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Influence of Temperature and Irradiance on Growth and Development of *Petunia X hybrida* 'Snow Cloud'

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William H. Carlson
Major professor

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# INFLUENCE OF TEMPERATURE AND IRRADIANCE ON GROWTH AND DEVELOPMENT OF *PETUNIA X HYBRIDA* 'SNOW CLOUD'

By

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# ABSTRACT

## The Effects of Temperature and Irradiance on the Growth and Development of Petunia x hybrida 'Snow Cloud'

by

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Petunia is one of the most popular bedding plants produced. The effects of 5 day temperatures and 5 night temperatures ranging from 10° to 30°C at irradiances of 13 and 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ were determined. Days to flower, leaf unfolding rate and number of lateral shoots produced were a function of average temperature. Leaf unfolding rate increased as average temperature increased, while days to flower and number of lateral shoots decreased. Fastest time to flower was achieved at 25° at the higher irradiance with delay and bud abortion occurring at higher temperatures. Plant height and average internode length increased as day temperature increased or irradiance decreased. Average lateral break length decreased with increasing day temperature but did not show an effect of night temperature. Plants at all treatments unfolded an average of 18.8 leaves on the mainstem by anthesis and required a minimum of 13 nodes on the mainstem before initiating a flower bud.

# ACKNOWLEDGMENTS

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Guidance Committee:

The paper format was adopted for this thesis in accordance with departmental and university regulations. Section I is to be submitted to the Journal of the American Society for Horticultural Science; Section II to HortScience.

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## Section II

# LITERATURE REVIEW

# INTRODUCTION

The petunia, or Petunia x hybrida Vilm., has been one of the most popular bedding plants since its introduction in the early 1850's, and is largely responsible for the birth of the bedding plant industry (Kaczperski et al., 1988). Although other bedding plant species have enjoyed rapid rises in popularity and have been labeled the number one bedding plant, the petunia has always been found in the top five (Anonymous, 1988; Lieberth, 1988; Mellon and Goldsmith, 1985).

Petunia x hybrida, a member of the Solanaceae family and native to South America, is a cross between two other species, Petunia axillaris and Petunia violacea. It was introduced to Europe by 1850 and to the United States by 1880 (Everett, 1981). Presently there are five classes of Petunia x hybrida. These are grandiflora singles, grandiflora doubles, multiflora singles, multiflora doubles and floribunda singles (Ball, 1985). The most commonly produced commercial varieties are the grandiflora and multiflora singles.

New cultivars of Petunia x hybrida are continually being introduced for commercial production, assuring the plant's popularity for some time to come. Because of this, a predictive model of plant growth and development would be an important addition to the available knowledge already used to grow petunias profitably.

Many environmental factors were recognized early as having an influence on plant growth (Hanson, 1917; Krizek et al., 1970; Mohr, 1964; Post, 1942; Roberts and Struckmeyer, 1938; Vince, 1964; Went, 1953; Zeevaart, 1976). Light, temperature, water, fertility levels and other factors can be manipulated alone or in various combinations to produce differing plant responses. Of these factors, light and temperature seem to have the greatest effect on petunia growth, as measured by days to flower and plant height (Carpenter and Carlson, 1974).

## LIGHT

### PHOTOPERIOD

Three separate characteristics of light can influence plant growth. These are duration, intensity and quality (Garner and Allard, 1920). The effects of duration, or photoperiod, have been studied in some depth. Garner and Allard were the first to discuss the concept of photoperiodism (1920). After studying the effects of day and night length on several plant species, they suggested the term 'photoperiodism' to describe the response of plants to the relative length of day and night.

In 1931, Alex Laurie (1931) demonstrated that flowering of several photoperiodic greenhouse crops could be controlled by lighting or shading the plants to obtain the desired response. He also demonstrated that rooting of cuttings of several plant species could be increased by extending the photoperiod during the rooting process. Through his work he was able to verify that photoperiodic manipulation was cost effective and had practical uses in commercial floriculture.

After Laurie's experiments, Withrow and Benedict (1936) showed that extending the photoperiod to 21 hours per day with incandescent lamps during the short days of winter increased dry weight gain and decreased time to flower in _Viola tricolor_ (pansy), _Mathiola incana_ (stock), and _Callistephus chinensis_ (aster). _Viola tricolor_ and _Callistephus chinensis_ also produced more flowers per plant under the extended photoperiod. _Mathiola incana_ produced less. Petersen (1955) later stated that the slow rate of plant growth during the low light conditions of winter was due more to the short photoperiod than the low light intensity. Therefore, extending the photoperiod, especially for seedlings and cuttings, would result in an increased growth rate.

Plants can be divided into one of several photoperiodic response groups (Salisbury, 1982). These groups are day neutral, quantitative short or long day, and qualitative short or long day. In most cases there are no distinct lines separating the different response groups. Instead, the response groups tend to blend together (Figure 1).

Roberts and Struckmeyer (1938, 1939) examined the effects of photoperiod on petunia and several other species of plants. They found that at a constant temperature of 12.8°C (55°F), flowering of petunia was induced by temperature and that the plants flowered under both long days (16 hour photoperiod) and short days ($9^1/_2$ hour photoperiod). When the plants were grown within the range of 17.2°-18.3°C (63°-65°F) or 21.1°-23.8°C (70°-75°F), they flowered only under long days, thus making them thermophotoperiodic. This concept was later stated by Post (1942).

Van der Veen and Meijer (1959) classified petunia as a non-obligate long day plant. Carpenter and Carlson (1974) reported that petunias became responsive to photoperiodic manipulations at the six-leaf stage, about 20 days after transplanting. The photoperiod supplied to the plant prior to this stage had no effect on days to flower or plant morphology. However, in the work of Piringer and Cathey (1960), petunia seedlings were exposed to long or short days up to the six-leaf stage. The seedlings given long days

Figure 1. Flowering responses of different hypothetical plants for various photoperiods. 1. A truly day-neutral plant, flowering about the same at all photoperiods. 2. Plant that is slightly but probably insignificantly promoted in its flowering by long-days. 3. and 4. Different degrees of a quantitative long-day response. 5. Qualitative or absolute long-day plant with a 12 hour critical photoperiod. 6. Qualitative short-day plant. 7. Quantitative short-day plant (Salisbury, 1982).

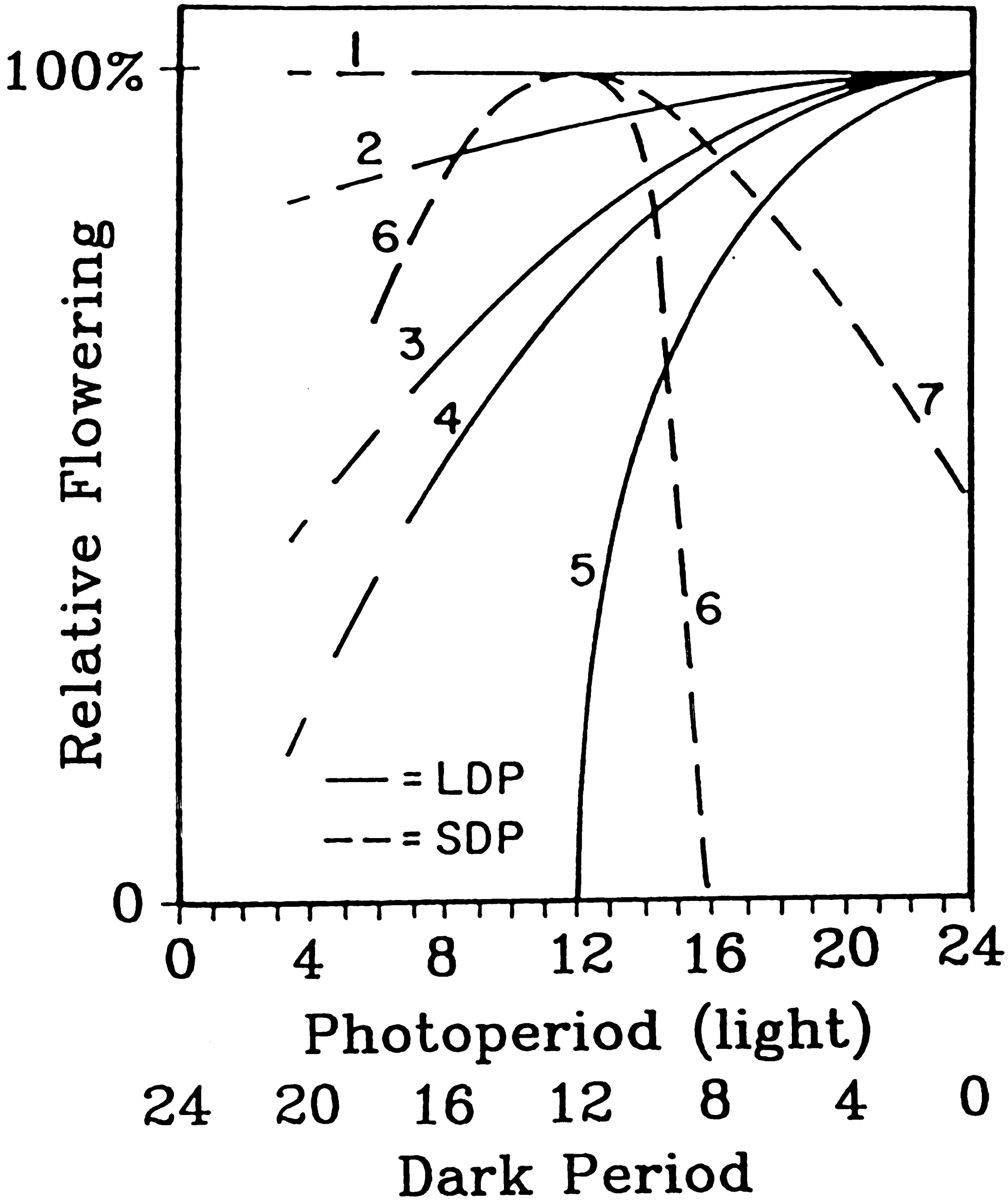

100%
0
Relative Flowering
1
2
3
4
5
6
6
7
— = LDP
– – = SDP
0
4
8
12
16
20
24
Photoperiod (light)
24
20
16
12
8
4
0
Dark Period

Figure 1

were taller and had a greater leaf area than seedlings exposed to short days even though both groups were at the same stage developmentally at the end of the experiment.

Days to flower can be greatly reduced in many plant species when grown under long days (Carpenter, 1974; Carpenter and Beck, 1973; Carpenter and Carlson, 1974; Hughes and Cockshull, 1966; Lane et al., 1965; Roberts and Struckmeyer, 1939; Seeley, 1955). Carpenter and Carlson (1974) were able to reduce time to flower by 30 to 45 days in petunias by growing them under long days instead of short days.

Besides flowering, photoperiod can affect other aspects of plant growth. Long days induce stem elongation in many plants (Vince-Prue, 1975). Elongation is accomplished by stimulating internode expansion during active growth. The increased internodes result in longer stems and taller plants (Carpenter and Carlson, 1974; Cathey and Piringer, 1961). In 1961, Cathey and Piringer (1961) discovered that when petunias were grown under an 8 hour photoperiod, the plants developed a rosette growth habit. This rosette growth was due to greatly shortened internodes. However, when the photoperiod was increased to either 16 or 24 hours the internodes elongated, resulting in taller plants with an alternate leaf pattern.

Another effect of photoperiod on petunia morphology was the reduction of the number and length of basal branches when the plants were grown under long days (Carpenter and Carlson, 1974). When grown under short days, the plants produced a large number of basal branches. However, when the photoperiod was extended to 16 or 24 hours, the number of branches was reduced along with the length of each individual branch. Similar results were reported by Wolnick and Mastalerz (1966). When petunias were grown under a 9 hour photoperiod, the plants branched freely. When the daylength was extended to 16 hours using incandescent bulbs, branching was inhibited. This inhibition however, may be more of a response to light quality, not photoperiod (Kasperbauer, 1971).

Length of photoperiod has been found to influence leaf size. Hughes and Cockshull (1966) obtained leaf areas 35% greater on petunias grown under long days when compared to those grown under short days. In either case, the plants had the same number of total leaves. Comparable results were later reported for Antirrhinum majus and Pelargonium x hortorum (Flint, 1960; Merritt and Kohl, 1985). Merritt and Kohl (1983) suggested that increased plant growth in Petunia x hybrida grown under long days was due to increased leaf size. This increase provided a larger sink for the plant prior to the closing of the plant canopy.

Different methods can be used to extend photoperiod. Lane, Cathey and Evans (1965) determined that for best plant growth, the most effective method of lengthening the day period was to provide light for 8 hours immediately preceding the natural photoperiod instead of extending the length at the end. However, Hughes and Cockshull (1966) stated that a 4 hour night break similar to lighting schedules to maintain a vegetative state in chrysanthemum was as effective as adding 8 hours of additional light to the natural photoperiod.

Many different types of lamps, if they produce sufficient intensity, can be used to extend the photoperiod (Carpenter and Beck, 1973; Carpenter and Carlson, 1974; Cathey and Campbell, 1975). However, some plant responses, such as flowering and stem elongation, are influenced by phytochrome conversion (Borthwick and Hendricks, 1960; Canham, 1966; Cathey, 1974; Holmes and Smith, 1977a; Lane et al., 1965; Mohr, 1962, 1964; Salisbury, 1961; Searle, 1965; Smith and Holmes, 1977; Vince, 1964; Zeevaart, 1976). Light sources high in red light would have a greater effect on reducing time to flower than those sources lacking red light (Carpenter, 1974; Doorenbos and Wellensiek, 1959). In 1974, Carpenter (1974) found that high pressure sodium lamps were one of the best sources to use in decreasing flowering time if low light levels were to be used. They also worked equally as well at high light levels, such as those found in supplemental lighting of the crop.

Photoperiod is a very important factor to consider when examining the effects of light on petunia growth. It affects not only time to flower but plant morphology as well. Photoperiod is easily controlled through the use of shadecloth and supplemental lighting, making it a useful tool for controlling petunia growth.

## INTENSITY

Benefits can be realized in many plant species when they are grown with supplemental light. Supplemental lighting is a term that refers to increasing the natural light levels received by the plants with one or more electrical light sources. When using supplemental light to extend the photoperiod of plants, low intensities can be used. However, if sufficiently high intensities are used, plant growth will be accelerated (Armitage et al., 1983; Carpenter, 1974; Carpenter and Anderson, 1972; Carpenter and Beck, 1973; Carpenter and Carlson, 1974; Krizek et al., 1968; Petersen, 1955).

Increasing the light intensity, especially during the low light levels of winter, has been shown to decrease the time to flower for several plant species. Early work by Withrow and Benedict (1936) showed a significant decrease in time to flower for Viola tricolor, Mathiola incana and Callistephus chinensis when the plants were grown with supplemental lights. Plants were illuminated with specially filtered incandescent lamps. The filters excluded infrared light with wavelengths longer than 1400 mu. Wavelengths in this range reportedly raised leaf temperatures $1^\circ$ to $2^\circ C$ and the filters eliminated this problem. As a result, time to flower for *Viola tricolor* was decreased 67%, for *Callistephus chinensis* 33% and for *Mathiola incana* 39% because of the additional irradiance.

Armitage et al. (Armitage and Tsujita, 1979; Armitage et al., 1981; Armitage et al., 1983) and Carpenter and Rodriguez (1971a) demonstrated in several studies that time to flower could be reduced in hybrid seed geraniums, a day neutral plant (Post, 1942), through the use of high intensity lighting, especially when the plants were illuminated from flower initiation to visible bud. This decrease was found to be true for several cultivars (Figure 2), and was shown to be an effect of cumulative photosynthetically active radiation (Craig and Walker, 1963; Erickson et al., 1980).

Carpenter and Beck (1973) reported substantial decreases in time to flower for several floricultural crops when grown with supplemental high intensity lighting. They grew petunias, impatiens, marigolds and zinnias under either natural winter light conditions, photoperiodic extensions with incandescent lamps or 24 hour continuous high intensity lighting. In all cases, the plants receiving the high intensity lighting flowered first, the extended photoperiod

Figure 2. The relationship between quantum flux density at an 18 hour photoperiod and number of days to flower for 3 cultivars of hybrid seed geranium, a: 'Sprinter Scarlet', b: 'Sooner Red' and c: 'Ringo'(Armitage et al., 1983).

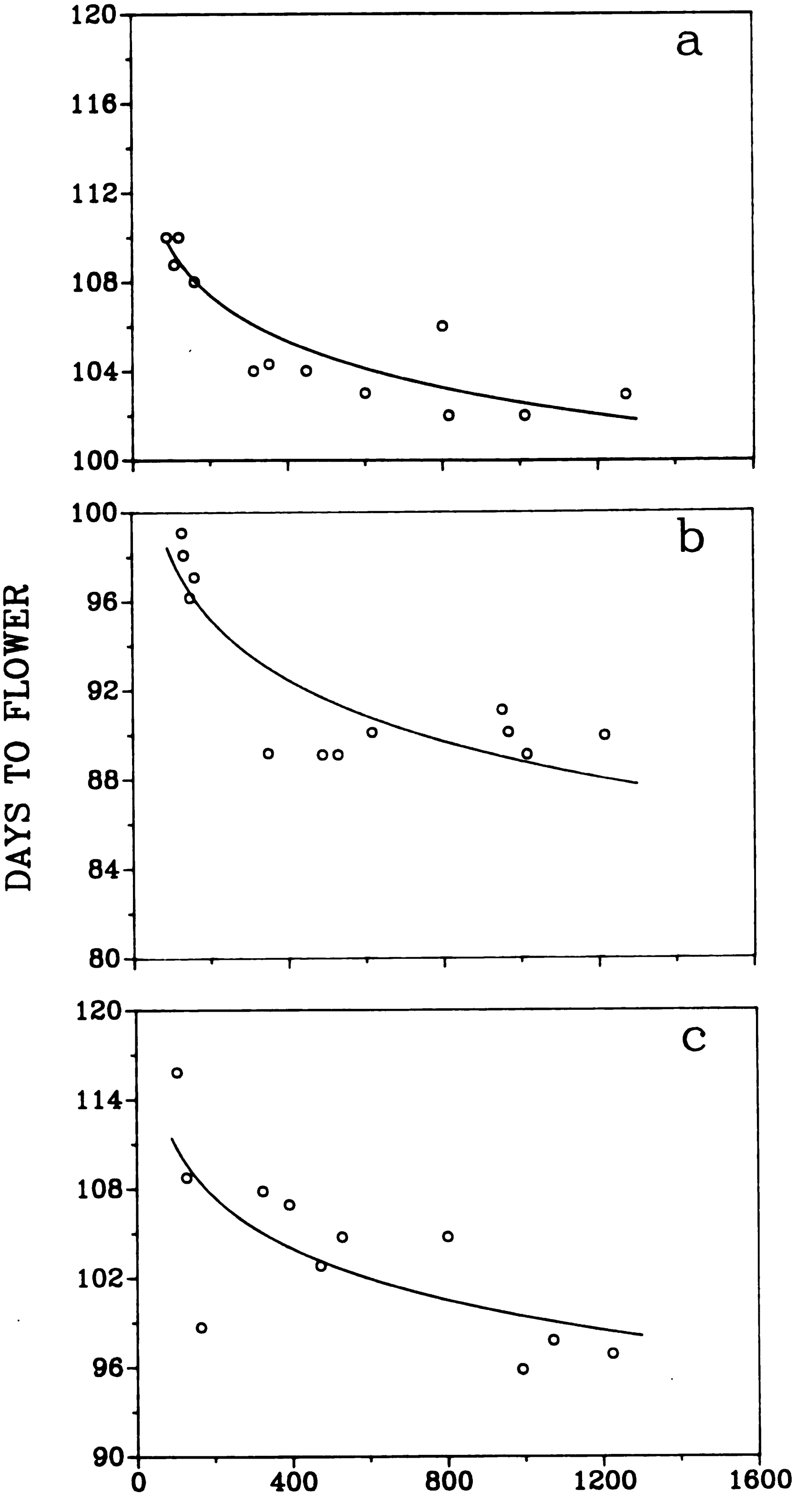


Figure 2 QUANTUM FLUX DENSITY ($\mu$mol $m^{-2}s^{-1}$)

plants second and the ones grown under natural light conditions last. These results, they stated, showed that the quicker flowering time was due to, at least in part, the high intensity lighting and not just a photoperiodic response.

