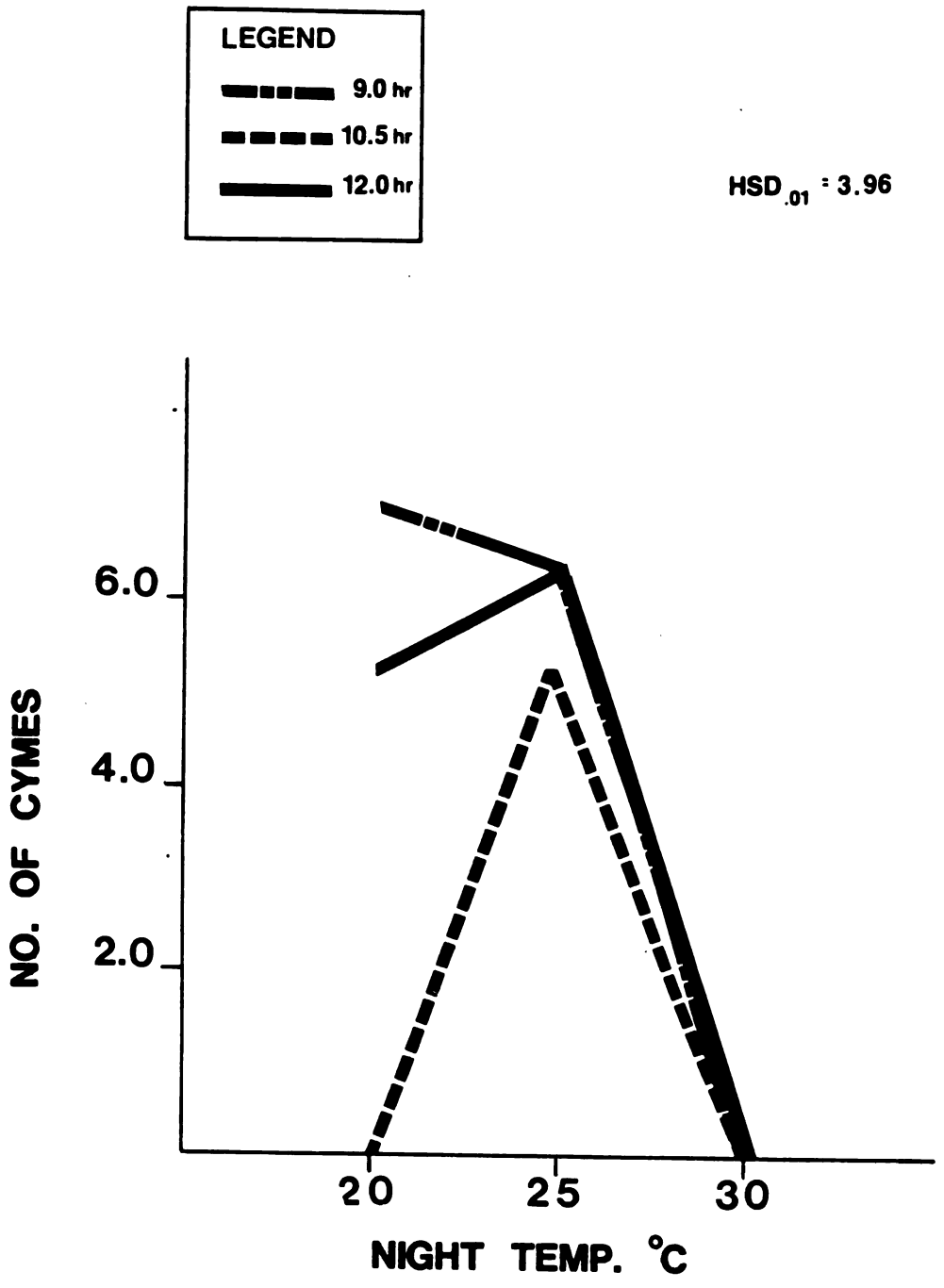

Fig. 1. Effect of day length and night temperature on flowering of 'Gelbe Melody' kalanchoe .