Carpenter and Carlson (1974) determined the effects of high intensity lighting on Petunia x hybrida. Plants were grown under the low light conditions of winter, under winter light conditions with the photoperiod extended with incandescent lamps at 10.8 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$ (50 f.c.) (Thimijan and Heins, 1983) or with 24 hour supplementary light provided from high pressure sodium lamps at 131.7 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$ (1000 f.c.). Three different cultivars were tested. Plants grown under the high pressure sodium lamps flowered an average of 45 days earlier than those plants grown under natural light conditions, and 17 days earlier than those grown under the 16 hour photoperiod (Table 1). They concluded that time to flower in Petunia x hybrida could be reduced by 2 days for every 1 day they were lit with high pressure sodium lamps.

Table 1. The effect of 3 lighting regimes on flowering of 3 cultivars of Petunia x hybrida (Carpenter and Carlson, 1974).

| | **DAYS TO FLOWER** | | |
|---|---|---|---|
| **TREATMENT** | **Happiness** | **White Magic** | **Blue Magic** |
| Natural Light | 83 | 85 | 92 |
| 16 Hour Inc. | 56 | 59 | 60 |
| 24 Hour HPS. | 38 | 42 | 45 |

Besides reducing time to flower, supplemental lighting of adequate intensity can be used to increase plant growth and quality. Carpenter and Rodriguez (1971b) showed in that they were able to obtain a higher percentage of flowering stems and a significant increase in the number of bottom breaks in three cultivars of cut roses by lighting them from 1800 hours to 0300 hours with fluorescent lamps. Similar results were obtained by Carpenter and Anderson (1972).

Pansy, stock and aster all experienced a significant increase in both fresh and dry weight when given supplemental lighting from incandescent lamps (Withrow and Benedict, 1936). Plants received 100 f.c. daily from 3 hours after sundown until dawn. In addition to the increase in fresh and dry weights, pansies produced longer stems and more flowers per plant when given supplemental light, although the diameters of individual flowers were less than those receiving only natural light conditions. Asters also produced longer stems and more flowers but had an increased flower diameter when given supplemental light. Stock, on the other hand, produced fewer flowers per plant though the stems were longer when given supplemental light.

Erickson et al. (1980) presented evidence that seed geraniums produced more lateral shoots and experienced decreased plant height but showed no difference in dry weight gain when lit with high pressure sodium lamps. In this experiment plants were lit 24 hours per day at a level of 40 micro-mol$\cdot s^{-1} \cdot m^{-2}$. Armitage et al. (1981) further demonstrated that specific leaf weight of hybrid seed geranium also increased with increasing intensity.

Krizek et al. (1968) stated that increased seedling growth for many bedding plant species could be obtained through the use of high intensity lighting. Seedlings grown with supplemental lights would be ready for transplanting sooner, have a greater fresh weight and display increased vigor over seedlings grown under natural light conditions.

In 1971 R. A. Norton (1971) outlined the benefits of supplemental light when used in Washington state and the northwest region of the country. Several bedding plant species, including petunia, were grown under natural light conditions or with supplemental lights provided by fluorescent lamps. Petunia showed a 246% increase in dry weight accumulation when they received the extra light. Other species tested showed equal or greater gains in dry weight.

Work by Carpenter and Beck (1973) showed that increased plant growth in petunias was obtained when the plants were supplemented with high pressure sodium lamps in addition to natural day light. Plants under the HPS lamps were slightly taller and had longer roots than plants grown only under natural day light.

In other work by Carpenter (1974), petunias were provided with 536 micro-mol$\cdot s^{-1} \cdot m^{-2}$ (10 w/ft$^2$) (Thimijan and

Heins, 1983) from high pressure sodium lamps for 24 hours a day in addition to natural daylight. When these plants were compared to petunias grown under normal winter light conditions, the lighted plants had increased basal branching, an increased fresh weight as well as a compact growth habit. The plants grown under the supplemental light were of greater quality than those grown under natural conditions.

Intensity also has an effect on the post production life of petunias. Armitage and Kowalski (1982) tested the effects of three light levels and three temperatures on the post production life of Petunia x hybrida 'Coral Sea'. At warm temperatures and high light levels, plants produced the greatest increase in dry weight. At lower temperatures, light level had less of an effect (Figure 3).

Like photoperiod, light intensity has been shown to have a profound effect on the growth and development of Petunia x hybrida. As a bedding plant, petunias are normally grown when natural light conditions are quite low. Increasing these low levels with supplemental light will produce a strikingly different plant.

Figure 3. Percentage of change in dry weight from day 1 of post harvest conditions for 'Coral Sea' petunia illuminated 13 hours day$^{-1}$ with fluorescent and incandescent lamps in: a. 10°, b. 20° or c. 30°C. High = high QFD (900 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$), Medium = medium QFD (600 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$), Low = low QFD (300 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$) (Armitage and Kowalski, 1982).

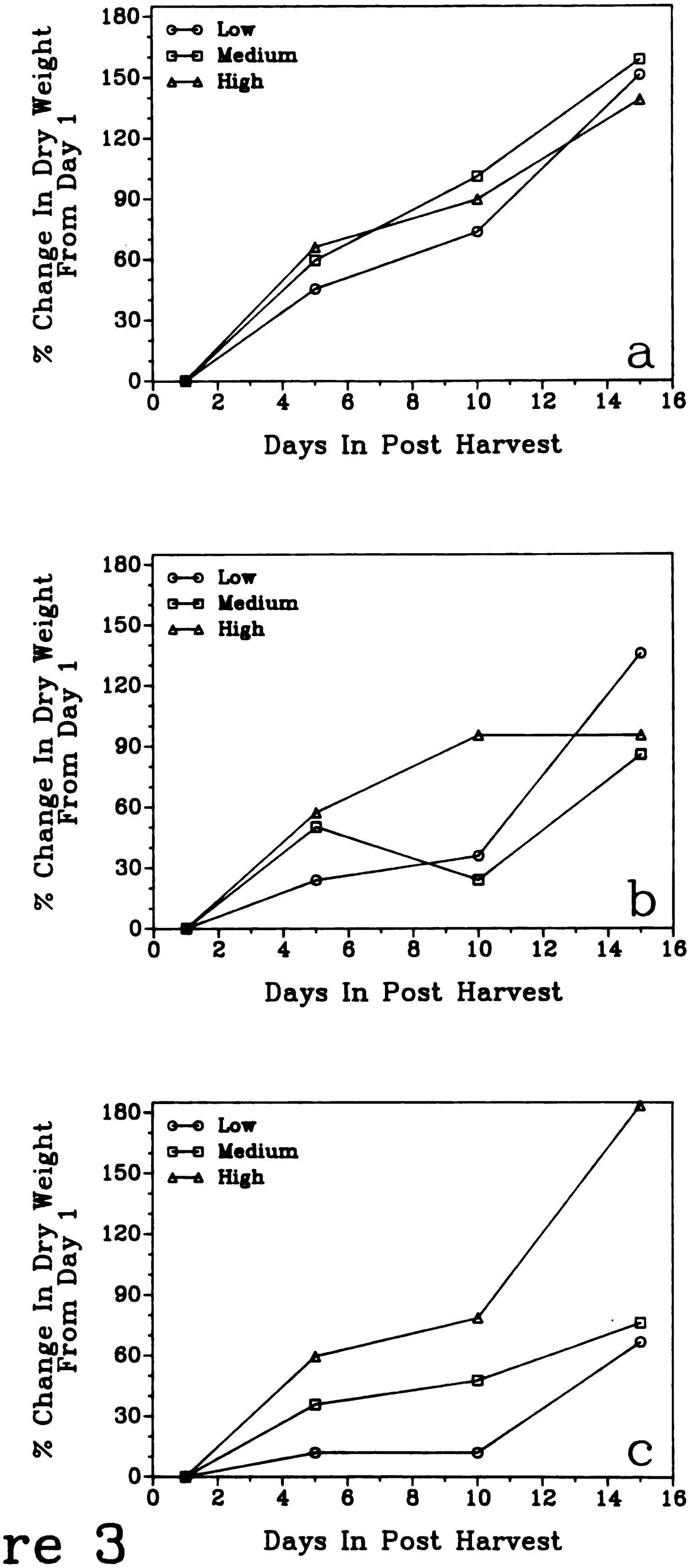

Low
Medium
High
% Change In Dry Weight From Day 1
Days In Post Harvest
0
30
60
90
120
150
180
0
2
4
6
8
10
12
14
16
a
b
c

Figure 3

## Quality

Light quality can greatly affect plant growth. Petunias and most other plants are highly responsive to light at wavelengths between 400 and 700 nanometers for photosynthesis and other plant processes (Figure 4) (Cathey and Campbell, 1977). The importance of light quality became apparent after Garner and Allard published a paper in 1920 that discussed the concept of photoperiod (1920). With the discovery of the manipulation of photoperiod to control flowering, the study of the effects of different light sources on plant growth became a highly researched area. Over the years many types of artificial lamps have been developed in an attempt to either imitate natural sunlight or at least develop light sources that will provide adequate plant growth using only necessary wavelengths. The spectral energy emission curves of several current light sources are presented (Figure 5) and can be compared to that of solar irradiation (Figure 6) (Cathey and Campbell, 1980).

Some of the earliest work with electric lighting came before Garner and Allard's landmark paper. As early as 1891, L. H. Bailey (1891) experimented with using electric arc lamps to increase growth of petunia and other plants. He discovered that petunias illuminated during the night grew much taller than plants grown under natural light conditions. However, the lamps Bailey used emitted large

Figure 4. Photosynthesis action spectrum for a) dim light and b) intense light (Cathey and Campbell, 1977).

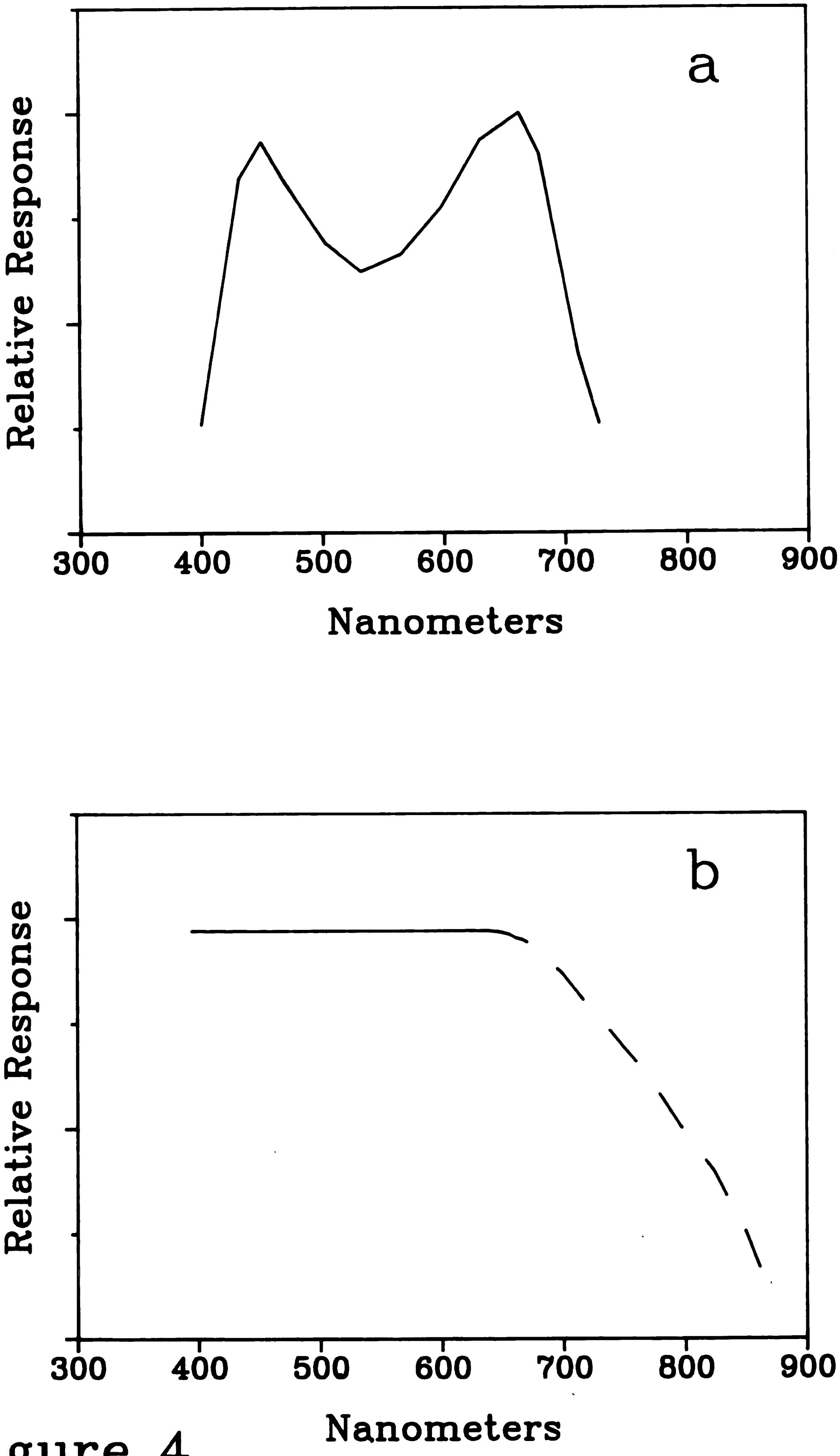
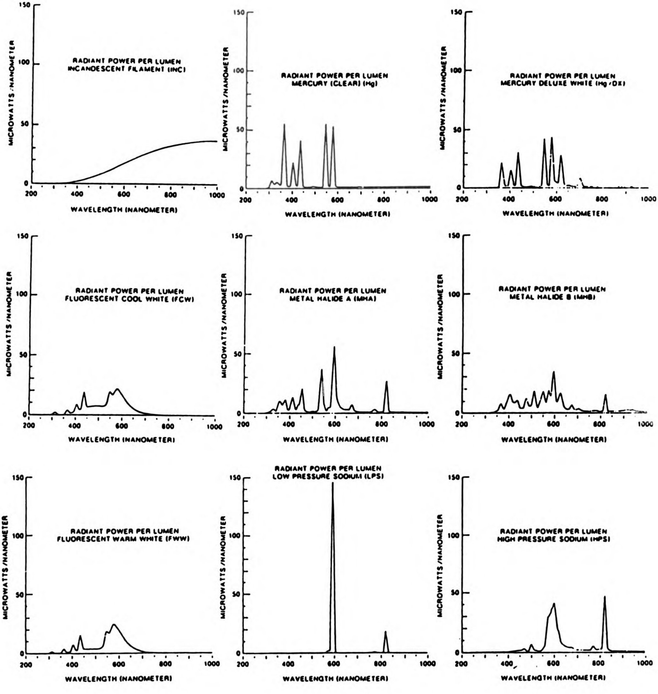

a
Relative Response
300
400
500
600
700
800
900
Nanometers
b
Relative Response
300
400
500
600
700
800
900
Nanometers

Figure 4

Figure 5. Spectral radiant power curves for some current horticultural lamps (adapted from Cathey and Campbell, 1980).



RADIANT POWER PER LUMEN
INCANDESCENT FILAMENT (INC)

RADIANT POWER PER LUMEN
MERCURY (CLEAR) (Hg)

RADIANT POWER PER LUMEN
MERCURY DELUXE WHITE (Hg/DX)

RADIANT POWER PER LUMEN
FLUORESCENT COOL WHITE (FCW)

RADIANT POWER PER LUMEN
METAL HALIDE A (MHA)

RADIANT POWER PER LUMEN
METAL HALIDE B (MHB)

RADIANT POWER PER LUMEN
FLUORESCENT WARM WHITE (FWW)

RADIANT POWER PER LUMEN
LOW PRESSURE SODIUM (LPS)

RADIANT POWER PER LUMEN
HIGH PRESSURE SODIUM (HPS)

Figure 5

Figure 6. Solar spectral irradiance (Cathey and Campbell, 1980).

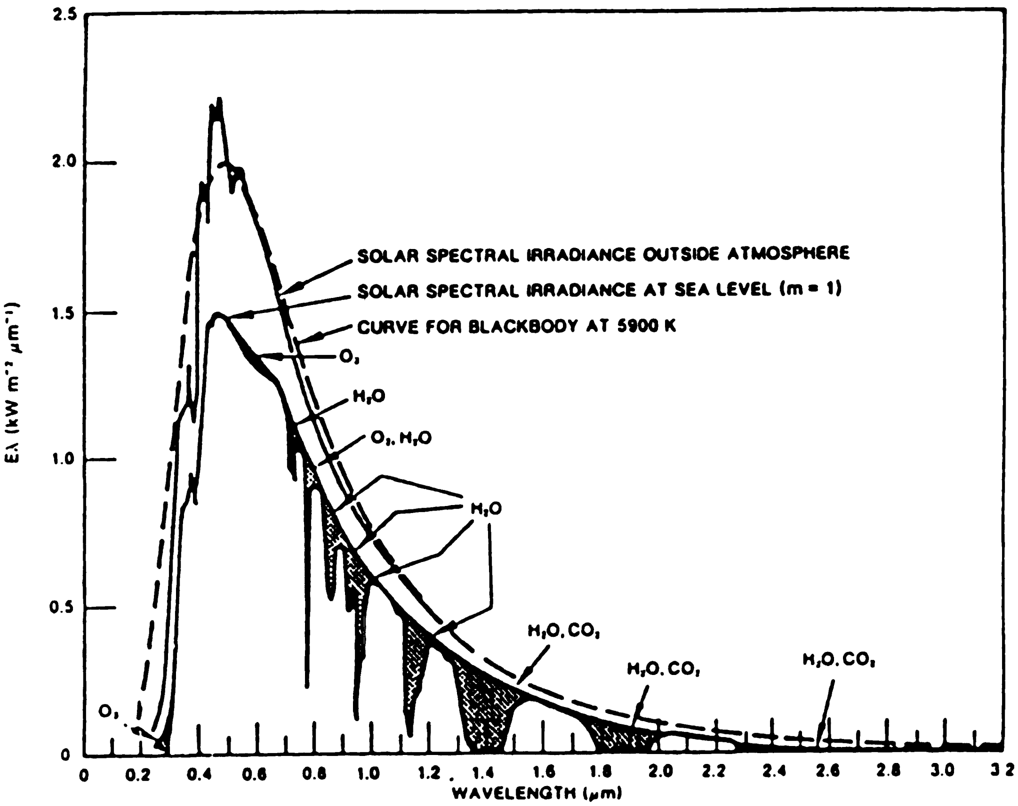

2.5
2.0
1.5
1.0
0.5
0
Eλ (kW m$^{-2}$ μm$^{-1}$)
SOLAR SPECTRAL IRRADIANCE OUTSIDE ATMOSPHERE
SOLAR SPECTRAL IRRADIANCE AT SEA LEVEL (m = 1)
CURVE FOR BLACKBODY AT 5900 K
$O_3$
$H_2O$
$O_2$, $H_2O$
$H_2O$
$H_2O, CO_2$
$H_2O, CO_2$
$H_2O, CO_2$
$O_3$
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
WAVELENGTH (μm)

Figure 6

amounts of ultraviolet rays that damaged the plants unless the light first passed through window glass to screen out the ultraviolet rays.

Much of the early work with light quality, or color, is now understood to be invalid (Kwack and Dunn, 1961; Van der Veen and Meijer, 1959). These early studies often reported conflicting and confusing accounts (Burns, 1933; Daster and Mehta, 1935; Popp, 1926; Shirley, 1929) most often because of the inability of these researchers to produce narrow wavelength bands for study. Many times, the eye was used to estimate light quality. Light that appeared blue to the human eye was termed blue light in research, red appearing light was used as red light and green appearing light as green light. Unfortunately, this system did not allow for the overlapping of the colors as seen by the human eye.

Withrow and Benedict (1936) tried to refine the study of light quality by using special filters to obtain narrower bands of wavelengths than previously obtained. Aster, stock and pansies were illuminated with one of eight colors, including a white light control, ranging from blue to infrared. They found that pansies grown under the orange/red light (about 650 nm and up) flowered earliest and produced the most flowers (19.1 flowers) when compared to the control (1.9 flowers), while plants grown under blue light (380-510 nm) produced the least (0.8 flowers). Similar results were found with aster. However, the orange/red wavelength inhibited branching in stock which decreased flower number. In all 3 species studied, the tallest plants were the ones grown under either orange/red or red (680 nm), and the greatest fresh and dry weight was produced by plants grown under orange/red. Green light (455-550 nm) plants produced the lowest dry weights and plants grown under the blue light appeared to be stunted.

After examining work of previous scientists, Post (1942) published a bulletin outlining the effects of light and temperature on various floricultural crops. He concluded that the visible part of the spectrum was important to plant growth, while the extremes in the ultraviolet and infrared regions were not important and could be detrimental to plant growth.

The advent of the fluorescent lamp greatly increased the accuracy with which light quality was studied. When coated with different phosphors, wide ranges of spectral composition could be achieved (Thomas and Dunn, 1967). As a result, fluorescent lamps became very popular for experimental use in the early 1940s and remained so until the late 1970s.

Naylor and Gerner (1940) compared incandescent lamps to fluorescent lamps and their effects on tomato and tobacco. They concluded that incandescent lamps emitted too much heat and produced poor growth and as a result were unsatisfactory to be used as a single light source. Plants grown under fluorescent lamps, however, were short, sturdy, had a deep green color and were superior to those grown under the incandescent lamps or natural winter conditions.

The work by Naylor and Gerner was later supported by Stoutemyer and Close (1946). Seedlings of several bedding plant species grew best when fluorescent lamps were used as a single light source. Since the fluorescent lamps emitted more energy in the lower region of the spectrum than incandescent (Figure 5), seedlings started under fluorescent were sturdier and of better quality than seedlings started under incandescent.

Particular wavelengths of light have been shown to affect several different plant processes. Wassink and Stolwijk (1956) stated that in experiments with etiolated peas and avena, phototropism showed the maximum response in the violet-blue spectral region. Red light exerted the greatest influence on leaf growth and internode inhibition in peas and beans, internode inhibition in barley seedlings, mesocotyl inhibition in avena and opening of the plumular hook in bean. In studies with light grown <u>Brassica</u> followed with 4 hours of spectral light, blue, violet and infrared radiation encouraged stem elongation immediately while other wavelengths inhibited it. Similar results were reported by Holmes and Smith (1977b).

The most noticeable effect of light quality on plant growth in early studies was the ability of some wavelengths to stimulate photoperiodic response while other wavelengths elicited diminished or no response (Downs et al., 1958; Piringer and Cathey, 1960; Van der Veen and Meijer, 1959). Work by Downs et al. (1958) showed that the far red wavelengths found in incandescent lamps promoted stem elongation. In several plant species, such as dill, millet, barley and wheat, stem elongation is necessary before initiation can occur. In these plants, then, incandescent lamps triggered flowering by promoting stem elongation.

Van der Veen and Meijer (1959) examined the effects of different wavelengths on flowering in Hyoscyamus niger, a long day plant, and Salvia occidentalis, a short day plant. The results of their study with Hyoscyamus niger are presented in Table 2. Flowering was encouraged by blue, high intensity red and infrared light wavelengths when supplied during long days, but flowering in response to night interruptions was very wavelength specific.

When a similar experiment was performed with Salvia occidentalis the same effects of wavelength on photoperiod were achieved (Table 3). They were able to conclude that when extending photoperiods of plants to manipulate flowering, quality of the light is as equally important as the length of exposure. They also concluded that while the color of the light has no actual influence on flower initiation, it does effect the daylength.

Table 2. The effect of color and time of application of light on flowering in *Hyoscyamus niger* (Van der Veen and Meijer, 1959).

| Photoperiod | Color | Night Break[z] | Effect | Flowering |
|---|---|---|---|---|
| 16 | blue | no | long-day | yes |
| 16 | green | no | short-day | no |
| 16 | red[y] | no | short-day | no |
| 16 | red[x] | no | long-day | yes |
| 16 | green + far red | no | long-day | yes |
| 10 | blue | blue | short-day | no |
| 10 | blue | green | long-day | yes |
| 10 | blue | red | long-day | yes |
| 10 | blue | far red | short-day | no |
| 10 | green | blue | short-day | no |
| 10 | green | green | short-day | no |
| 10 | green | red | short-day | no |
| 10 | green | far red | short-day | no |
| 10 | red | blue | short-day | no |
| 10 | red | green | short-day | no |
| 10 | red | red | short-day | no |
| 10 | red | far red | short-say | no |

[z] 2.5 hours lighting during the middle of the dark period.
[y] Low intensity. (Exact intensity not stated.)
[x] High intensity. (Exact intensity not stated.)

Table 3. The effect of color and time of application of light on flowering in *Salvia occidentalis* (Van der Veen and Meijer, 1959).

| Photoperiod | Color | Night Break[z] | Effect | Flowering |
|---|---|---|---|---|
| 16 | blue | no | long-day | no |
| 16 | green | no | short-day | yes |
| 16 | red[y] | no | short-day | yes |
| 16 | red[x] | no | long-day | no |
| 16 | green + far red | no | long-day | no |
| 10 | blue | blue | short-day | yes |
| 10 | blue | red | long-day | no |
| 10 | blue | far red | short-day | yes |
| 10 | green | blue | short-day | yes |
| 10 | green | red | short-day | yes |
| 10 | green | far red | short-day | yes |
| 10 | red | blue | short-day | yes |
| 10 | red | red | short-day | yes |
| 10 | red | far red | short-say | yes |

[z] 2.5 hours lighting during the middle of the dark period.
[y] Low intensity. (Exact intensity not stated.)
[x] High intensity. (Exact intensity not stated.)

The early 1960s saw many new types of lamps introduced for commercial and experimental use. The best plant growth could be achieved by using a balance of wavelengths of light with peaks in certain key areas to attain desired results. This effect was often obtained by mixing several sources of fluorescent lamps with incandescent since red and blue light seemed to control most plant processes (Carpenter, 1974).

Helson (1965) reported an experiment in which cool white fluorescent lamps were compared to Gro-Lux lamps, a commercial brand of fluorescent lamp developed for plant growth. The spectral emission curves of the two types of fluorescent lamps can be compared in Figure 7 (Thomas and Dunn, 1967). They found that tomato plants grew to similar heights under both types of fluorescent lamps when used alone, and that plant height could be increased for both light sources by adding incandescent. Also, the Gro-Lux lamps, with their increased output in the red area, combined with incandescent, allowed plants to produce greater leaf area and dry weight when compared to cool white fluorescent and incandescent.

The duration of exposure to a particular wavelength was shown to affect the plant response (Vince, 1964). Blue light promoted internode elongation in *Tropaeolum majus* when the exposure was brief, but inhibited internode elongation as the period of exposure increased (Figure 8).

Figure 7. Spectral emission curve of a) cool-white fluorescent lamp and b) Gro-Lux lamp (Thomas and Dunn, 1967).

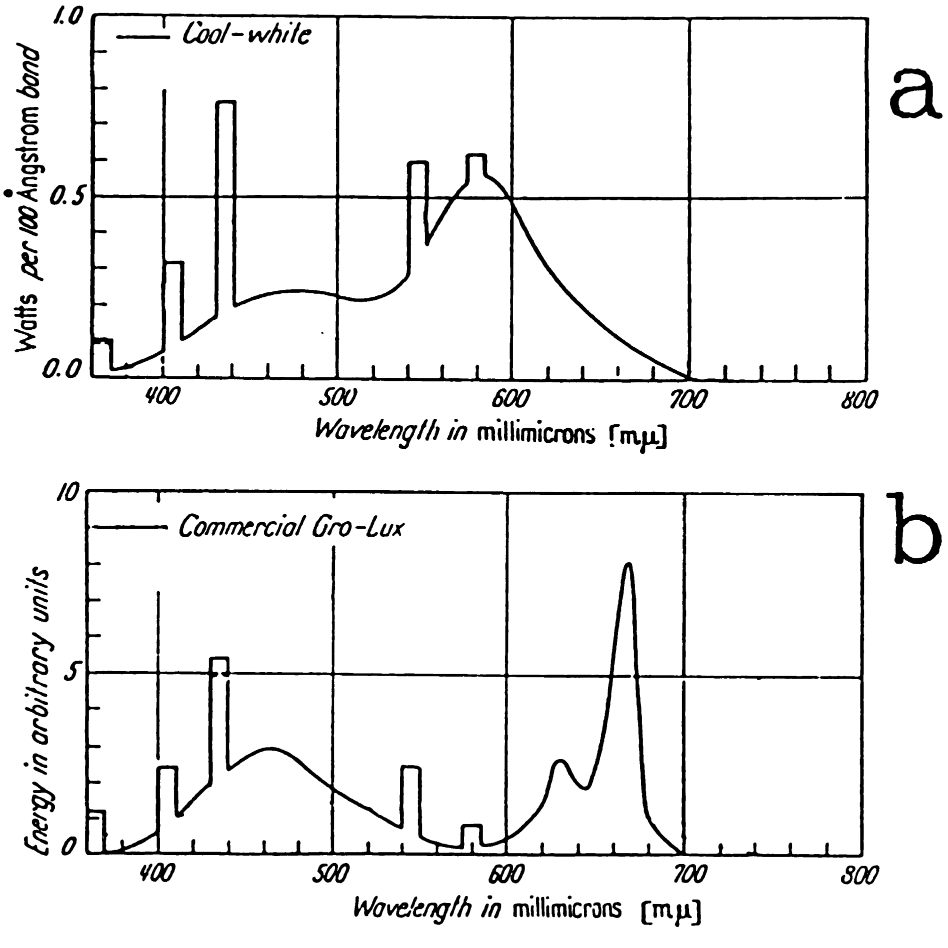

1.0
Cool-white
a
Watts per 100 Ångstrom band
0.5
0.0
400
500
600
700
800
Wavelength in millimicrons [mμ]
10
Commercial Gro-Lux
b
Energy in arbitrary units
5
0
400
500
600
700
800
Wavelength in millimicrons [mμ]

Figure 7

Figure 8. The effect of irradiation on internode elongation in <u>Tropaeolum majus</u>, showing the change in relative effectiveness of red and blue light as the daily duration of illumination is increased (Vince, 1964).

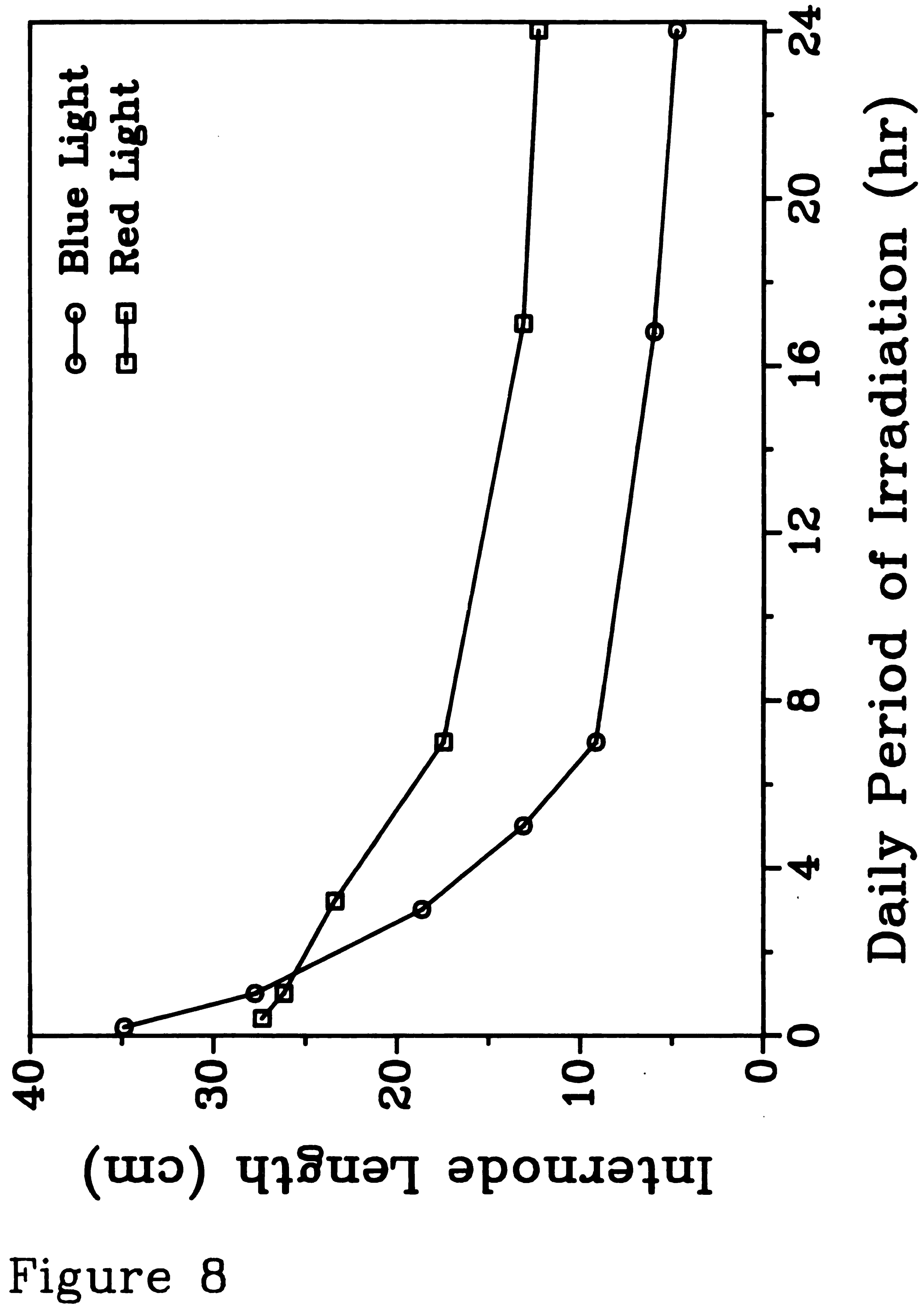

Blue Light
Red Light
Internode Length (cm)
0
10
20
30
40
Daily Period of Irradiation (hr)
0
4
8
12
16
20
24

Figure 8

Petunias were being researched extensively at this time and much of that research included the effects of light quality (Boodley, 1963; Cathey and Campbell, 1975; Lane et al., 1965; Ogawara and Ono, 1958; Piringer and Cathey, 1960; Van der Veen and Meijer, 1959; Wolnick and Mastalerz, 1966). Red light was shown to accelerate seed germination in light sensitive seeds (Borthwick et al., 1952; Downs et al., 1958; Morgan and Smith, 1981). This acceleration was also shown to be true in petunia (Ogawara and Ono, 1958). The germination percentage was greatly increased when seeds were exposed to red light rather than green or blue.

Van der Veen and Meijer (1959) demonstrated the effects of light color on stem elongation and growth habit of petunia. They stated that the petunia first maintains a rosette growth habit, followed by a period of elongated growth and finally flowering. When plants were exposed to blue light, the rosette habit was absent and the plant flowered quickly on an elongated stem. If the plants are given green or red light, the rosette habit remained and the plants flowered late, if at all. The effect of the red light could be reversed if the plants were exposed to alternating days of red light and far red light. With the exposure to far red light, the rosette habit was broken and the petunia plant elongated and flowered. Similar conclusions were later reached by Boodley (1963) and

Piringer and Cathey (1960). Piringer and Cathey (1960) grew petunias under 8 hours of natural light conditions and then extended the photoperiod with 8 hours of fluorescent or incandescent lamps. The incandescent lamps provided the plants with large amounts of far red irradiation and the petunias flowered 2-3 weeks earlier, depending on cultivar, than their counterparts grown with fluorescent lamps as a supplemental source.

Light quality has also been shown to affect lateral branching in petunia and other plants (Bogorad and McIlrath, 1960; Kasperbauer, 1971; Tucker, 1976; Tucker and Mansfield, 1972; Vince-Prue, 1977; Wolnick and Mastalerz, 1966). Petunias exposed to far red light flowered earlier than controls grown under natural short days, but exhibited none of the lateral branching. Similar results were shown for Xanthium (Bogorad and McIlrath, 1960; Tucker and Mansfield, 1972), tobacco (Kasperbauer, 1971), tomato (Tucker, 1976) and fuschia (Vince-Prue, 1977).

Quality of light is known to affect many aspects of plant growth. Quality can influence germination, time to flower, branching patterns and other plant characteristics. Some wavelengths have antagonistic effects on others, especially red and far red (Morgan and Smith, 1981; Van der Veen and Meijer, 1959). Thus, light quality is very important when considering light sources for studying plant growth.

Duration, intensity and quality are of equal importance for plant growth. Light for plant growth can not be selected on the basis of one characteristic to the exclusion of the other two. Each characteristic of light -- duration, intensity and photoperiod -- can exert a profound effect on plant growth. The researcher must decide before hand what type of plant characteristics are desired, and then choose a light source that will balance duration, intensity and quality to obtain the desired results.

## Temperature

The effects of temperature are many and can vary from plant to plant. Went (1953) indicated that physiological effects can occur in plants at temperatures ranging from 0° to 40°C, though plant injury results at either extreme of this range. Went also discussed the concept of optimum temperature for plant growth. Optimum temperatures were different from plant to plant and even plant part to plant part. He found that tomato roots grew best at 30°C while cotton roots grew best at 25°, sunflower roots at 20° and pea roots at 10°. And even though tomato roots grew best at 30°, stems elongated fastest in tomato at only 18°.