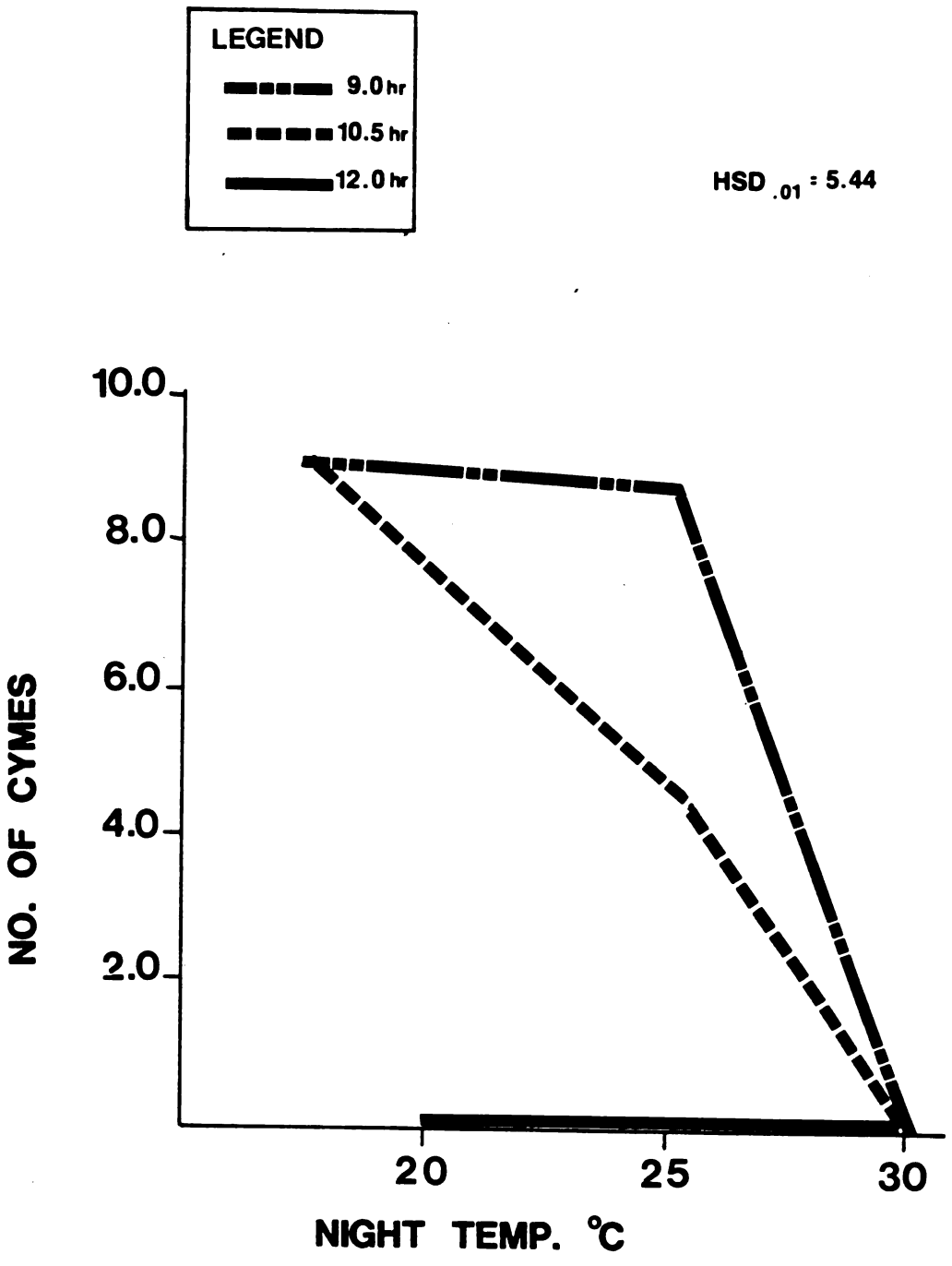

Fig. 2. Effect of day length and night temperature on flowering of 'Mace' kalanchoe .

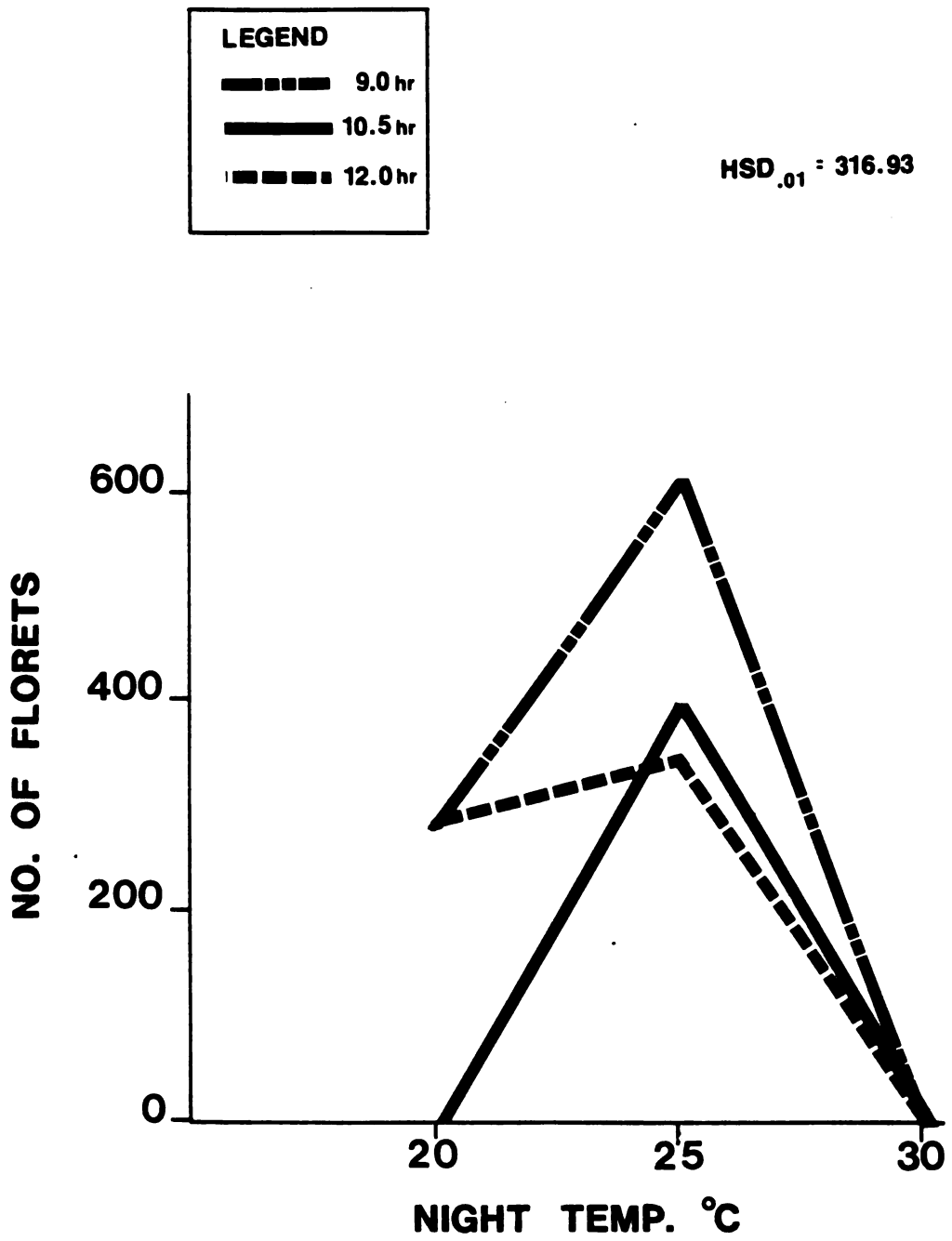

Fig. 3. Effect of night temperature and photoperiod on flowering response of " Gelbe Melody ".