Several early studies discussed the effects of temperature on flowering (Cathey, 1954; Furuta and Nelson, 1953; Hanan, 1959; Post, 1940). Furuta and Nelson (1953) grew chrysanthemums at temperatures from 21.7° to 37.8°C (71° to 100°F). Buds were formed at all temperatures but did not develop at 37.8°. Buds formed at 29.4° (85°F) did develop but flowering was delayed by 11 days. Post (1940) and Cathey (1954) both found that low night temperatures prevented bud formation in chrysanthemum, delayed flowering, and reduced the total number of buds. Hanan (1959) performed a similar experiment with carnation but studied the effects of day temperature. Decreasing day temperature from 23.9° to 11.1°C (75° to 52°F) likewise delayed flowering but had no effect on total flowers formed.

In other studies of the effects of temperature and flowering, Smith and Langhans (1962) determined that night temperature had a greater effect on time to flower in Easter lilies than did day temperature. However, the plants were exposed to night temperatures for $15^1/_2$ hours and day temperatures for $8^1/_2$ hours possibly skewing the results. Litlere and Strømme (1975) found that temperatures above 25°C delayed flower initiation in hydrangea. Temperatures in this range also increased the number of blind shoots, thus reducing flower number.

In some plants, temperature may effect some stages of flowering but not all. Armitage et al. (1981) found that temperature highly influenced flowering in seed geranium from the stage of visible bud to anthesis, but had little effect from initiation to visible bud. Similar results were reported by White and Polys (1987).

Wilson (1966) examined the effects of temperature on growth rate in plants. He investigated the effects of temperature on net assimilation rate, relative growth rate and relative leaf area growth rate in maize, rape and sunflower. The plants had an optimum temperature for these factors between 20° and 30°C, in which the rate peaked and then dropped off (Figure 9).

Petunia growth is greatly influenced by temperature (Holcomb and Mastalerz, 1985; Krizek et al., 1970; Krizek et al., 1972; Krizek et al., 1968; Mastalerz, 1965; Merritt and Kohl, 1982; Shedlosky and White, 1987; Wolnick and Mastalerz, 1966). At the seedling stage, the plants require a higher temperature than what is needed for satisfactory growth at later stages (Holcomb and Mastalerz, 1985; Krizek et al., 1970; Krizek et al., 1972; Krizek et al., 1968). Increased temperatures at the seedling stage promoted faster growth and sturdier seedlings (Krizek et al., 1968). Early growers of petunias routinely used low temperatures, usually 10° to 15.6°C (50° to 60°F) to promote branching. However Krizek et al. (1970) recommended that better results through increased growth could be obtained by growing petunias and most other bedding plants at 26.7° to 29.4° (80° to 85°) days and 21.1° to 23.9°C (70° to 75°F) nights during the seedling stage.

Figure 9. The effects of temperature on: a) net assimilation rate, b) relative growth rate and c) relative leaf area growth rate for maize (Wilson, 1966).

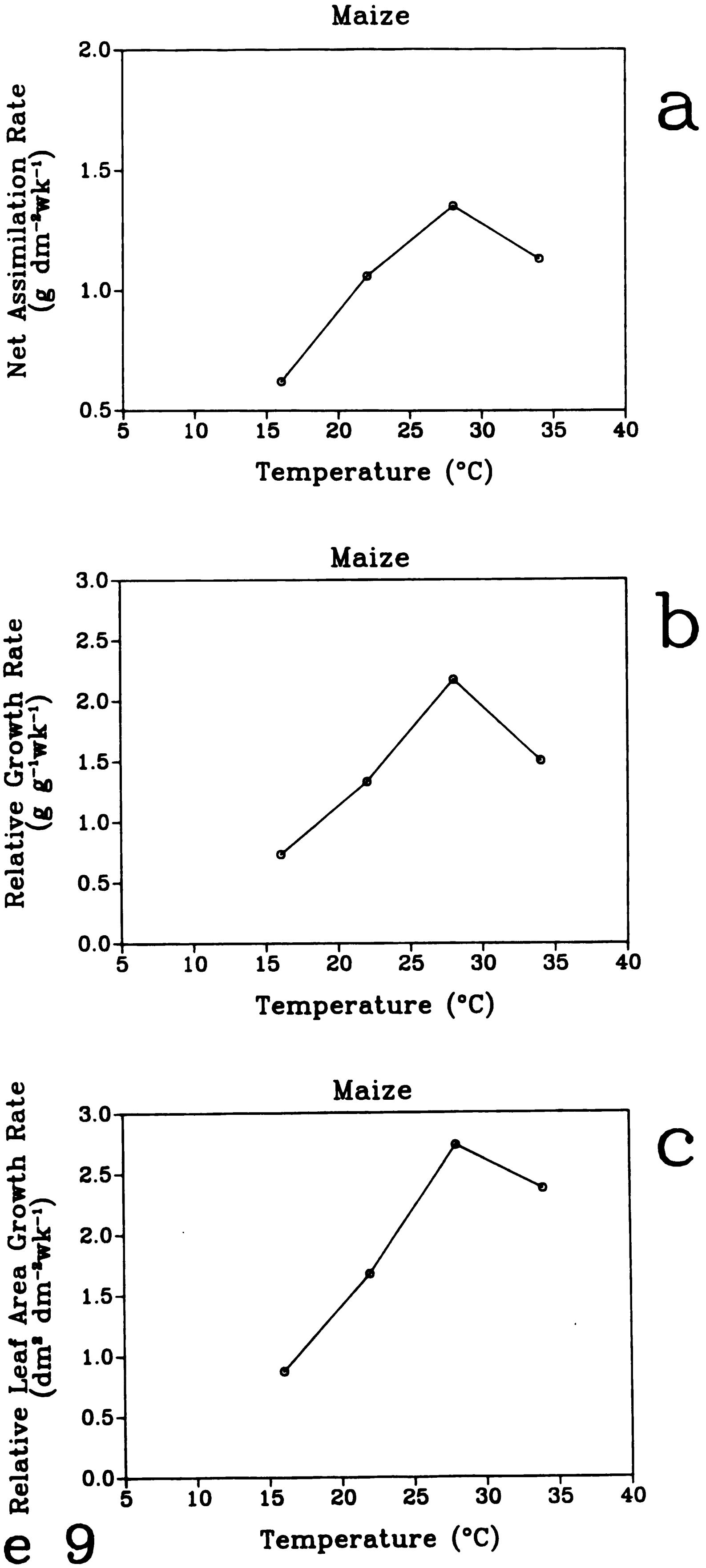

Maize
Net Assimilation Rate (g dm$^{-2}$wk$^{-1}$)
2.0
1.5
1.0
0.5
5
10
15
20
25
30
35
40
Temperature (°C)
a
Maize
Relative Growth Rate (g g$^{-1}$wk$^{-1}$)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
5
10
15
20
25
30
35
40
Temperature (°C)
b
Maize
Relative Leaf Area Growth Rate (dm$^{2}$ dm$^{-2}$wk$^{-1}$)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
5
10
15
20
25
30
35
40
Temperature (°C)
c

Figure 9

In a later study by Krizek et al. (1972), petunias were grown under one of the following temperature regimes: 18° days/12° nights, 24° days/18° nights or 30° days/24°C nights. Day temperatures corresponded to a 16 hour photoperiod. Fourteen days after transplanting, the lowest temperature combination was found to be severely limiting to petunia growth, while the the other two temperature combinations greatly enhanced growth. At 30° days/24° nights and 24° days/18° nights plants showed an increase in fresh weight of the tops, dry weight of the tops, total leaf area and number of nodes developed when compared to the lowest temperature combination. However, the authors stated that the highest temperature combination during later stages of growth would be detrimental to the plant. They did not suggest a stage of plant growth in which detrimental effects would be detected.

Early research on petunias and temperature usually involved night temperature because it was easier to control than day temperature, especially in the early spring (Carlson and Rowley, 1980). Piringer and Cathey (1960) examined the effect of night temperatures ranging from 10° to 26.7°C (50° to 80°F) on petunias. They found that as night temperatures decreased, stem length and internode length decreased while time to flower and the number of basal branches increased, confirming results they reported in a previous experiment (Cathey and Piringer, 1961).

In a study by Seeley (1955), the effect of night temperature on flowering in petunia was investigated. Petunias were grown at night temperatures of 10° or 15.6°C (50° or 60° F) under natural light conditions during April and May. Petunias grown at both temperatures were short and compact, but plants grown at 15.6° night temperatures flowered earlier, had an increased number of flowers with a greater fresh weight and increased flower diameter than those grown at 10°.

In general, overall plant growth and development was slowed in petunias as temperatures dropped below 15.6°C (60°) (Cathey and Campbell, 1975; Wolnick and Mastalerz, 1966). Total crop time to produce a flowering plant is approximately eleven weeks when the plants are grown at 10°C (50°F) (Boodley 1970) but only eight weeks if 15.6° (60°) temperatures are maintained (Carlson and Mischel, 1980).

Fluctuating temperatures were compared to constant temperatures by Mastalerz (1965). In his experiment, petunias were exposed to one of four temperature regimes for four weeks after transplanting. Plant gain was measured by comparing fresh weight. Lowest fresh weight gain was seen at the coolest temperature combination of 10°C (50°F) NT and 15.6° (60°) DT. Greatest fresh weight gain was obtained when the plants were grown at a constant 26.7° (80°) DT and NT. The most important fact from this experiment came from two middle treatments. Both received an average 18.3° (65°)

temperature over each twenty-four hour period, but one group was grown at a constant 18.3° while the second was grown at 10° for the 12 hour night and 26.7° for the 12 hour day. Plants grown at 18.3° constant temperature had a final fresh weight of 2.5 grams, while the plants grown at fluctuating temperatures attained a final fresh weight of only 1.8 grams.

In recent years, root zone heating has been examined for its practicality in the production of petunias and other bedding plants (Merritt and Kohl, 1982; Shedlosky and White, 1987). Merritt and Kohl (1982) exposed seedlings of _Petunia x hybrida_ 'Snow Cloud' to 2 root zone temperatures. The first ranged from 15.6° to 19.4°C and the second 21° to 35°. The plants were also divided into 2 photoperiods of 9 or 13 hours and air temperatures of 15.6° nights and 21° days that corresponded to the 9 hour photoperiod. Plants were grown in their respective environments for 25 days. Within each photoperiod, plants grown at the higher root zone temperature showed an increase in mainstem, branch and total leaf area and an increased dry weight when compared to the lower temperature in the same photoperiod.

In a similar study by Shedlosky and White (1987), White Cascade petunias were grown at several combinations of night temperatures ranging from 7° and 21°C soil temperature and 7° or 16° air temperatures. The results are presented in Table 4. In treatments without root zone heating, the plants at the warmer (16°) night temperature produced greater fresh and dry weights than the cooler temperature as would be expected. However, if soil temperatures were increased to 21°, similar results were obtained for both fresh and dry weights for either air temperature.

Table 4. The effects of night air and soil temperatures on the mean fresh and dry weights of White Cascade petunia (adapted from Shedlosky and White, 1987).

| **Treatment Temp** | | | |
|---|---|---|---|
| **Air (°C)** | **Soil (°C)** | **Fresh wt. (g)** | **Dry wt. (g)** |
| 7 | Ambient | 48.4 | 2.4 |
| 16 | Ambient | 66.0 | 3.7 |
| 16 | 16 | 85.9 | 4.6 |
| 16 | 21 | 93.7 | 4.5 |
| 7 | 16 | 73.8 | 4.0 |
| 7 | 21 | 90.0 | 4.6 |

Temperature has been shown to exert a major influence on plant growth and development. Temperature can affect germination, time to flower and plant morphology. Temperature can affect plant growth as night temperature, day temperature or average temperature. In most cases, however, temperature does not act alone but interacts with other environmental factors such as light. These interactions, then, are an important consideration in plant growth.

## Temperature-Light Interaction

Rarely do plant responses result from single environmental factors. More often, plant responses are due to a combination of several different factors (Blackman, 1919; Cathey and Piringer, 1961; Garner and Allard, 1920; Krizek et al., 1972; Lane et al., 1965; Merritt and Kohl, 1982; Piringer and Cathey, 1960; Roberts and Struckmeyer, 1938, 1939; Seeley, 1955; Wolnick and Mastalerz, 1966). The interaction of temperature, light and other factors was recognized early. In 1917 Hanson (1917) described an interaction of several environmental factors by observing their different effects on leaves from the outer and inner portion of the crown of trees in a forest. Gilbert (1926) stated that temperature was found to be a determining factor in influencing time of flower primordia formation in Xanthium, but that this temperature effect was closely associated to the relative day length.

Miller (1960) studied the effects of adjusting the night temperature to the amount of light received during the day. Snapdragons were grown during the winter at night temperatures of 15.6°, 10° or 4.4°C (60°, 50° or 40°F). After bright, sunny days, treatments were each adjusted upward 5.6° (10°) for the night. On days of average intensity, all treatments remained the same. On dark, cloudy days, the treatments at 15.6° and 10° were each adjusted down 5.6°.

Adjusting temperatures upward after sunny days resulted in decreased time to flower and slightly smaller plants, showing an interaction between light intensity and night temperature. However, shifting downward after a dark day had no effect.

Armitage et al. (1981) demonstrated a different type of interaction in seed geraniums. Bud initiation and development from germination to visible bud was highly dependent on light intensity and temperature had little effect. However, from visible bud to flower, flower bud development was highly dependent on temperature, with no effect from light intensity.

Early work with petunia was conducted by Roberts and Struckmeyer (1938, 1939). They demonstrated a strong interaction between photoperiod and temperature as related to flowering in petunia. They grew petunias and several other types of plants at 2 photoperiods, 9 and 16 hours, and three temperature regimes ranging from 12.8° to 23.8°C (55° to 75°F). The results for petunia are presented in Table 5.

Table 5. The effects of temperature and photoperiod on flowering in petunia (Roberts and Struckmeyer, 1939).

| | **Temperature (°C)** | | |
|---|---|---|---|
| **Photoperiod (hours)** | **21.1°-23.8° (warm)** | **17.2°-18.3° (intermediate)** | **12.8° (cool)** |
| 16 | Flowered | Flowered | Flowered |
| 9 | No Flower | No Flower | Flowered |

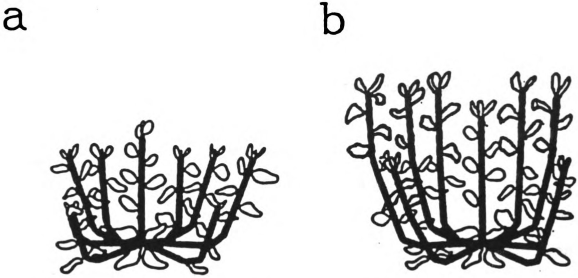
Petunias were shown to flower under long days at any temperature, but under short days only at temperatures below 17.2°. They concluded that flowering in petunia could be induced by long days at any temperature and during short days flowering was induced only by low temperature. This idea was later restated by Post (1942). He said that if petunias are to flower before April, during short day conditions, they must be grown with cool temperatures or flowering will not occur until the natural photoperiod is long enough to induce flowering. However, the petunia was later shown to be a non-obligate long day plant (Van der Veen and Meijer, 1959).

Piringer and Cathey (1960) demonstrated the interaction of photoperiod and temperature on lateral branching in petunia. They found that if plants were grown with a 16 hour photoperiod at temperatures of 15.6°C (60°F) and above, the majority of the plants would be single stemmed with little or no lateral branching. However, if plants were grown at a 9 hour photoperiod at temperatures between 10°C (50°F) and 15.6°, they would be very branched and compact. At temperatures between 10° to 15.6° and a 16 hour photoperiod, the plants would branch but develop only half as many branches as the plants at the same temperature but shorter photoperiod. Finally, under short days and temperatures above 15.6°, plants would be slightly branched with longer internodes than branches of plants grown at cooler temperatures (Figure 10).

Merritt and Kohl (1982) studied the effect of root temperature in combination with photoperiod on petunia growth. The plants were grown at high (24°C) or low (15.6°) soil temperatures and 9 or 13 hour photoperiods. Air temperature was maintained at 21° DT and 15.6° NT and adjusted to the 9 hour photoperiod for all four treatments. Responses obtained were similar to those of other experiments dealing with temperature or photoperiod. A high soil temperature under short day conditions produced the most lateral branches while high soil temperatures and long days produced the fewest. However, the high soil temperature and long days did produce the greatest leaf area and dry weight gain as would be expected. Plants grown under cool soil temperatures in combination with short days produced the least amount of leaf area and experienced the lowest dry weight gain. These results are similar to results obtained by Carpenter and Carlson (1974) in their study of photoperiod and by Seeley (1955) in his study of temperature.

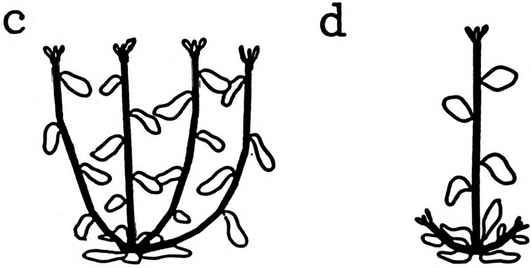
The separate effects of light and temperature on plant growth are difficult to evaluate. Plants have optimum conditions for growth (Went, 1953), but environmental factors are closely related. A petunia will have an optimum temperature for growth at a given light intensity, but this optimum will change if the light intensity is changed.

Figure 10. The effect of temperature and photoperiod on lateral branch formation in petunia for: a) 9 hour photoperiod, temperature less than 15.6°C, b) 9 hour photoperiod, temperature greater than 15.6°, c) 16 hour photoperiod, temperature less than 15.6° and d) 16 hour photoperiod, temperature greater than 15.6° (adapted from Wolnick and Mastalerz, 1966).



9 Hour Photoperiod
Temperature < 15.6°C

9 Hour Photoperiod
Temperature > 15.6°C



16 Hour Photoperiod
Temperature < 15.6°C

16 Hour Photoperiod
Temperature > 15.6°C

Figure 10

Likewise, other factors such as humidity and nutrient status may alter optimum light and temperature levels. Therefore, light and temperature effects are best discussed in relation to each other and other environmental factors.

## Miscellaneous Factors

Many factors other than light and temperature influence plant growth. Plant responses to temperature, light levels and duration can be generated through other means. Jeffcoat (1977) showed that basal branching similar to that found under short day photoperiods or cool temperatures could also be induced by the addition of cytokinins to the plants. Short height as found in petunias produced at cool temperatures, short photoperiods or high intensity supplemental lighting could also be induced by foliar applications of daminozide or other plant growth regulators (Cathey et al., 1965; Cathey and Piringer, 1961; Wolnick and Mastalerz, 1966). Gibberellins have been found to decrease time to flower (Evans and Lyons, 1988; Lyons and Widmer, 1983) and cause stem elongation (Pressman et al., 1985). Thus, many factors other than light and temperature can influence plant growth.

## **Plant Growth Analysis**

Quantifying plant growth for the purpose of making predictions about growth and development can be divided into two categories, the classical approach and the functional approach. Williams (1946) described a method for determining relative growth rate. Relative growth rate was defined as the ratio between the change of plant dry weight over time to the total plant dry weight. Similar ratios have been defined as a method of predicting plant growth (Cooper and Thornley, 1976; Fukai and Silsbury, 1978; McMurtrie and Wolf, 1983). Studies that use ratios fall into the category of the classical approach.