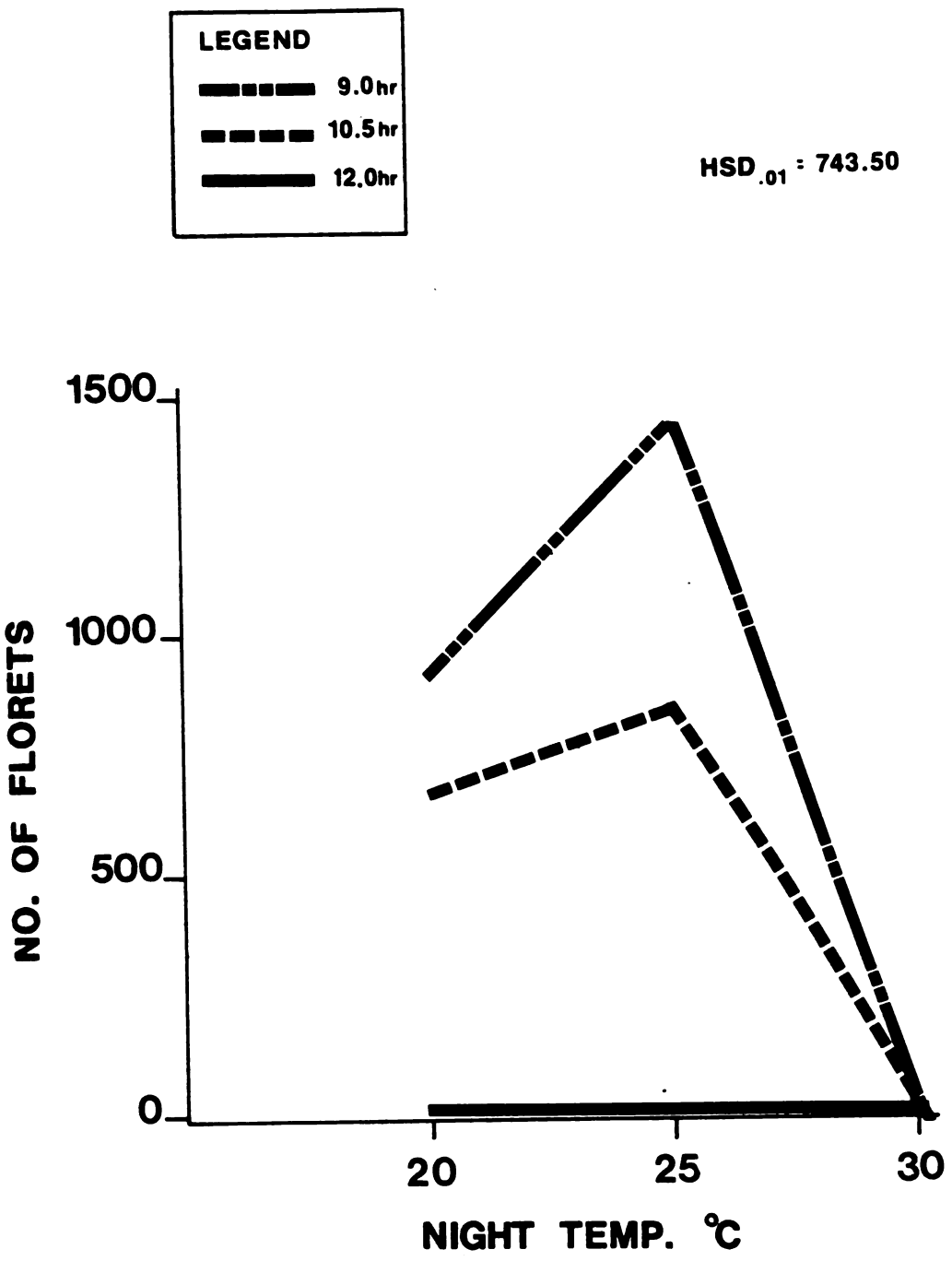

Fig. 4. Effect of night temperature and photoperiod on flowering response of " Mace " .

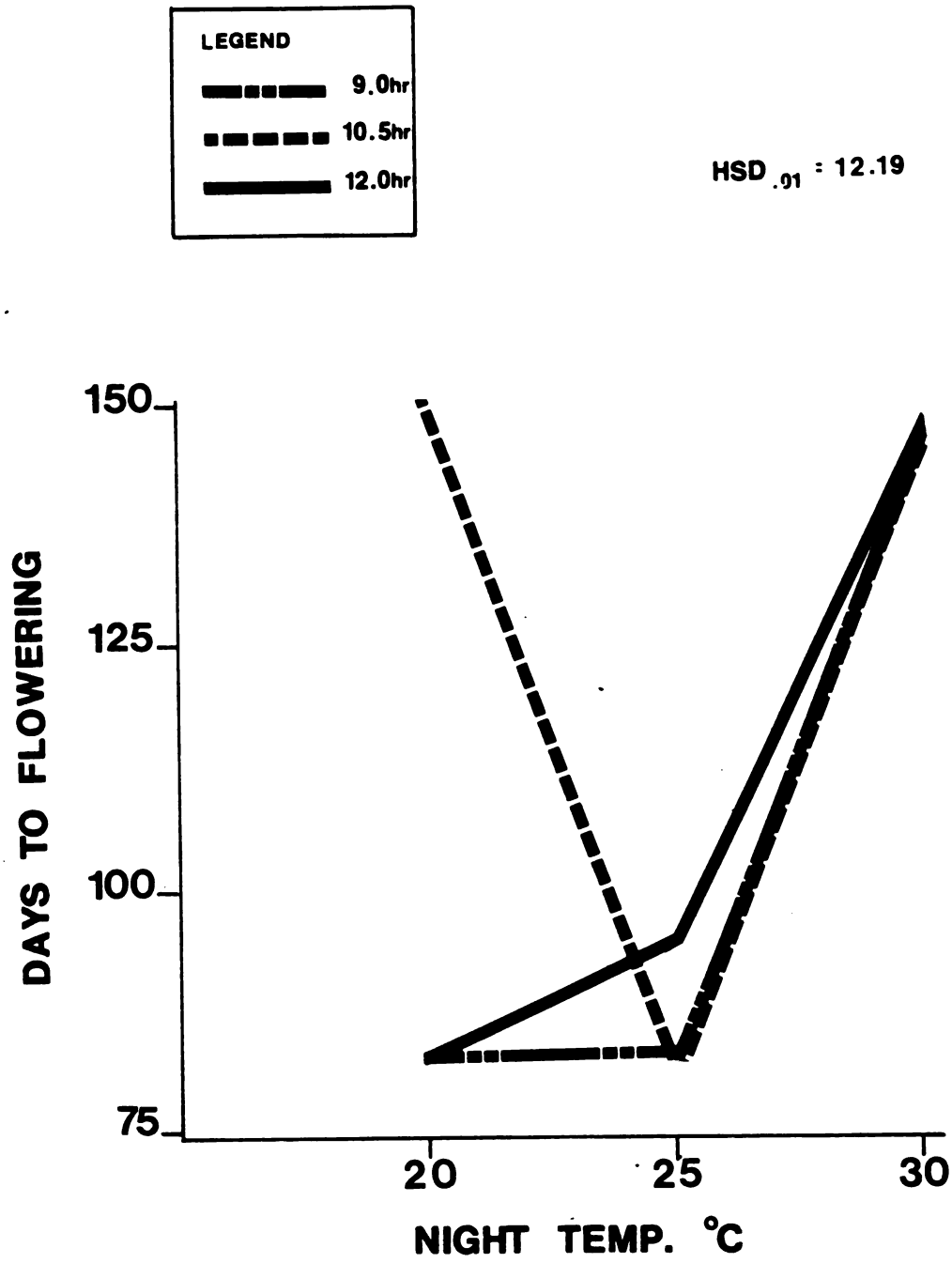

Fig. 5 Effect of night temperature and photoperiod on average days to first open floret for 'Gelbe Melody' .

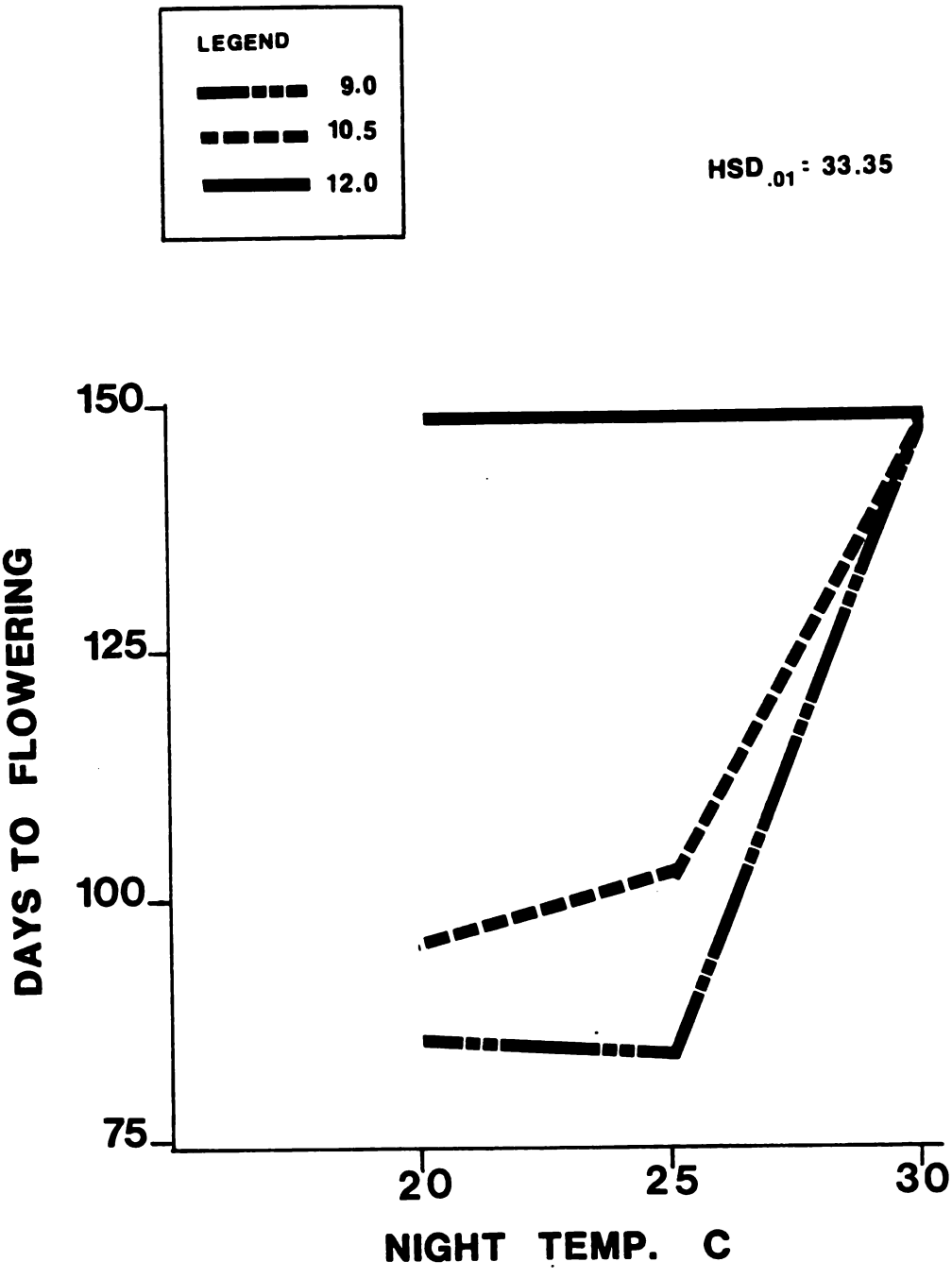

Fig. 6. Effect of night temperature and photoperiod on average days to first open floret for 'Mace'.