The functional approach for plant growth study involves fitting mathematical functions to raw data using regression analysis. Many functions have been developed and adapted for describing plant growth (Erickson, 1976; Hunt, 1978; Richards, 1959). In 1976, a model was specified as a set of mathematical equations that quantitatively represented a particular system (Thornley, 1976). The term modeling is now commonly applied to the functional approach of data analysis as relating to plant growth and development.

Two extensive reviews of the literature have been made recently on plant growth analysis (Hopper, 1985; Karlsson, 1984). For this reason, a detailed review will not be made here.

## Conclusion

Plant growth is a complex process that is not easily broken down into separate components. The previous literature review examined two of the most influential aspects of the environment, light and temperature. These two factors are the easiest to study because they are the easiest to control (Carlson and Rowley, 1980). While the influence of other factors can not be totally eliminated, their effects can be minimized and held constant to enable the researcher to study light and temperature effects with some accuracy.

Modeling plant growth demands a high degree of accuracy if the model produced is to have any value. The best predictive model is the simplest one that will still be reliable in predicting plant growth. The model to be developed for Petunia x hybrida will use only light and temperature because these two factors can be used to accurately predict plant growth. The data from these two parameters will be developed into predictive equations which will then be the basis for the model.

## LITERATURE CITED

Anonymous. 1988. Floriculture crops 1987 summary. National Agric. Stat. Serv., Agric. Stats. Board. USDA, Washington D.C.

Armitage, A. M. and M. J. Tsujita. 1979. The effect of supplemental light source, illumination and quantum flux density on the flowering of seed-propagated geraniums. J. Hort. Sci. 54(3):195-198.

Armitage, A. M., W. H. Carlson, and J. A. Flore. 1981. The effect of temperature and quantum flux density on the morphology, physiology and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 106(5):643-647.

Armitage, A. M. and T. Kowalski. 1982. Effects of light intensity and air temperature in simulated post production environment on Petunia hybrida Vilm. J. Amer. Soc. Hort. Sci. 108(1):115-118.

Armitage, A. M., C. E. Sams, R. M. Miranda, W. H. Carlson and J. A. Flore. 1983. The effect of quantum flux density and net photosynthetic rate on morphology and time to flower of hybrid geraniums. Scientia Hort. 21:273-282.

Bailey, L. H. 1891. Some preliminary studies of the influence of the electric arc lamp upon greenhouse plants. Cornell Univ. Agric Exp. Sta. Bul. No. 30. pp.82-110.

Ball, V. 1985. Petunia, p.607-609. In: V. Ball (ed.). The Ball Red Book, 14th edition. Reston Publishing, Reston, Virginia.

Blackman, V. H. 1919. The compound interest law and plant growth. Ann. Bot. 33:353-360.

Bogorad, L. and W. J. McIlrath. 1960. Effect of light quality on axillary bud development in Xanthium. Plant Physiol. 35:Suppl. 32.

Boodley, J. W. 1963. Fluorescent lights for starting and growing plants. NY State Flower Growers Bul. No. 206:1-3.

Boodley, J. W. 1970. Influence of container size on petunia growth. New York State Flor. Ind. Bul. No.1 p.4-5.

Borthwick, H. A., S. B. Hendricks, M. W. Parker, E. H. Toole and V. K. Toole. 1952. A reversible photoreaction controlling seed germination. Proc. Nat. Acad. Sci. 38:662-666.

Borthwick, H. A. and S. B. Hendricks. 1960. Photoperiodism in plants. Science 132:1223-1228.

Burns, G. R. 1933. Photosynthesis in various portions of the spectrum. Plant Physiol. 8:247-262.

Canham, A. E. 1966. Artificial Light in Horticulture. Centrex Publishing. Eindhoven, England.

Carlson, W. H. and J. M. Mischel. 1980. Producing petunias for profit. Cooperative Extension Bulletin E-1375. Michigan State University, East Lansing, Michigan.

Carlson, W. H. and E. M. Rowley. 1980. Bedding plants, p.479-521. In: R. A. Larson (ed.). Introduction to floriculture. Academic Press, NY.

Carpenter, W. J. 1974. High intensity lighting in the greenhouse. Research Report 255. Michigan State University Printing.

Carpenter, W. J. and G. A. Anderson. 1972. High intensity supplementary lighting increases yields of greenhouse roses. J. Amer. Soc. Hort. Sci. 97(3):331-334.

Carpenter, W. J. and G. R. Beck. 1973. High intensity supplementary lighting of bedding plants after transplanting. HortScience 8(6):482-483.

Carpenter, W. J. and W. H. Carlson. 1974. Comparison of photoperiodic and high intensity lighting on the growth and flowering of Petunia x hybrida Vilm. The Michigan Florist 52:16-24.

Carpenter, W. J. and R. C. Rodriguez. 1971a. Earlier flowering of geranium cv. Carefree Scarlet by high intensity supplemental light treatment. HortScience 6(3):206-207.

Carpenter, W. J. and R. C. Rodriguez. 1971b. Supplemental lighting effects on newly planted and cut-back greenhouse roses. HortScience 6(3):207-208.

Cathey, H. M. 1954. Chrysanthemum temperature study. C. The effect of night, day and mean temperature upon the flowering of Chrysanthemum morifolium. Proc. Amer. Soc. Hort. Sci. 64:499-502.

Cathey, H. M. 1974. Participation of phytochrome in regulating internode elongation of Chrysanthemum morifolium (Ramat.) Hemsl. J. Amer. Soc. Hort. Sci. 99(1):17-23.

Cathey, H. M. and L. E. Campbell. 1975. Effectiveness of five vision-lighting sources on photo-regulation of 22 species of ornamental plants. J. Amer. Soc. Hort. Sci. 100(1):65-71.

Cathey, H. M. and L. E. Campbell. 1977. Plant productivity: new approaches to efficient sources and environmental control. Transactions ASAE-1977.

Cathey, H. M. and L. E. Campbell. 1980. Light and lighting systems for horticultural plants. Hort. Rev. 2:491-537.

Cathey, H. M., J. Halperin and A. A. Piringer. 1965. Relation of n-dimethylaminosuccinamic acid to photoperiod, kind of supplementary light and night temperature, in its effect on the growth and flowering of garden annuals. Hort. Res. 5:1-12.

Cathey, H. M. and A. A. Piringer. 1961. Relation of phosfon to photoperiod, kind of supplemental light and night temperature on growth and flowering of garden annuals. Proc. Amer. Soc. Hort. Sci. 77:608-619.

Cooper, A. J. and J. H. M. Thornley. 1976. Response of dry matter partitioning, growth and carbon and nitrogen levels in the tomato plant to changes in root temperature: experiment and theory. Ann. Bot. 40:1139-1152.

Craig, R. and D. E. Walker. 1963. The flowering of Pelargonium hortorum 'Bailey' seedlings as affected by cumulative solar energy. Proc. Amer. Soc. Hort. Sci. 83:772-776.

Daster, R. H. and R. J. Mehta. 1935. The study of the effect of blue-violet rays on photosynthesis. Ann. Bot. 49:809-821.

Doorenbos, J. and S. J. Wellensiek. 1959. Photoperiodic control of floral induction. Ann. Rev. Plant Physiol. 10:147-184.

Downs, R. J., H. A. Borthwick and A. A. Piringer. 1958. Comparison of incandescent and fluorescent lamps for lengthening photoperiods. Proc. Amer. Soc. Hort. Sci. 71:568-578.

Erickson, R. O. 1976. Modeling of plant growth. Ann. Rev. Plant Physiol. 27:407-434.

Erickson, V. L., A. Armitage, W. H. Carlson and R. M. Miranda. 1980. The effect of cumulative photosynthetically active radiation on the growth and flowering of the seedling geranium, Pelargonium x hortorum 'Bailey'. HortScience 15(6):815-817.

Evans, M. R. and R. E. Lyons. 1988. Photoperiodic and gibberellin-induced growth and flowering responses of Gaillardia x grandiflora. HortScience 23(3):584-586.

Everett, T. H. 1981. Petunia. p.2574-2577. In: The Illustrated New York Botanical Garden Encyclopedia of Horticulture. Vol. 8. Garland Publishing, New York.

Flint, H. L. 1960. Relative effects of light duration and intensity on growth and flowering of winter snapdragon (Antirrhinum majus L.). Proc. Amer. Soc. Hort. Sci. 75:769-773.

Fukai, S. and J. H. Silsbury. 1978. A growth model for Trifolium subturraneum L. Swards. Aust. J. Agric. Res. 29:51-65.

Furuta, T. and K. S. Nelson. 1953. The effect of high night temperatures on the development of chrysanthemum flower buds. Proc. Amer. Soc. Hort. Sci. 61:548-550.

Garner, A. A. and H. A. Allard. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. J. Agric. Res. 18:553-606.

Gilbert, B. A. 1926. Interrelation of relative day length and temperature. Bot. Gaz. 81(3):1-24.

Hanan, J. J. 1959. Influence of day temperatures on growth and flowering of carnations. Proc. Amer. Soc. Hort. Sci. 74:692-703.

Hanson, H. C. 1917. Leaf structure as related to environment. Am. J. Bot. 4:533-570.

Helson, V. A. 1965. Comparison of gro-lux and cool-white fluorescent lamps with and without incandescent as light sources used in plant growth rooms for growth and development of tomato plants. Can. J. Plant Sci. 45:461-466.

Holcomb, E. J. and J. W. Mastalerz. 1985. Seeding and seedling production, p.87-125. In: J. W. Mastalerz and E. J. Holcomb (eds.). Bedding plants III. Penn. Flower Growers.

Holmes, M. G. and H. Smith. 1977a. The function of phytochrome in the natural environment-- I. Characterization of daylight for studies in photomorphogenesis and photoperiodism. Photochem. and Photobio. 25(6):533-538.

Holmes, M. G. and H. Smith. 1977b. The function of phytochrome in the natural environment-- IV. Light quality and plant development. Photochem. and Photobio. 25(6):551-557.

Hopper, D. A. 1985. Investigation of modeling the growth of the hybrid seed geranium (Pelargonium x hortorum Bailey 'Red Elite'). MS thesis. Michigan State University.

Hughes, A. P. and K. E. Cockshull. 1966. Effects of night-break lighting on bedding plants. Exp. Hort. 16:44-52.

Hunt, R. 1978. Plant growth analysis. Studies in biology No. 96. Edward Arnold LTD., London.

Jeffcoat, B. 1977. Influence of the cytokinin, 6-benzylamino-9-(tetrahydropyran-2-yl)-9H-purine, on the growth and development of some ornamental crops. J. Hort. Sci. 52(1):143-153.

Kaczperski, M. P., W. H. Carlson, R. D. Heins and J. Biernbaum. 1988. Petunias: Designed by cool days/warm nights. Grower Talks 52(1):37-39.

Karlsson, M. G. 1984. Influence of temperature and irradiance on growth and development of Chrysanthemum morifolium 'Bright Golden Anne'. MS thesis. Michigan State University.

Kasperbauer, M. J. 1971. Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. Plant Physiol. 47:775-778.

Krizek, D. T., W. A. Bailey and H. H. Klueter. 1970. A head start program for bedding plants through controlled environments. In: W. H. Carlson (ed.) Proc. 3rd BPI Conf. 43-53.

Krizek, D. T., H. H. Klueter and W. A. Bailey. 1972. Effects of day and night temperature and type of container on the growth of $F_1$ hybrid annuals in controlled environments. Amer. J. Bot. 59(3):284-289.

Krizek, D. T., W. A. Bailey, H. H. Klueter and H. M. Cathey. 1968. Controlled environments for seedling production. Comb. Proc. Inter. Plant Prop. Soc. 18:273-281.

Kwack, B. H. and S. Dunn. 1961. Effects of light quality on plant maturity. I. Duration of growth, nutrient supply and photoperiod. Lloydia 24(2):75-80.

Lane, H. C., H. M. Cathey and L. T. Evans. 1965. The dependence of flowering in several long-day plants on the spectral composition of light extending the photoperiod. Amer. J. Bot. 52(10):1006-1014.

Laurie, A. 1931. Photoperiodism-Practical application to greenhouse culture. Proc. Amer. Soc. Hort. Sci. 27:319-322.

Lieberth, J. A. 1988. It was a very good year. Greenhouse Grower 6(10):30-32.

Litlere, B. and E. Strømme. 1975. The influence of temperature, daylength and light intensity on flowering in Hydrangea macrophylla (Thunb.) Ser. Acta Hort. 51:285-298.

Lyons, R. E. and R. E. Widmer. 1983. Effects of $GA_3$ and NAA on leaf lamina unfolding and flowering of Cyclamen persicum. J. Amer. Soc. Hort. Sci. 108(5):759-763.

Mastalerz, J. W. 1965. Constant vs alternating temperatures compared for best plant growth. Bul. Penn. Flower Growers 61:5.

McMurtrie, R., and L. Wolf. 1983. A model of competition between trees and grass for radiation, water and nutrients. Ann. Bot. 52:449-458.

Mellon, A. and G. Goldsmith. 1985. Sun plants, p. 431-458. In: E. J. Holcomb and J. W. Mastalerz (eds.). Bedding plants III. Penn. Flower Growers.

Merritt, R. H. and H. C. Kohl Jr. 1982. Effect of root temperature and photoperiod on growth and crop productivity efficiency of petunia. J. Amer. Soc. Hort. Sci. 107(6):997-1000.

Merritt, R. H. and H. C. Kohl Jr. 1983. Crop productivity efficiency of petunias in the greenhouse. J. Amer. Soc. Hort. Sci. 108(4):544-548.

Merritt, R. H. and H. C. Kohl Jr. 1985. Photoperiod and soil temperature effects on crop productivity efficiency and growth of seedling geraniums in the greenhouse. J. Amer. Soc. Hort. Sci. 110(2):204-207.

Miller, R. O. 1960. Growth and flowering of snapdragons as affected by night temperatures adjusted in relation to light intensity. Proc. Amer. Soc. Hort. Sci. 75:761-768.

Mohr, H. 1962. Primary effects of light on growth. Ann. Rev. Plant Physiol. 13:465-488.

Mohr, H. 1964. The control of plant growth and development by light. Bio. Rev. 39:87-112.

Morgan, D. C. and H. Smith. 1981. Non-photosynthetic responses to light quality, p. 109-134. In: O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (eds.). Physiological plant ecology. I. Responses to the physical environment. Springer-Verlag, NY.

Naylor, A. W. and G. Gerner. 1940. Fluorescent lamps as a source for light for growing plants. Bot. Gaz. 101:715-716.

Norton, R. A. 1971. Supplementary lighting of selected annual bedding plants in coastal Washington state. Acta Hort. 22:131-141.

Ogawara, K. and K. Ono. 1958. The effects of light on the germination of <u>Petunia hybrida</u> seeds. Hort. Assoc. Japan J. 27:276-281.

Petersen, H. 1955. Artificial light for seedlings and cuttings. New York State Flower Growers Bul. No. 122. p.2-3.

Piringer, A. A. and H. M. Cathey. 1960. Effect of photoperiod, kind of supplemental light and temperature on the growth and flowering of petunia plants. Proc. Amer. Soc. Hort. Sci. 76:649-660.

Pressman, E, Z. Hittin and S. Izhar. 1985. Dwarfism caused by floral-bud removal in petunia and its reversal by gibberellin. Ann. Bot. 55:189-193.

Post, K. 1940. The relationship of temperature to flower bud formation in chrysanthemum. Proc. Amer. Soc. Hort. Sci. 37:1003-1006.

Post, K. 1942. Effects of daylength and temperature on growth and flowering of some florists crops. Cornell Univ. Agric. Exp. Sta. Bul. 787:1-70.

Popp, H. W. 1926. A physiological study of the effect of light of various ranges of wave-length on the growth of plants. Amer. J. Bot. 13:706-736.

Richards, F. J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

Roberts, R. H. and B. E. Struckmeyer. 1938. The effects of temperature and other environmental factors upon the photoperiodic responses of some of the higher plants. J. Agric. Res. 56:633-677.

Roberts, R. H. and B. E. Struckmeyer. 1939. Further studies of the effects of temperature and other environmental factors upon the photoperiodic responses of plants. J. Agric. Res. 59:699-709.

Salisbury, F. B. 1961. Photoperiodism and the flowering process. Ann. Rev. Plant Physiol. 12:293-326.

Salisbury, F. B. 1982. Photoperiodism. Hort. Rev. 4:66-105.

Searle, N. E. 1965. Physiology of flowering. Ann. Rev. Plant Physiol. 16:97-118.

Seeley, J. G. 1955. Petunias for sale 8 weeks after potting. Bul. Penn. Flower Growers. 51:1,4-7.

Shedlosky, M. E. and J. W. White. 1987. Growth of bedding plants in response to root-zone heating and night temperature regimes. J. Amer. Soc. Hort. Sci. 112(2):290-295.

Shirley, H. L. 1929. The influence of light intensity and light quality upon the growth of plants. Amer. J. Bot. 16:353-390.

Smith, D. R. and R. W. Langhans. 1962. The influence of day and night temperatures on the growth and flowering of the Easter lily (Lilium longiflorum Thunb. var Croft). Proc. Amer. Soc. Hort. Sci. 80:593-598.

Smith, H. and M. G. Holmes. 1977. The function of phytochrome in the natural environment-- III. Measurement and calculation of phytochrome photoequilibria. Photochem. and Photobio. 25(6):547-550.

Stoutemyer, V. T. and A. W. Close. 1946. Rooting cuttings and germinating seeds under fluorescent and cold cathode lighting. Proc. Amer. Soc. Hort. Sci. 48:309-325.

Thimijan, R. W. and R. D. Heins. 1983. Photometric, radiometric and quantum light units of measure: a review of procedures for interconversion. HortScience 18(6):818-822.

Thomas, A. V. Jr., and S. Dunn. 1967. Plant growth with new fluorescent lamps. I. Fresh and dry weight yields of tomato seedlings. Planta 72:198-207.

Thornley J. H. M. 1976. Mathematical models in plant physiology, a quantitative approach to problems in plant and crop physiology. Academic Press Inc., London.

Tucker, D. J. 1976. Effect of far-red light on the hormonal control of side shoot growth in the tomato. Ann. Bot. 40:1033-1042.

Tucker, D. J. and T. A. Mansfield. 1972. Effects of light quality on apical dominance in Xanthium strumarium and the associated changes in endogenous levels of abscisic acid and cytokinins. Planta 102:140-151.

Van der Veen, R. and G. Meijer. 1959. Light and plant growth. MacMillan Company, New York.

Vince, D. 1964. Photomorphogenesis in plant stems. Biol. Rev. 39:506-536.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw-Hill, New York.

Vince-Prue, D. 1977. Photocontrol of stem elongation in light-grown plants of Fuschia hybrida. Planta 133:149-156.

Wassink, E. C. and J. A. J. Stolwijk. 1956. Effects of light quality on plant growth. Ann. Rev. Plant Physiol. 7:373-400.

Went, F. W. 1953. The effect of temperature on plant growth. Ann. Rev. Plant Physiol. 59:699-709.

White, J. W. and S. M. Polys. 1987. Photon flux and leaf temperature effects on flower initiation and early development of 'Red Elite' geraniums. J. Amer. Soc. Hort. Sci. 112(6):945-950.

Williams, R. F. 1946. The physiology of plant growth with special reference to the concept of net assimilation rate. Ann. Bot. 10:41-71.

Wilson, J. W. 1966. Effect of temperature on net assimilation rate. Ann. Bot. N.S. 30(120):753-761.

Withrow, R. B. and H. M. Benedict. 1936. Photoperiodic responses of certain greenhouse annuals as influenced by intensity and wavelength of artificial light used to lengthen the daylight period. Plant Physiol. 11:225-249.

Wolnick, D. J. and J. W. Mastalerz. 1966. Response of petunia cultivars to selected combinations of electric light, photoperiod, temperature and B-Nine. Bul. Penn. Flower Growers. 62:1-7,21.

Zeevaart, J. A. D. 1976. Physiology of flower formation. Ann. Rev. Plant Physiol. 27:321-348.

# SECTION I

# The Influence of Temperature and Irradiance on the Growth and Development of Petunia x hybrida Vilm.

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Additional index words. Day temperature, night temperature, average daily temperature.

Abstract. Petunia x hybrida 'Snow Cloud' plants were grown under 25 temperature combinations ranging from 10° to 30°C and at PPF levels of 100 or 200 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$ (6.5 and 13 mol$\cdot$day$^{-1}\cdot$m$^{-2}$, respectively). Days to flower was a quadratic function of average temperature, with 25°C being the optimum

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temperature for minimal time to flower at 13 $mol \cdot day^{-1} \cdot m^{-2}$. Plant height increased linearly and average internode length increased quadraticly as day temperature increased. The number of lateral shoots decreased quadraticly as average temperature increased, and the average length of each shoot decreased quadraticly as day temperature increased.

A fundamental objective of most commercial establishments growing bedding plants is to produce a crop meeting the quality standards of the market in the shortest time possible. Growers may manipulate irradiance, photoperiod, temperature, nutrition and other factors alone or in combinations to achieve the desired results. Thus production time relies heavily on past experience of the grower and the techniques used to produce the crop. Many times this method results in substandard plant quality or inefficient production methods.

The plant's response to the environment has been used to develop production strategies to increase the efficiency of producing floricultural crops (Grueber et al., 1986; Karlsson et al., 1983; Karlsson et al., 1988). Much of the research involving irradiance and temperature effects on Petunia x hybrida, a popular bedding plant (Lieberth, 1988), was conducted 15 to 30 years ago (Boodley, 1970; Carpenter and Carlson, 1974; Mastalerz, 1965; Seeley, 1955) and many of the suggested production techniques are now outdated. Only recently has interest in this area of petunia research been renewed (Armitage and Kowalski, 1982; Merritt and Kohl, 1982; Merritt and Kohl, 1983). The purpose, therefore, of this study is to determine the influence of irradiance and temperature on the growth and development of petunia so that new production strategies can be developed for the crop.

## Materials and Method

Petunia seeds of the cultivar 'Snow Cloud' were sown in No. 406 plug trays (plug size:1.5 X 1.5 X 2.0 cm, 3.0 ml by volume) containing a commercial peat-lite mix (Michigan Peat Co., Sandusky, MI). Plug trays were covered with clear polyethylene and placed under constant light at 200 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$ (17.3 mol$\cdot$day$^{-1}\cdot$m$^{-2}$) and a 23°C constant temperature. The polyethylene was removed after 5 days and the plug trays were placed on capillary matting. Ten days after sowing, the seedlings were transplanted into 9 cm pots (345 ml by volume) filled with the same commercial peat-lite mix. Plants were irrigated as necessary to prevent water stress and fertilized with 10.7 mM nitrogen and 3.18 mM potassium from $CaNO_3$ and $KNO_3$ at each irrigation.

The seedlings were placed in 1 of 5 walk in 5.85 m$^2$ growth chambers maintained at either a constant 10°, 15°, 20°, 25° or 30°C air temperature. Seedlings were placed at a spacing of 123.5 plants $m^{-2}$. Each chamber was maintained at an 18 hour photoperiod and divided to provide photosynthetic photon flux (PPF) levels of 100 or 200 micro-$mol \cdot s^{-1} \cdot m^{-2}$ (6.5 and 13 $mol \cdot day^{-1} \cdot m^{-2}$, respectively). Plants were moved among growth chambers to supply a factorial combination of 5 day temperatures (DT), 5 night temperatures (NT) and 2 PPF levels. Changes between NT and DT corresponded with the change in photoperiod.

Leaf temperatures were measured with a Sensortek BAT-12R meter and Omega copper-constanstan thermocouple. The difference between temperature set points and leaf temperature was less than 1.5°C; temperature set points were used for data analysis. PPF was provided by a mixture of cool-white fluorescent and incandescent bulbs (input wattage 90:10, respectively) and PPF levels were adjusted by raising the lamps to maintain the proper PPF at the canopy top. PPF levels were determined with a LI-COR LI-185A meter and LI-190SB quantum sensor.

Data were collected for each treatment at time of flowering. The experiment was terminated 120 days after sowing the seed, at which time data were collected on remaining plants not reaching flowering. Data collected included days from sowing to flower, plant height, average internode length, number of lateral shoots and average lateral shoot length. A plant was in flower when the outer edge of the corolla reflexed perpendicular to the corolla tube. Plant height was measured from the soil line to the top of the mainstem. Average internode length was determined for the internodes on the mainstem and did not include any lateral shoots. Lateral shoots were counted and measured if they had attained a minimum length of 4 mm and were measured from the point of attachment to the mainstem to the end of the stem of the shoot.

## Results and Discussion

Plants grown at a constant 10°C temperature at either irradiance and those grown at 15° NT and 10° DT at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ did not flower within 120 days from sowing (Table 1). Days to flower was determined to be a function of average temperature (AVG) for each irradiance (Figure 1). As AVG increased, days to flower decreased. Plants grown under 13 $mol \cdot day^{-1} \cdot m^{-2}$ flowered 3 to 23 days before their respective counterparts at the lower irradiance except the 2 highest AVG (25° NT/30° DT and constant 30°), which showed no significant difference in time to flower between the 2 irradiances. Irradiance had more of an effect in reducing time to flower at the lower AVG than at the higher AVG. Isopleth plots were developed from the equations to show the response of time to flower to varying NT and DT at an 18 hour photoperiod (Figure 2).

Increasing air temperature has long been known to decrease time to flower in petunia (Seeley, 1955). It has also been shown that increasing the soil temperature while maintaining commercial production air temperatures would produce similar results (Merritt and Kohl, 1982). Plants in this study , grown at 13 $mol \cdot day^{-1} \cdot m^{-2}$, showed a significant decrease in flowering time as the average air temperature approached 25°, with higher temperatures slightly delaying the crop. This delay may have been due, at least in part, to the increased bud abortion experienced at the higher average temperature (data not reported). Similar bud abortion was found at the lower irradiance also.

Raising the irradiance from 6.5 to 13 $mol \cdot day^{-1} \cdot m^{-2}$ decreased time to flower in petunia (Figure 1) by up to 3 weeks. High intensities of fluorescent lights (287 $micro\text{-}mol \cdot s^{-1} \cdot m^{-2}$) used to supplement natural light conditions when growing petunias were shown to decrease time to flower by up to 12 days when compared to plants receiving low intensity incandescent lighting to extend the photoperiod (Carpenter and Beck, 1973). In our study, plants flowered in 67 days when grown at an average air temperature of 20° at an irradiance of 6.5 $mol \cdot day^{-1} \cdot m^{-2}$. However, when the intensity was doubled to provide a total irradiance of 13 $mol \cdot day^{-1} \cdot m^{-2}$, the plants flowered in only 56 days. At the higher irradiance, the average temperature could be lowered to 15° and still flower at the same time as the ones grown at 20° at the lower irradiance. The plants could be supplied with a high night temperature with little heating during the day and result in fuel savings for commercial applications using heat blankets since a smaller area is heated at night to the warmer temperature. Time to flower would not increase.

Plant height (Table 2, Figure 3) increased as DT increased or irradiance decreased. Plant height was influenced more by low irradiance at 30° DT than at 10° DT. Plants grown at 10° DT and an irradiance of 13 $\mathrm{mol \cdot day^{-1} \cdot m^{-2}}$ were similar in height to those grown at the lower irradiance and corresponding night temperature. However, as DT increased, the difference in plant height at the same NT/DT combination increased when the two irradiances were compared (Figure 4). Plants grown under 13 $\mathrm{mol \cdot day^{-1} \cdot m^{-2}}$ at 30° DT were up to 6 cm shorter than plants grown under 6.5 $\mathrm{mol \cdot day^{-1} \cdot m^{-2}}$ and 30° DT. Plants grown at 20° constant temperature at either irradiance were much taller than expected based on the data collected from plants from the other treatments. Since this response could not be reproduced in subsequent trials, it was considered anomalous and data from these treatments were not used in data analysis for plant height or average internode length.

Plant height was dependent on internode length since all plants flowered with a similar number of nodes on the mainstem. The effects of DT and irradiance on average internode length were similar to their effects on plant height (Table 3). As DT increased, average internode length increased significantly. Likewise, plants at the lower irradiance had longer average internode length than plants at the higher irradiance. The effect of NT was less significant than either DT or irradiance (Figure 5).

Krizek et al. (1972) reported that increasing both DT and NT increased plant height in petunia seedlings. However, they only used 3 temperature regimes in which an increase in NT accompanied an increase in DT. They did not discuss separate effects of NT and DT, just the combined effects.

The difference between day temperature and night temperature (DIF) has been shown to influence internode length and plant height (Erwin et al., 1989). Internode length increases as DIF increases. DIF did not have as great effect in this experiment as has been seen in other plants. However, the 18 hour photoperiod may have decreased the effect of DIF, and DIF may have been more apparent if a shorter photoperiod was selected.

The number of lateral shoots formed by the plants was a function of average temperature (Table 4). Plants formed a similar number of lateral shoots at both irradiances. As average temperature increased, the number of lateral shoots decreased (Figure 6). The average length of each lateral shoot varied widely within each plant. However, average length was strongly influenced by day temperature (Table 5). As day temperature increased, the average length decreased. Night temperature had no effect.

Previous work showed that higher temperatures decreased lateral branching in petunia (Carpenter, 1974; Carpenter and Carlson, 1974; Piringer and Cathey, 1960) similar to the results found in this study. Petunia and other crops have shown increased lateral branching when light intensity increased (Carpenter, 1974; Erickson et al., 1980). An increase in lateral branching under a higher intensity was not evident from our data. However, the higher intensity used in this study (200 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$), was not as high as intensities used in other experiments (533 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$ (Carpenter, 1974)).

Plant quality is the main underlying factor to consider when selecting combinations of irradiance, day temperatures and night temperatures for forming plant production strategies for petunia. Plant growth can be increased by raising temperatures (Krizek et al., 1972), but this increased growth rate will also result in lower plant quality by increasing plant height and reducing lateral branching (Merritt and Kohl, 1982; Piringer and Cathey, 1960). Lateral branching and reduced plant height, resulting in increased quality, can be obtained by lowering the growing temperatures. However, this will result in a corresponding delay in time to flower and an extended production period. Individual growers must first determine the quality their particular market will demand. Only then can a proper selection of combinations of temperature and irradiance be made to produce petunias of desired quality in the shortest time.

## Literature Cited

Armitage, A. M. and T. Kowalski. 1982. Effects of light intensity and air temperature in simulated post production environment on Petunia hybrida Vilm. J. Amer. Soc. Hort. Sci. 108(1):115-118.

Boodley, J. W. 1970. Influence of container size on petunia growth. New York State Flor. Ind. Bul. No. 1 pp.4-5.

Carpenter, W. J. 1974. High intensity lighting in the greenhouse. Research Report 255. Michigan State University Printing.

Carpenter, W. J. and G. R. Beck. 1973. High intensity supplementary lighting of bedding plants after transplanting. HortScience 8(6):482-483.

Carpenter, W. J. and W. H. Carlson. 1974. Comparison of photoperiodic and high intensity lighting on the growth and flowering of Petunia x hybrida Vilm. The Michigan Florist 52:16-24.

Erickson, V. L., A. Armitage, W. H. Carlson and R. M. Miranda. 1980. The effect of cumulative photosynthetically active radiation on the growth and flowering of the seedling geranium, Pelargonium x hortorum 'Bailey'. HortScience 15(6):815-817.

Erwin, J. E., R. D. Heins and M. G. Karlsson. 1989. Thermomorphogenesis in Lilium longiflorum. Amer. J. Bot. 76(1):47-52.

Grueber, K. L., W. E. Healy, H. B. Pemberton and H. F. Wilkins. 1986. Easter lily leaf unfolding rate as influenced by temperature. Minn. State Flor. Bul. 35(6):1-4.

Karlsson, M., R. D. Heins and W. H. Carlson. 1983. Development of environmental strategies based on plant growth models. Acta Hort. 147:153-160.

Karlsson, M. G., R. D. Heins and J. E. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113(1):70-74.

Krizek, D. T., H. H. Klueter and W. A. Bailey. 1972. Effects of day and night temperature and type of container on the growth of $F_1$ hybrid annuals in controlled environments. Amer. J. Bot. 59(3):284-289.

Lieberth, J. A. 1988. It was a very good year. Greenhouse Grower 6(10):30-32.

Mastalerz, J. W. 1965. Constant vs alternating temperatures compared for best plant growth. Bul. Penn. Flower Growers 61:5.

Merritt, R. H. and H. C. Kohl Jr. 1982. Effect of root temperature and photoperiod on growth and crop productivity efficiency of petunia. J. Amer. Soc. Hort. Sci. 107(6):997-1000.

Merritt, R. H. and H. C. Kohl Jr. 1983. Crop productivity efficiency of petunias in the greenhouse. J. Amer. Soc. Hort. Sci. 108(4):544-548.

Piringer, A. A. and H. M. Cathey. 1960. Effect of photoperiod, kind of supplemental light and temperature on the growth and flowering of petunia plants. Proc. Amer. Soc. Hort. Sci. 76:649-660.

Seeley, J. G. 1955. Petunias for sale 8 weeks after potting. Bul. Penn. Flower Growers. 51:1,4-7.

Table 1. Mean number of days to flower for *Petunia x hybrida* 'Snow Cloud' in response to day and night temperatures between 10° and 30°C, and irradiances of 13 or 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ for an 18 hour photoperiod.

| Night temperature (°C) | Day temperature (°C) | | | | |
|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 |
| 13 $mol \cdot day^{-1} \cdot m^{-2}$ | | | | | |
| 10 | NF | 77 | 60 | 51 | 49 |
| 15 | 105 | 74 | 57 | 50 | 49 |
| 20 | 83 | 68 | 56 | 50 | 49 |
| 25 | 74 | 64 | 53 | 46 | 49 |
| 30 | 66 | 57 | 51 | 46 | 52 |
| 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ | | | | | |
| 10 | NF | 100 | 74 | 58 | 54 |
| 15 | NF | 89 | 67 | 56 | 54 |
| 20 | 101 | 81 | 67 | 55 | 52 |
| 25 | 87 | 69 | 59 | 52 | 51 |
| 30 | 82 | 66 | 56 | 52 | 51 |

Significance

| | |
|---|---|
| NT | *** |
| DT | *** |
| Irradiance | *** |
| NT X DT | *** |
| NT X Irradiance | *** |
| DT X Irradiance | *** |
| NT X DT X Irradiance | *** |

---

*** Significant at the .1% level.

NF - Treatments did not flower within 120 days from sowing.

Table 2. Mean plant height in centimeters for *Petunia x hybrida* 'Snow Cloud' in response to day and night temperatures between 10° and 30°C, and irradiances of 13 or 6.5 mol·day$^{-1}$·m$^{-2}$ for an 18 hour photoperiod.

| Night temperature (°C) | Day temperature (°C) | | | | |
|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 |
| 13 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | 11.3 | 12.5 | 17.5 | 21.6 | 21.6 |
| 15 | 11.7 | 12.2 | 15.2 | 19.4 | 22.9 |
| 20 | 11.2 | 12.0 | 25.4 | 22.1 | 23.0 |
| 25 | 12.7 | 14.2 | 19.1 | 19.5 | 20.8 |
| 30 | 13.3 | 13.8 | 19.4 | 21.5 | 25.3 |
| 6.5 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | 11.8 | 17.8 | 20.6 | 23.3 | 27.1 |
| 15 | 12.6 | 17.9 | 21.3 | 27.6 | 26.7 |
| 20 | 14.6 | 16.9 | 27.0 | 25.2 | 28.6 |
| 25 | 16.6 | 16.3 | 21.6 | 26.1 | 27.5 |
| 30 | 13.5 | 16.4 | 23.3 | 25.2 | 37.5 |

| Significance | |
|---|---|
| NT | *** |
| DT | *** |
| Irradiance | *** |
| NT X DT | *** |
| NT X Irradiance | NS |
| DT X Irradiance | *** |
| NT X DT X Irradiance | *** |

---

$^{NS,\ ***}$ Nonsignificant and significant at the .1% level, respectively.

Table 3. Mean average internode length in centimeters for *Petunia x hybrida* 'Snow Cloud' in response to day and night temperatures between 10° and 30°C, and irradiances of 13 or 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ for an 18 hour photoperiod.

| Night temperature (°C) | Day temperature (°C) 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|
| 13 $mol \cdot day^{-1} \cdot m^{-2}$ | | | | | |
| 10 | 0.6 | 0.6 | 1.0 | 1.1 | 1.2 |
| 15 | 0.6 | 0.9 | 0.8 | 1.1 | 1.3 |
| 20 | 0.6 | 0.7 | 1.4 | 1.2 | 1.3 |
| 25 | 0.6 | 0.7 | 1.0 | 1.0 | 1.1 |
| 30 | 0.7 | 0.7 | 1.1 | 1.3 | 1.2 |
| 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ | | | | | |
| 10 | 0.7 | 1.0 | 1.2 | 1.4 | 1.5 |
| 15 | 0.7 | 1.0 | 1.3 | 1.6 | 1.5 |
| 20 | 0.8 | 1.0 | 1.6 | 1.5 | 1.5 |
| 25 | 0.9 | 0.9 | 1.2 | 1.5 | 1.5 |
| 30 | 0.8 | 0.9 | 1.4 | 1.4 | 1.9 |

| Significance | |
|---|---|
| NT | * |
| DT | *** |
| Irradiance | *** |
| NT X DT | * |
| NT X Irradiance | NS |
| DT X Irradiance | *** |
| NT X DT X Irradiance | *** |

---

[NS, *, ***] Nonsignificant, significant at the 5% and .1% levels, respectively.

Table 4. Mean lateral shoot number for *Petunia x hybrida* 'Snow Cloud' in response to day and night temperatures between 10° and 30°C, and irradiances of 13 or 6.5 mol:day$^{-1}$:m$^{-2}$ for an 18 hour photoperiod.

| Night temperature (°C) | Day temperature (°C) | | | | |
|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 |
| 13 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | 8.2 | 8.0 | 8.0 | 7.0 | 5.0 |
| 15 | 7.4 | 7.0 | 7.0 | 6.0 | 4.6 |
| 20 | 8.4 | 7.8 | 6.4 | 4.6 | 4.4 |
| 25 | 8.0 | 7.8 | 7.0 | 4.4 | 4.2 |
| 30 | 8.4 | 8.2 | 7.6 | 5.2 | 3.4 |
| 6.5 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | 7.4 | 7.2 | 7.2 | 6.0 | 3.8 |
| 15 | 7.2 | 7.0 | 6.4 | 5.4 | 3.0 |
| 20 | 7.4 | 7.4 | 5.0 | 4.6 | 3.6 |
| 25 | 7.6 | 7.0 | 6.4 | 2.8 | 2.6 |
| 30 | 8.8 | 8.4 | 4.6 | 3.4 | 3.8 |

| Significance | |
|---|---|
| NT | *** |
| DT | *** |
| Irradiance | *** |
| NT X DT | *** |
| NT X Irradiance | NS |
| DT X Irradiance | NS |
| NT X DT X Irradiance | NS |

---

NS, *** Nonsignificant and significant at the .1% level, respectively.