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Development of the Inflorescence of Two Cultivars of Kalanchoe Using Scanning Electron Microscopy

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Abstract: The development of the apical meristem of 'Mace' and 'Gelbe Melody' kalanchoe was examined under photoinductive conditions. Using scanning electron microscopy, the transition from vegetative to reproductive stages was followed. After 18 short day cycles (SD), the meristem became dome-shaped and axillary buds developed. The development of the dichasial cyme was evident after 28 SD cycles. 'Mace' and 'Gelbe Melody' formed petal and stamen primordia after 35 SD cycles; the gynoecium primordia developed after 49 SD cycles. Differences in foliage size and shape were reflected in the foliar primordia of each cultivar.

INTRODUCTION

As a preliminary to their work on radiation-induced mutations, Stein and Stein (5) investigated the development of the shoot apex of Kalanchoe cv. Brilliant Star. Using longitudinal sections and light microscopy (LM), they described the changes in the meristem from the vegetative through the reproductive state. Timing for this sequence was determined under SD conditions.

While sectioning provides internal detail, the form of the

floral parts can be difficult to reconstruct (4). Scanning electron microscopy (SEM) illustrates surface features; images of intact apices can be formed using an electron beam (3). Photomicrographs have a three-dimensional quality, with a greater depth of field than with LM (3).

The development of the floral organs of 'Mace' and 'Gelbe Melody' kalanchoe was studied using SEM. The pattern of floral initiation and the time sequence of their development under standard forcing procedures (1) was recorded.

MATERIALS AND METHODS

Commercially rooted vegetative cuttings of 'Mace' and 'Gelbe Melody' kalanchoe have a rapid response to SD treatment: 14 SD cycles at 17°C night temperature was required for floral induction (1).

A pasteurized mixture of peat/loam/perlite (1:1:1 by volume) was used as the growing medium. It was amended with superphosphate at 1 kg/m^3; the pH of the soil mix was approximately 6.2.

The plants were grown in 7.5 cm square plastic containers and fertilized with a constant liquid feed system with 200 ppm N and K_2O and later supplemented with 200 ppm N, P_2O_5, and K_2O. The pots were leached with water once a week.

The cuttings were potted upon arrival and grown under LD conditions until April 19, 1978 (3 weeks). Incandescent light at 100 W/m^2 for 4 hours (11:00 PM to 3:00 AM) provided the artificial LD conditions. Inductive conditions were maintained by pulling black sateen cloth at 5:00 PM and removing it at 8:00 AM daily. The plants were grown under artificial SD and natural light intensity for 8 weeks,

or visible bud. At this time they were returned to LD conditions.

Greenhouse temperatures were maintained at 17°C night and 21°C day temperature. Night temperatures did not exceed 21°C during the shading period; day temperatures did not exceed 30°C.

The experiment was a completely randomized design, using 44 plants for each cultivar. This allowed 8 plants for determination of complete floral development and 4 plants for each sampling date. Samples were taken at start of SD, and after the following numbers of SD cycles: 7,14,18,21,25,28,35,49.

Data were recorded on the 8 intact plants when all plants had fully flowered (July 10, 1978). This included number of days to first floret and pictures of representative plants.

Sample apices were trimmed to cubes no larger than 5mm. They were refrigerated overnight at 2-5°C in formalin, glacial acetic acid, ethanol and distilled water (10:5:45:40) (FAA).

Samples were dehydrated in an ethanol series (50%, 60%, 70%, 80%, 90%, 100%) for a minimum of 20 minutes for each solution with one repetition of 100% ethanol. They were then critical point dried (CPD) in a Denton DCP-1 dryer using liquid CO_2 on the same day. Samples were held in a vacuum desiccator until ready for mounting and viewing.

The excised apices were mounted on International Scientific Instrument Co (ISI) stubs with Tube-Koat (G.C. Electronics Co., Rockford, Illinois.). They were sputter-coated with gold for 4 minutes in a Film-Vac, Inc. Mini-Coater. The tissues were viewed with an ISI Super-Mini SEM using a 15 kv accelerating potential and Photo-Micrographs taken. Coated stubs were stored in a vacuum desiccator until further use.

RESULTS AND DISCUSSION

'Mace' remained vegetative after 14 SD cycles (Fig. 1A, 1B). The last pair of leaves were formed at this time. The doming of the apical meristem and the development of the axial buds after 18 SD (Fig. 1C) signalled the change to a reproductive phase. Subsequent leaves were smaller and bract-like, probably the intermediate bract-like leaves which subtend the inflorescence.

Following the decussate phyllotaxy, the inflorescences developed at 90^{o} to the last structure formed (Fig. 1C). After 25 SD cycles (Fig. 1E), the scale-like bracts had formed. The development of the dichasium became apparent after 28 SD cycles (Fig. 1F). The excised areas were leaves (L) or the bract-like leaf (BL).

Petal primordia were well-formed after 35 SD cycles (Fig. LG). The floret is slightly distended along the horizontal axis, although florets were generally symmetrical and even in shape. Eight stamen primordia were also formed after 35 SD cycles (Fig. 1G). Sepals have been removed to show petals and stamens more clearly.