Table 5. Mean lateral shoot length in centimeters for Petunia x hybrida 'Snow Cloud' in response to day and night temperatures between 10° and 30°C, and irradiances of 13 or 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ for an 18 hour photoperiod.

| Night temperature (°C) | Day temperature (°C) 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|
| 13 $mol \cdot day^{-1} \cdot m^{-2}$ | | | | | |
| 10 | 8.1 | 8.2 | 6.0 | 2.7 | 1.3 |
| 15 | 7.7 | 8.2 | 7.0 | 2.4 | 1.8 |
| 20 | 8.7 | 7.4 | 4.1 | 2.3 | 0.8 |
| 25 | 8.4 | 8.3 | 7.2 | 2.6 | 1.2 |
| 30 | 9.7 | 7.7 | 6.5 | 2.0 | 0.9 |
| 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ | | | | | |
| 10 | 8.1 | 8.1 | 6.5 | 2.4 | 0.8 |
| 15 | 7.2 | 5.6 | 4.5 | 1.7 | 0.6 |
| 20 | 8.1 | 7.2 | 3.2 | 2.1 | 1.9 |
| 25 | 9.6 | 7.8 | 3.7 | 1.7 | 1.3 |
| 30 | 7.4 | 5.6 | 4.0 | 3.0 | 1.0 |

| Significance | |
|---|---|
| NT | NS |
| DT | *** |
| Irradiance | * |
| NT X DT | NS |
| NT X Irradiance | NS |
| DT X Irradiance | NS |
| NT X DT X Irradiance | NS |

---

NS, *, *** Nonsignificant, significant at the 5% and .1% levels, respectively.

Figure 1. Days to flower for <u>Petunia x hybrida</u> 'Snow Cloud' in response to average daily temperature between 10° and 30°C for:

a) 13 mol·day$^{-1}$·m$^{-2}$

(Days to Flower = $190.205-(11.1917*AVG)+(0.219176*AVG^2)$)

$r^2 = .915$

b) 6.5 mol·day$^{-1}$·m$^{-2}$

(Days to Flower = $212.741-(11.7045*AVG)+(0.211953*AVG^2)$)

$r^2 = .937$

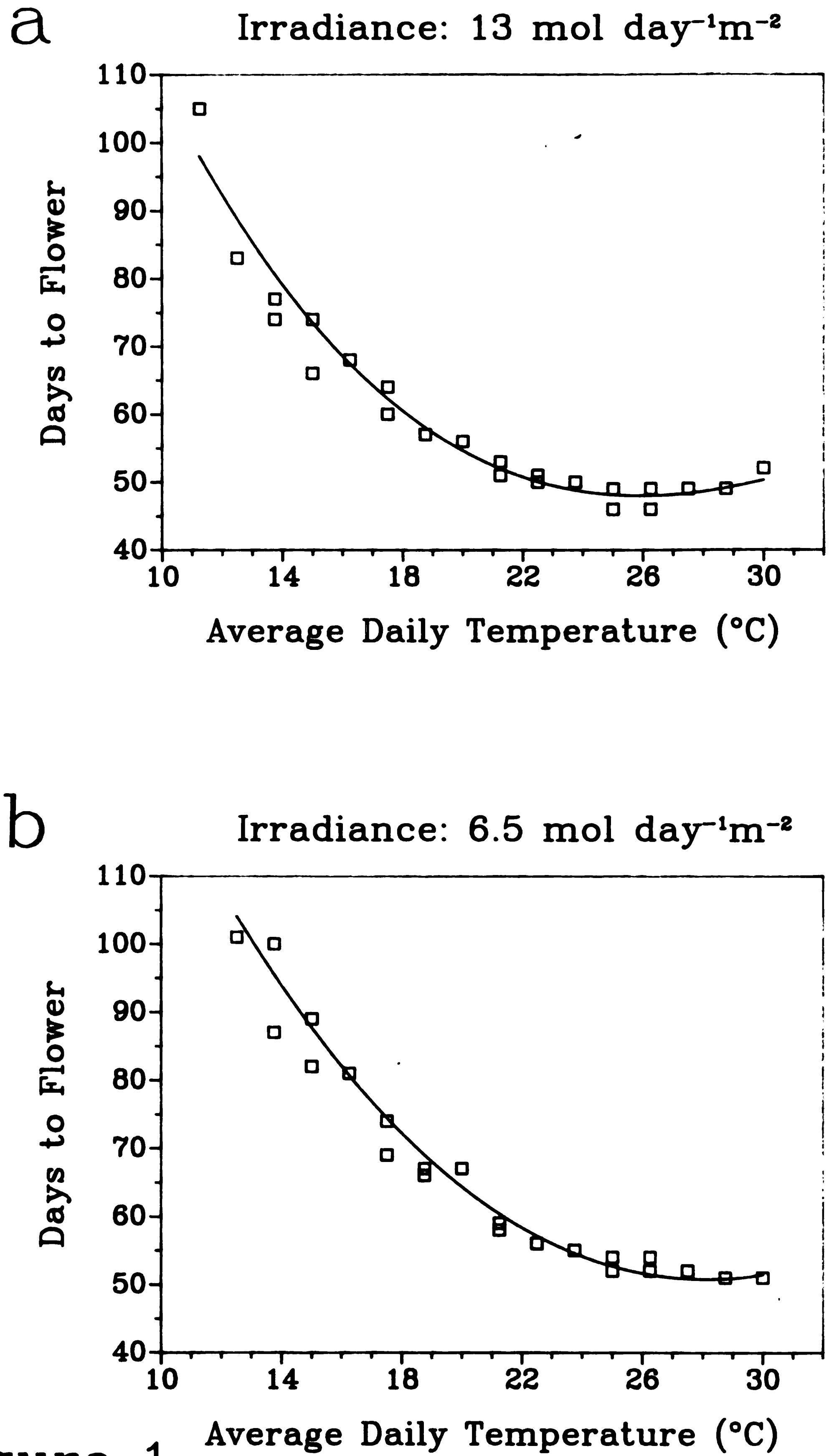

a
Irradiance: 13 mol day$^{-1}$m$^{-2}$
Days to Flower
110
100
90
80
70
60
50
40
10
14
18
22
26
30
Average Daily Temperature (°C)
b
Irradiance: 6.5 mol day$^{-1}$m$^{-2}$
Days to Flower
110
100
90
80
70
60
50
40
10
14
18
22
26
30
Average Daily Temperature (°C)

Figure 1

Figure 1. Days to flower for <u>Petunia x hybrida</u> 'Snow Cloud' in response to average daily temperature between 10° and 30°C for:

a) 13 $mol \cdot day^{-1} \cdot m^{-2}$

(Days to Flower = $190.205-(11.1917*AVG)+(0.219176*AVG^2)$)

$r^2 = .915$

b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$

(Days to Flower = $212.741-(11.7045*AVG)+(0.211953*AVG^2)$)

$r^2 = .937$

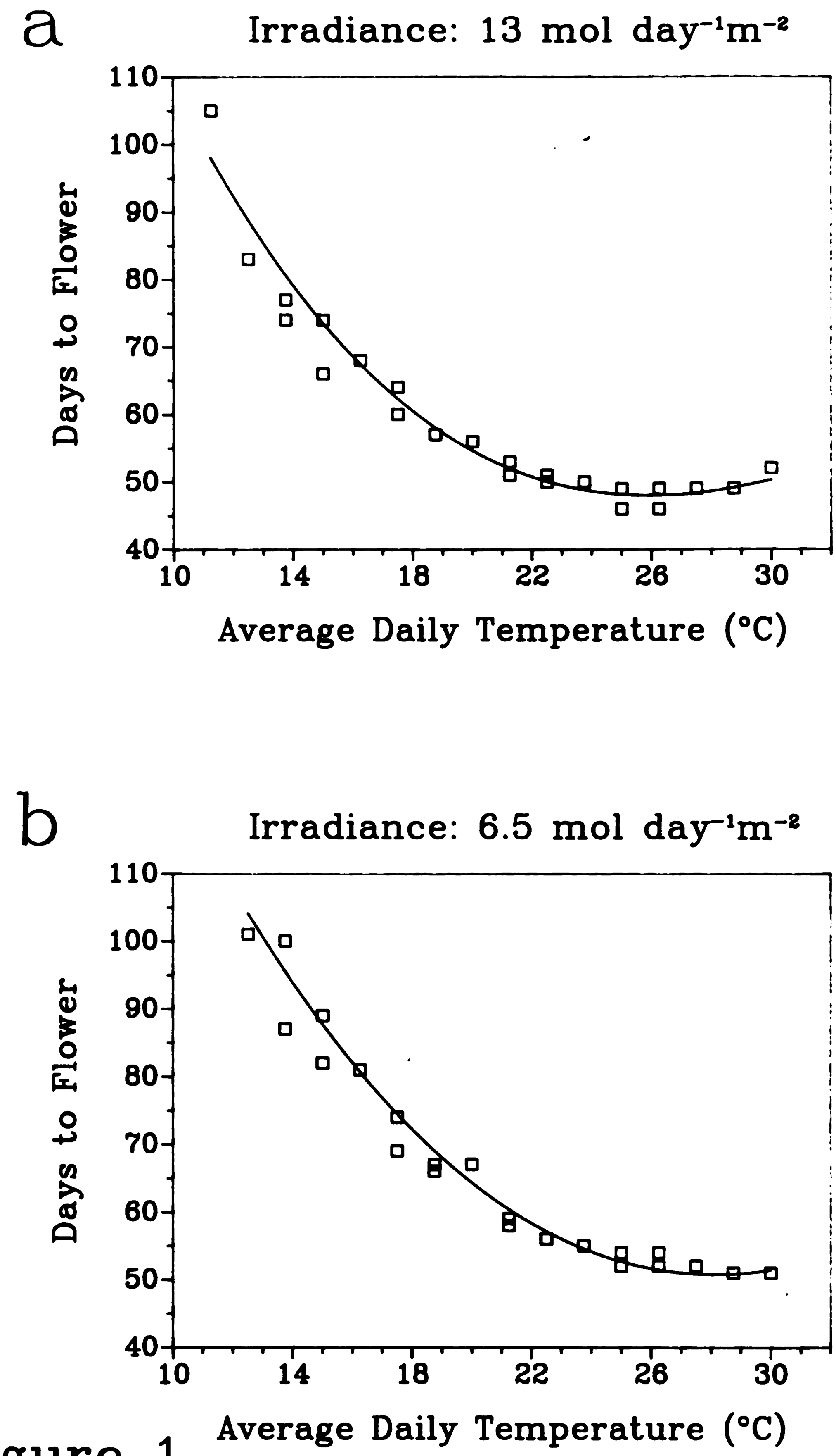

a
Irradiance: 13 mol day$^{-1}$m$^{-2}$
Days to Flower
110
100
90
80
70
60
50
40
10
14
18
22
26
30
Average Daily Temperature (°C)
b
Irradiance: 6.5 mol day$^{-1}$m$^{-2}$
Days to Flower
110
100
90
80
70
60
50
40
10
14
18
22
26
30
Average Daily Temperature (°C)

Figure 1

Figure 1. Days to flower for Petunia x hybrida 'Snow Cloud' in response to average daily temperature between 10° and 30°C for:

a) 13 $mol \cdot day^{-1} \cdot m^{-2}$

(Days to Flower = $190.205-(11.1917*AVG)+(0.219176*AVG^2)$)

$r^2 = .915$

b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$

(Days to Flower = $212.741-(11.7045*AVG)+(0.211953*AVG^2)$)

$r^2 = .937$

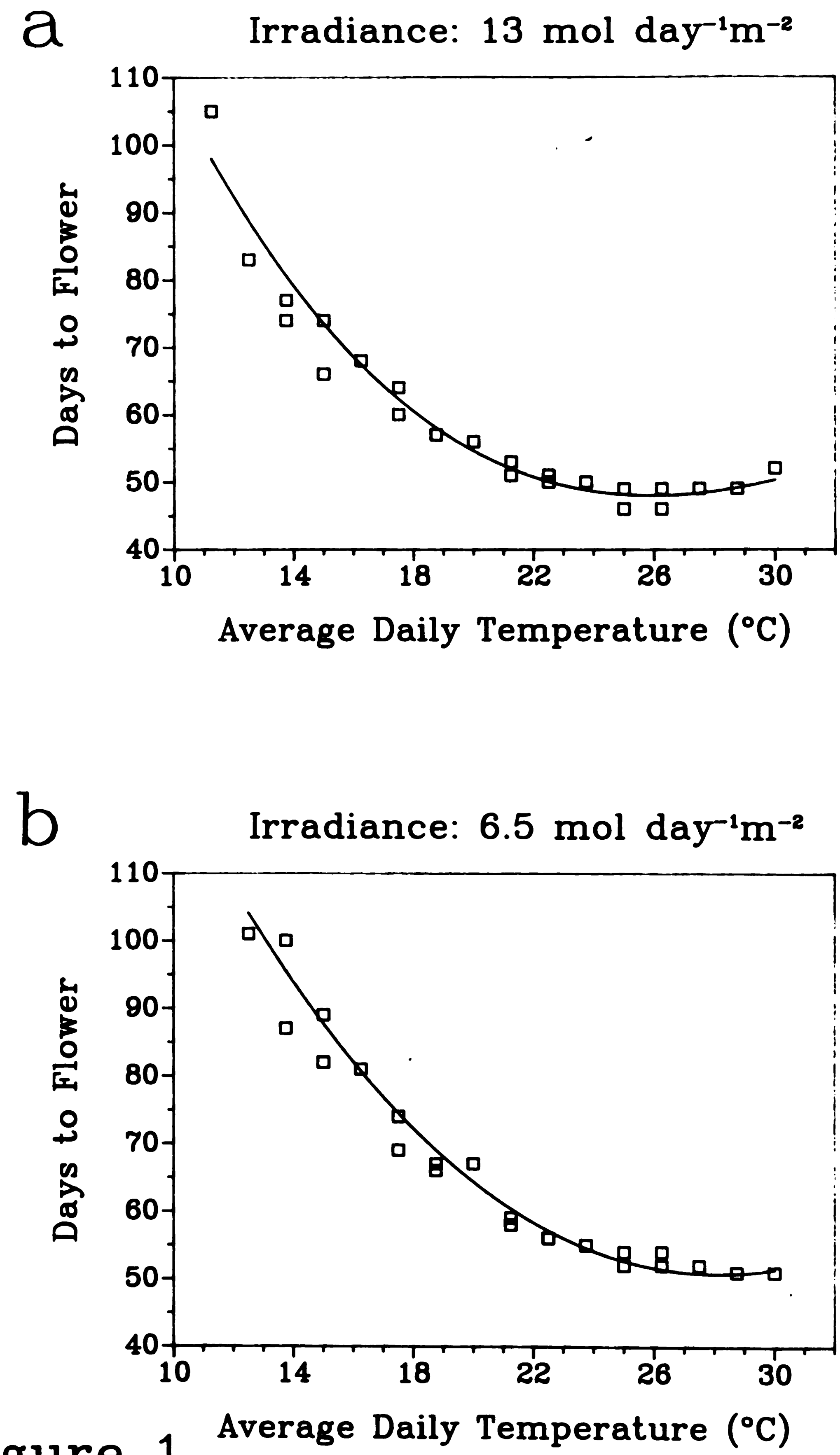
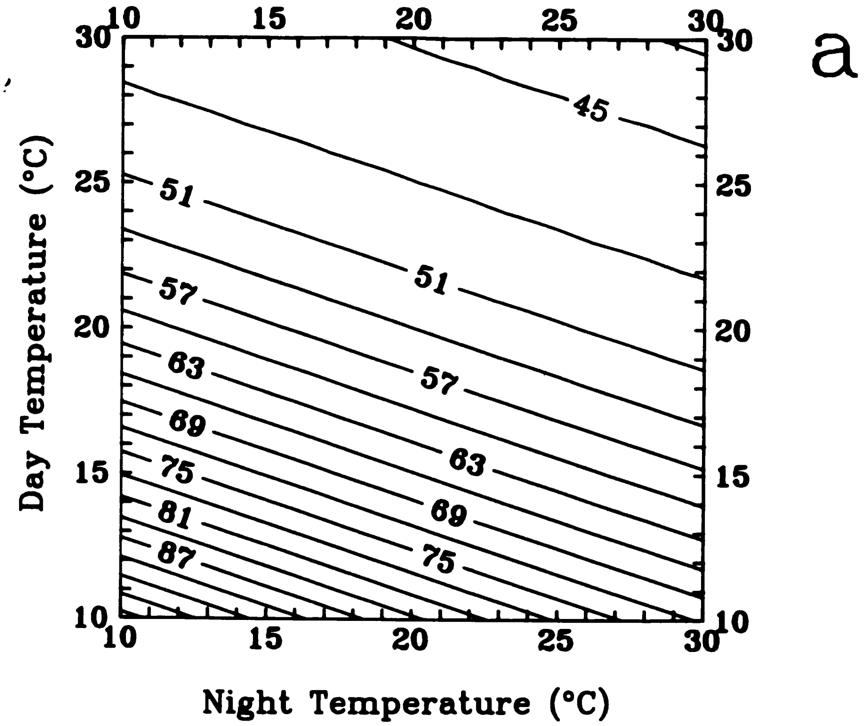

a
Irradiance: 13 mol day$^{-1}$m$^{-2}$
110
100
90
80
70
60
50
40
Days to Flower
10
14
18
22
26
30
Average Daily Temperature (°C)
b
Irradiance: 6.5 mol day$^{-1}$m$^{-2}$
110
100
90
80
70
60
50
40
Days to Flower
10
14
18
22
26
30
Average Daily Temperature (°C)

Figure 1

Figure 2. Isopleth plots of days to flower for varying combinations of night and day temperature between 10° and 30°C for Petunia x hybrida 'Snow Cloud' at a) 13 $mol \cdot day^{-1} \cdot m^{-2}$ and b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$.