The gynoecium primordia, with four carpels, was well developed after 49 SD cycles. However, the advanced development of the apex caused technical difficulties in preserving the entire structure through the fixation and preservation process.

'Gelbe Melody' developed in a similar manner (Fig. 2, 3). After 18 SD cycles, the apical meristem formed a dome; the leaf primordia became more bract-like in shape (Fig. 2C, 2D).

Axillary bud development was evident after 25 SD cycles (Fig. 2E) along with the beginnings of the dichasium. Sepal primordia were well-developed after 28 SD cycles (Fig. 2F) with faint bulges

of the stamen primordia just visible.

The four petals arose in the junctions of the sepals (Fig. 3A). The eight stamens were formed either adnate to the petals or at their junction. The shape of the flower is somewhat rectangular at this point. This shape did not persist in the fully developed flowers.

The petals were well-developed after 49 SD cycles, with fusion of the petals of the petals becoming evident (Fig. 3C, 3D, 3E). The four carpellate gynoecium also appeared at this time (Fig. 3D). At anthesis, the carpels were basally connate, with separate styles and glandular stigmas.

The leaf and bract primordia of 'Mace' and 'Gelbe Melody' differed in shape and form (Fig. 1, 2) reflecting differences in the fully developed foliage of the cultivars. The change in the size and shape of the apical dome after 18 SD cycles coincided with Stein and Stein's observations on 'Brilliant Star' kalanchoe (5).

The dichasium developed in a similar manner in both cultivars, with the central floret flanked by two lateral florets (Fig. 1F, 2E). These florets marked the development of the main axes of the inflorescence which was characterized by a central floret and several dichasia, each of which has a central floret (2). The sequence of the appearance of florets in the inflorescence proceded from the central florets outward along the cincinni, in a scorpioid pattern. The distal or central floret reached anthesis earliest; the central florets of each dichasium generally flowered in pairs downward along the central axis. Slight irregularities in this pattern, i.e. rate and extent of development of secondary bifurcations, were noted; more pronounced deviations were found under marginal conditions of induction (2, 6).

The androecium primordia appeared after 35 SD cycles in both 'Mace' and 'Gelbe Melody', more than 10 days earlier than in 'Brilliant Star' (5). Both 'Mace' and 'Gelbe Melody' had a shorter response time, flowering an average of 5-10 days earlier than 'Brilliant Star' (Carlson-unpublished data). However, the gynoecium primordia appeared at about the same time in all cultivars.

The irregular flower shape was evident in 'Mace' and 'Gelbe Melody' (Fig. 1G, 3B). The tubular corolla was forming in the final micrograph of 'Gelbe Melody' (Fig. 3E), showing the fusion of petals.

Fig. 1. Scanning electron micrographs of main shoot apices of Kalanchoe cv. Mace.

A. Vegetative apex. 45° tilt, X 100. 7 SD cycles. Leaf primordia (L) present.

B. Vegetative apex. 45° tilt, X 100. 14 SD cycles.

C. Transitional apex. 0° tilt, X 50. 18 SD cycles. Axillary buds (AX) developed; bract-like leaves (BL) formed.

D. Transitional apex. 45° Tilt, X 110. 21 SD cycles.

E. Reproductive apex. 45° tilt, X 120. 25 SD cycles. Scale-like bracts (B) visible.

F. Reproductive apex. 0° tilt, X 60. 28 SD cycles. Pattern of dichasium apparent.

G. Reproductive apex. 0° tilt, X 96. 35 SD cycles. Sepals (S) dissected, petal (P) primordia present, Stamens (St) forming.

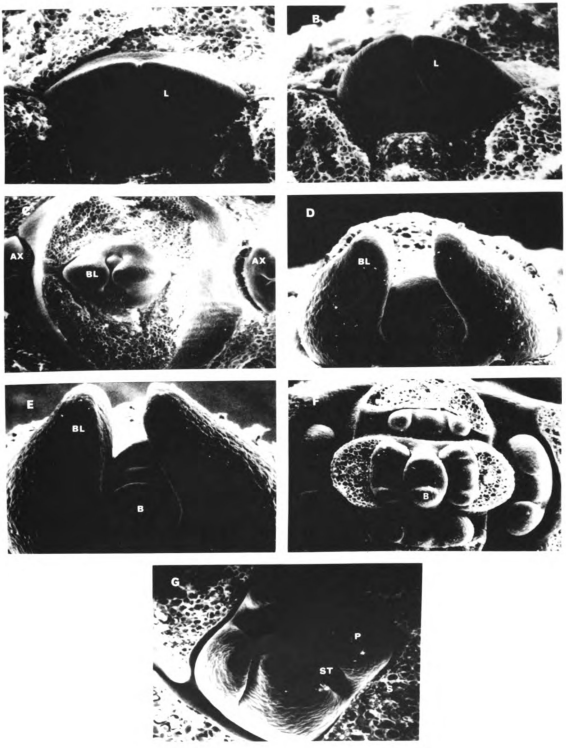

Fig. 1.

Fig. 2. Scanning electron micrographs of terminal shoot apices of Kalanchoe blossfeldiana cv. Gelbe Melody.

A. Vegetative apex. 30° tilt, X 200. 7 SD cycles. Leaf (L) primordia forming.

B. Vegetative apex. 40° tilt, X 200. 14 SD cycles.

C. Transitional apex. 55° tilt, X 110. 18 SD cycles.

D. Transitional apex. 45° tilt, X 110. 21 SD cycles. Bract-like leaves (BL) formed.

E. Reproductive apex. 45° tilt, X 72. 25 SD cycles. Bract (B) primordia present.

F. Reproductive apex. 10° tilt, X 50. 28 SD cycles. Sepal (S) primordia well-formed.

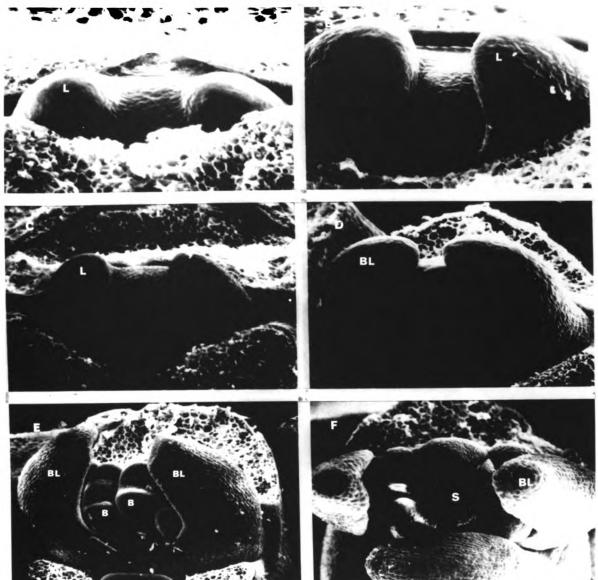

Fig. 2.

Fig. 3. Scanning electron micrographs of shoot apices of Kalanchoe blossfeldiana cv. Gelbe Melody.

A. Reproductive apex. 45° tilt, X 100. 35 SD cycles
4 sepals (S), 4 petals (P), 8 stamens (St) present.

B. Reproductive apex. 0° tilt, X 120. 35 SD cycles.

C. Reproductive apex. 20° tilt, X 30. 49 SD cycles.

D. Reproductive apex, 0° tilt, X 60. 49 SD cycles.
4 carpels (C) formed.

E. Reproductive apex. 0° tilt, X 18. 49 SD cycles.
Central floret (CF), Lateral floret (LF).

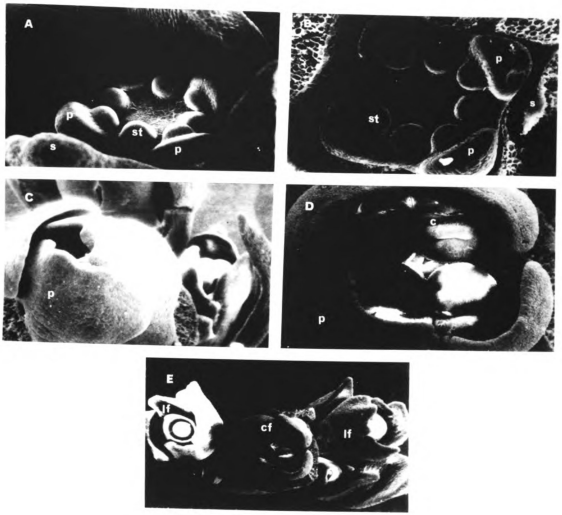

Fig. 3.

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Effects of High Night Temperature on Nine Cultivars of Kalanchoe

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Abstract: Nine cultivars of kalanchoe were evaluated under greenhouse conditions for response to high temperatures. 'Goddess', 'Rhumba', 'Rotkappchen' and 'Tabasco' were unaffected by night temperatures of 25-30°C. Individual plants of 'Toltec' and Montezuma' were incompletely flowered under high night temperatures. 'Adagio' and 'Pixie' showed some partial initiation under both high and low (17-20°C) night temperatures, indicating a need for increased treatment beyond the 28 short day cycles. Most of the cultivars were slightly delayed in flowering time with high night temperatures.

INTRODUCTION

Early kalanchoe cultivars with bright red flowers are grown from seed for Christmas and Valentine's Day (1). As new hybrids were developed and grown year round, difficulties in timing and quality were encountered particularly during periods of high night temperatures. Efforts to negate the inhibitory effects of high night temperatures through growth regulators were unsuccessful (5). Pertuit (4) demonstrated that increased short day (SD) cycles could compensate for a lower night temperature; however, the inhibitory effects of high night temperatures could not be overcome

even after 5 months of SD treatment (5).

Harder (3) noted the importance of temperature during the inductive period. Plants subjected to high temperatures (30°C) reacted much the same as plants receiving insufficient SD treatment. Partial initiation resulted, with a reduction in branching of the inflorescences, fewer florets and enlarged bracts (phyllody).

Breeding efforts have been directed towards developing 'heat-resistant' cultivars, among other desirable traits. Many of the recent introductions resulted from that breeding program.

To evaluate cultivars for heat tolerance under greenhouse conditions, nine cultivars were tested for their ability to initiate flowers at high night temperatures during the SD induction period.

MATERIALS AND METHODS

The commercially rooted vegetative cuttings, 'Goddess', 'Montezuma', 'Tabasco', 'Toltec',[1] and 'Adagio', 'Nugget', 'Pixie', 'Rotkappchen' and 'Rhumba' were used in this study.[2] The Aztec series were pinched 3 weeks before shipping, while the latter cultivars were terminal cuttings.

On arrival the cuttings were potted in a pasteurized mix of

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[1]Plant material supplied by Pan American Plant Co., West Chicago, Ill. 60185.

[2]Plant material supplied by Mikkelsen's, Inc., Ashtabula, Ohio 44004.

peat, loam and perlite (1:1:1 by volume), amended with superphosphate at a rate of 1 kg/m^3. The pH of the mix was approximately 6.2. The plants were grown in 7.5 cm square plastic containers and were fed on a constant liquid feed system with 200 ppm N and K_2O and later supplemented with 200 ppm N, P_2O_5 and K_2O. The pots were leached thoroughly once a week.

To maintain vegetative conditions, the plants were kept under LD conditions until treatments were applied. Artificial LD were supplied by means of 4 hours of incandescent light at 100 W/m^2 from 11:00 PM to 3:00 AM.

The treatments were set up in the same greenhouse. One black cloth was placed near an evaporative cooling system and a temperature of 17-20^{o}C was maintained under the cloth at night. The second black cloth was positioned away from the cooling system; a rubber heating pad, thermostatically controlled, was also placed under the cloth. (Plants were not grown on the pad). Temperatures ranged from 25-30^{o}C during the shading period.

Black sateen cloth was pulled at 5:00 PM and removed at 8:00 AM. This treatment commenced on June 21, 1978 and ended 4 weeks later on July 19, 1978.

The plants were in a completely randomized design under each black cloth. There were 5 replications per cultivar per treatment.

When all plants had flowered, data were recorded. Flowering dates were noted when the first floret opened on each plant. Visual observations on the degree of flowering were determined as follows:

vegetative - no florets or reproductive growth

transitional - incomplete development of cymes, limited number of florets, enlargment of bracts.

flowering - completely developed cymes, abundant florets, bracts of normal size (minute, scale-like).

RESULTS AND DISCUSSION

With the exceptions of 'Adagio' and 'Pixie', all plants given low night temperatures (17-20°C) came into complete flower (Table 1). All 'Adagio' plants and 20% of 'Pixie' plants at low night temperatures were transitional. 'Adagio' and 'Pixie' probably required a greater number of SD cycles for complete floral induction under these conditions.

'Goddess', 'Rhumba', Rotkappchen' and 'Tabasco' were unaffected by high night temperatures (25-30°C) (Table 1). All plants in both treatments were fully flowered; the number of days to first floret was not significantly different for the two treatments with these cultivars (Table 2).

'Toltec' and 'Montezuma' were relatively unaffected by night temperature, with 80% of the plants under high temperatures in complete flower. The number of days to flowering was not significantly different. With 'Nugget', all plants at high night temperatures were transitional; 'Pixie' produced 80% transitional flowering with high night temperatures.

The earliest response was observed with 'Goddess', 'Montezuma', 'Rhumba', 'Tabasco' and 'Toltec', all of which flowered in fewer than 60 days from the start of SD treatment. Most of the cultivars exhibited a slight delay in flowering time under high night

temperature; 'Goddess' and 'Nugget' were the two exceptions to this trend.

From these results, an understanding of some of the factors involved in the formation of insufficient kalanchoe inflorescences begins to emerge. Deviations of temperature, daylength and duration of treatment resulted in plants unsuited for sale (3). Cultivars differ in their requirements of temperature and number of SD cycles (2,4). With the wide choice of cultivars available, the commercial producer can avoid cultivars which are heat-sensitive for summer production under uncooled greenhouse conditions.

Table 1. Percentage of vegetative, transitional and flowering plants of nine cultivars of kalanchoe grown under high and low night temperatures.[z]

Cultivar	Night Temperature	% Vegetative	% Transitional	% Flowering
Adagio	high	-	100	-
	low	-	100	-
Goddess	high	-	-	100
	low	-	-	100
Montezuma	high	-	20	80
	low	-	-	100
Nugget	high	-	100	-
	low	-	-	100
Pixie	high	-	80	20
	low	-	20	80
Rhumba	high	-	-	100
	low	-	-	100
Rotkappchen	high	-	-	100
	low	-	-	100
Tabasco	high	-	-	100
	low	-	-	100
Toltec	high	-	20	80
	low	-	-	100

[z]High night temperature = 25-30°C; low night temperature = 17-20°C.

Table 2. Effect of night temperature on average days to first open floret for cultivars of kalanchoe.

	Night Temperature	
	Days to First Floret	
Cultivar	High (25-30°C)	Low (17-20°C)
Adagio	65.0	59.2
Goddess	54.2	54.2
Montezuma	56.6	52.8
Nugget	68.0	69.6
Pixie	70.8	59.6
Rhumba	54.8	53.0
Rotkappchen	69.0	63.8
Tabasco	54.0	52.6
Toltec	56.6	54.2
$HSD_{.01}$	6.52	

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APPENDIX

TABLE 1. Effect of night temperature and photoperiod on flowering of 'Gelbe Melody' and 'Mace' kalanchoe.

CULTIVAR	NIGHT TEMP (°C)	PHOTO-PERIOD (HR)	NO. OF LATERAL CYMES	NO. OF CYMES	NO. OF FLORETS	NO. OF LATERAL FLORETS	NO. OF TERMINAL FLORETS	DAYS TO FLOWER
Gelbe Melody	20°	9.0	5.5	6.5	285.0	155.8	129.2	84.5
		10.5	0	0	0	0	0	150.0
		12.0	4.0	4.8	288.0	126.0	162.0	84.2
	25°	9.0	4.3	5.3	613.8	342.8	271.0	84.2
		10.5	2.7	3.7	404.3	131.2	273.2	84.7
		12.0	4.3	5.2	350.0	247.3	102.7	96.2
	30°	9.0	0	0	0	0	0	150.0[z]
		10.5	0	0	0	0	0	150.0[z]
		12.0	0	0	0	0	0	150.0[z]
Mace	20°	9.0	8.0	9.0	912.3	661.3	251.0	86.2
		10.5	6.8	7.7	669.8	550.2	219.7	96.3[y]
		12.0	0	0	0	0	0	150.0[z]
	25°	9.0	7.8	8.8	1415.5	1093.5	322.0	84.8
		10.5	4.0	4.8	839.2	537.5	301.7	103.3[y]
		12.0	0	0	0	0	0	150.0[z]
	30°	9.0	0	0	0	0	0	150.0[z]
		10.5	0	0	0	0	0	150.0[z]
		12.0	0	0	0	0	0	150.0[z]
	$HDS_{.01}$		4.72	5.06	637.06	520.12	201.78	25.42

[y]Not all plants in treatment flowering

[z]Plants did not flower by termination of experiment