Irradiance: 13 mol·day$^{-1}$·m$^{-2}$



Irradiance: 6.5 mol·day$^{-1}$·m$^{-2}$

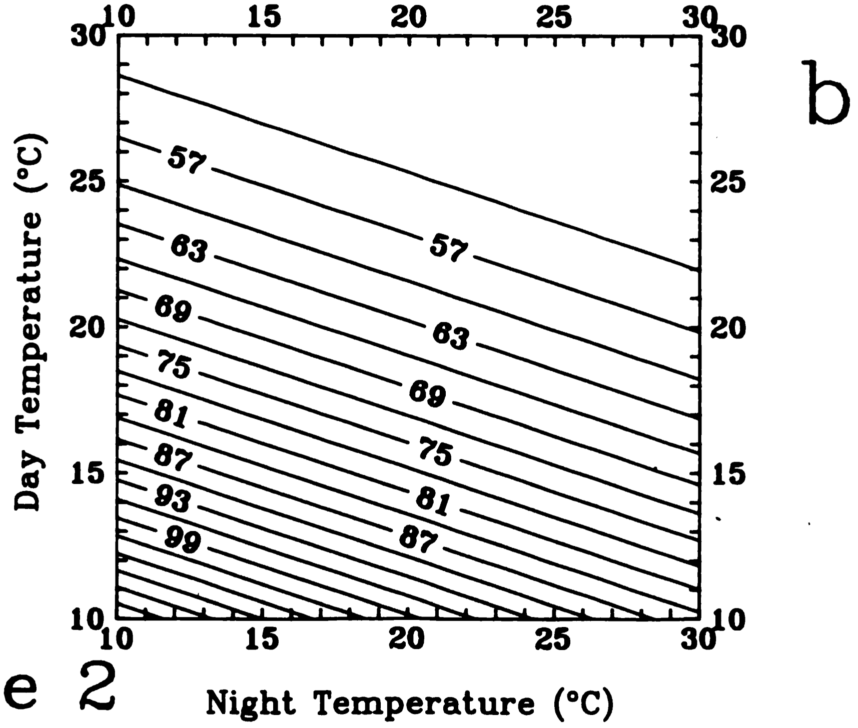


Figure 2

Figure 3. Isopleth plots of plant height in centimeters for varying combinations of night and day temperature between 10° and 30°C for _Petunia x hybrida_ 'Snow Cloud' at:

a) 13 $mol\cdot day^{-1}\cdot m^{-2}$

(Plant height = 3.78643+(0.3204*DT)+(0.35232*AVG))

$r^2=.750$

b) 6.5 $mol\cdot day^{-1}\cdot m^{-2}$.

(Plant height = 3.01463+(0.40296*DT)+(0.5216*AVG))

$r^2=.810$

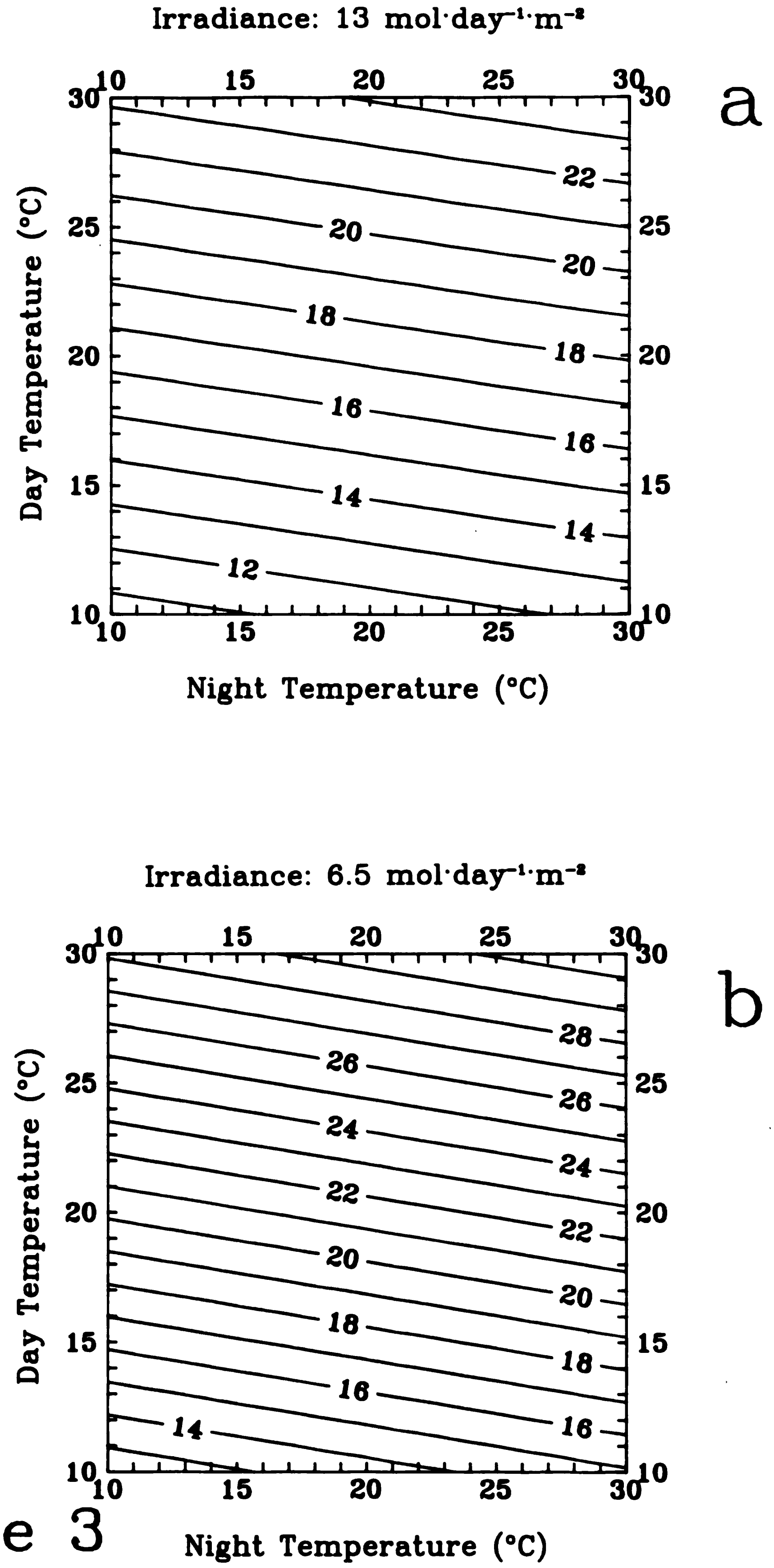

Irradiance: 13 mol·day⁻¹·m⁻²
a
Day Temperature (°C)
Night Temperature (°C)
10
15
20
25
30
12
14
16
18
20
22
Irradiance: 6.5 mol·day⁻¹·m⁻²
b
14
16
18
20
22
24
26
28

Figure 3

Figure 3. Isopleth plots of plant height in centimeters for varying combinations of night and day temperature between 10° and 30°C for <u>Petunia x hybrida</u> 'Snow Cloud' at:

a) 13 $mol \cdot day^{-1} \cdot m^{-2}$

(Plant height = 3.78643+(0.3204*DT)+(0.35232*AVG))

$r^2$=.750

b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$.

(Plant height = 3.01463+(0.40296*DT)+(0.5216*AVG))

$r^2$=.810

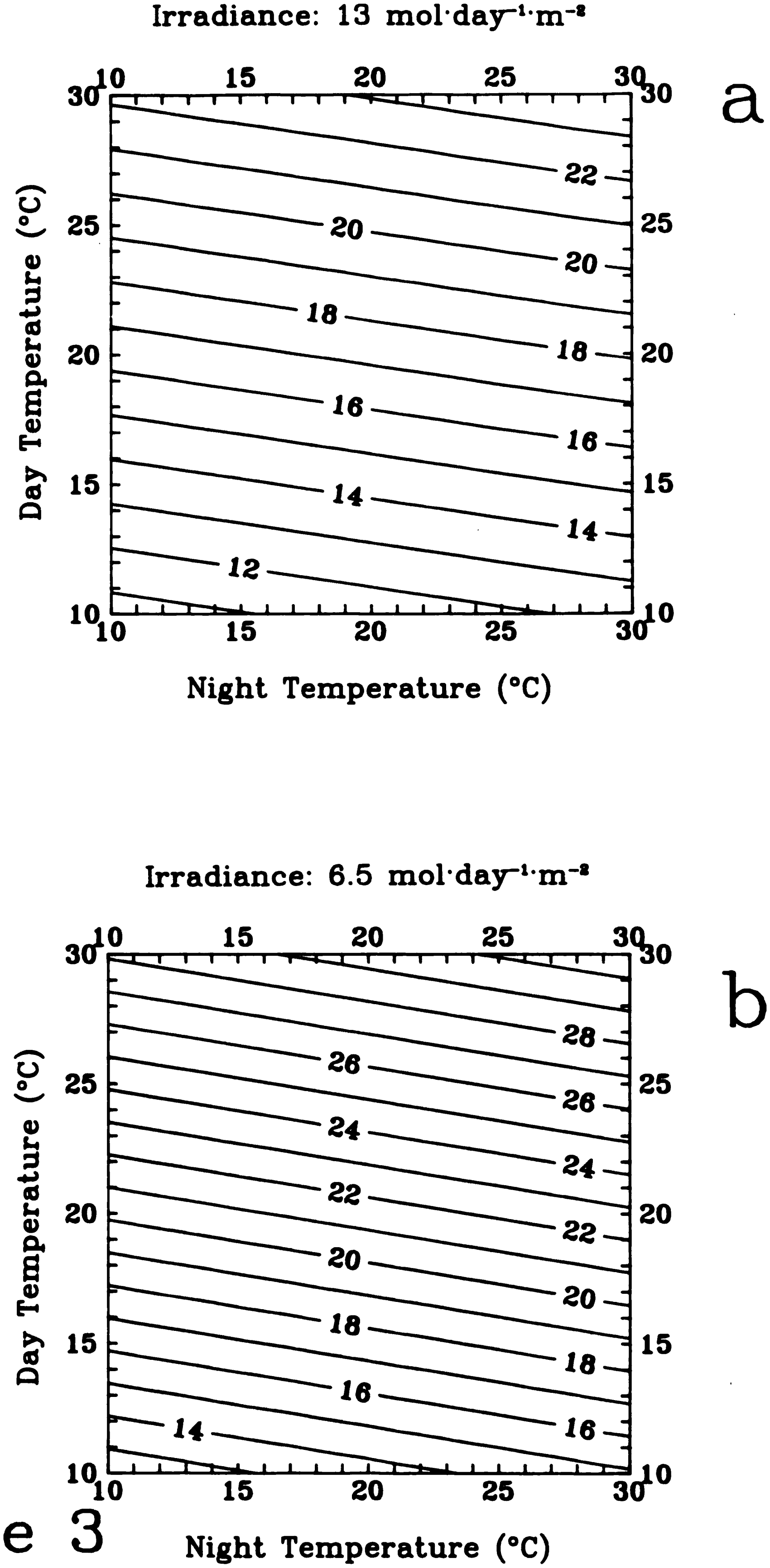

Irradiance: 13 mol·day$^{-1}$·m$^{-2}$
a
Day Temperature (°C)
Night Temperature (°C)
10
15
20
25
30
12
14
14
16
16
18
18
20
20
22
Irradiance: 6.5 mol·day$^{-1}$·m$^{-2}$
b
14
16
16
18
18
20
20
22
22
24
24
26
26
28

Figure 3

Figure 4. Plant height in centimeters for Petunia x hybrida 'Snow Cloud' at 30°C NT and DT between 10° and 30° at irradiances of 13 and 6.5 $mol \cdot day^{-1} \cdot m^{-2}$.

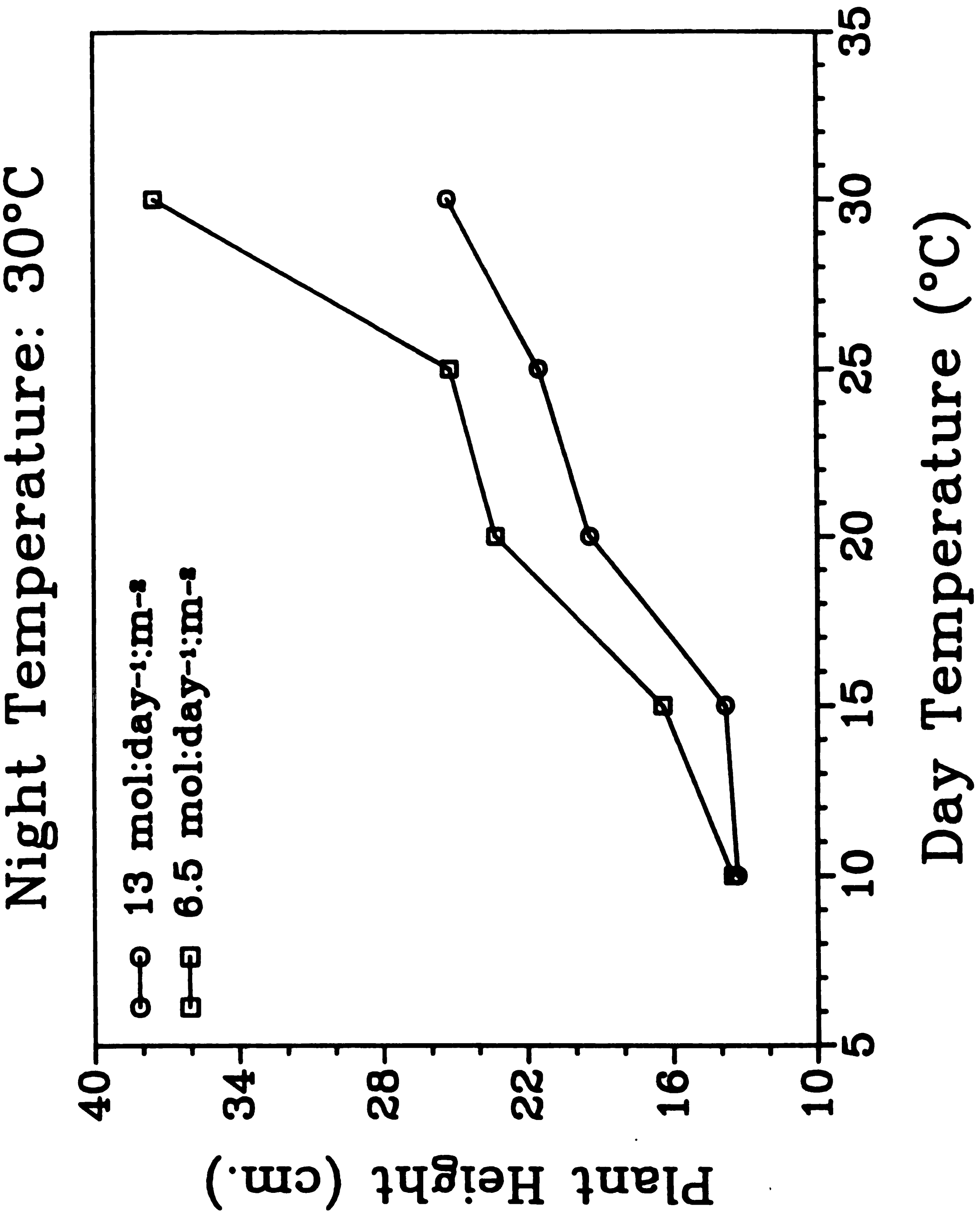

Night Temperature: 30°C
13 mol·day⁻¹·m⁻²
6.5 mol·day⁻¹·m⁻²
Plant Height (cm.)
40
34
28
22
16
10
5
10
15
20
25
30
35
Day Temperature (°C)

Figure 4

Figure 5. Isopleth plots of average internode length in centimeters for varying combinations of night and day temperature between 10° and 30°C for Petunia x hybrida 'Snow Cloud' at:

a) 13 $mol \cdot day^{-1} \cdot m^{-2}$

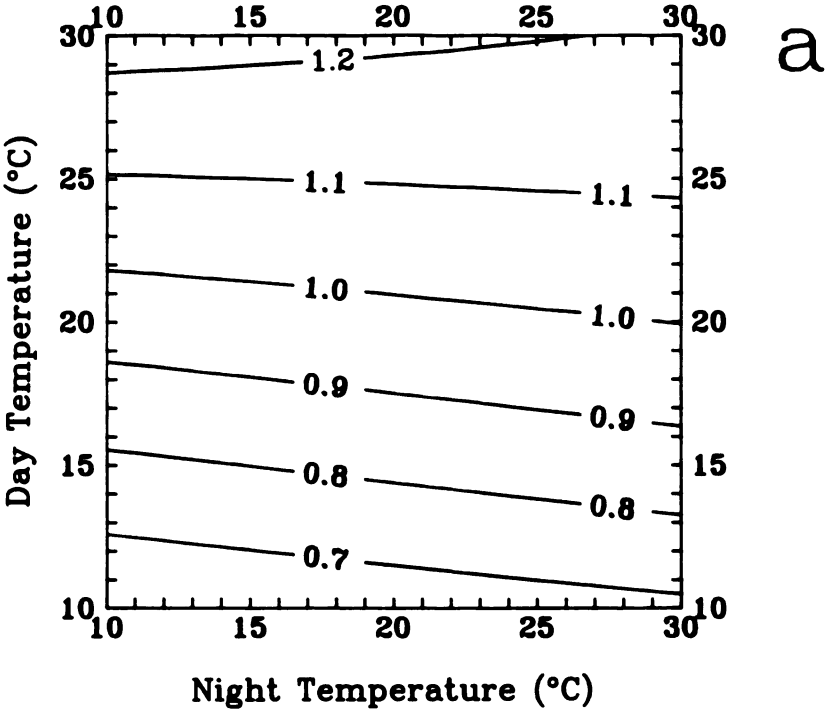
(Average internode length = 0.143507 + (0.037663*DT) + (0.00063527*DT*NT) - (0.000023821*NT*$DT^2$))

$r^2$=.733

b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$.

(Average internode length = 0.13144 + (0.069617*DT) - (0.0009204*$DT^2$) + (0.000011519*NT*$DT^2$))

$r^2$=.809


Irradiance: 13 mol·day$^{-1}$·m$^{-2}$

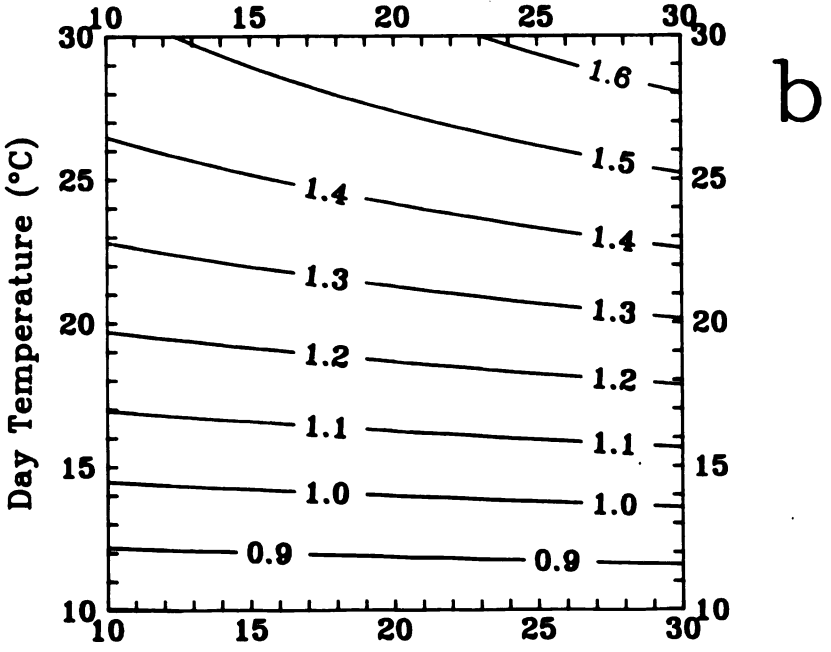

Irradiance: 6.5 mol·day$^{-1}$·m$^{-2}$

Figure 5

Figure 6. Lateral shoots formed by Petunia x hybrida 'Snow Cloud' in response to average daily temperature between 10° and 30°C for:

a) 13 $mol \cdot day^{-1} \cdot m^{-2}$

(Number of shoots = $9.29607-(0.00634*AVG^2)$)

$r^2 = .837$

b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$

(Number of shoots = $8.85987-(0.00723*AVG^2)$)

$r^2 = .801$

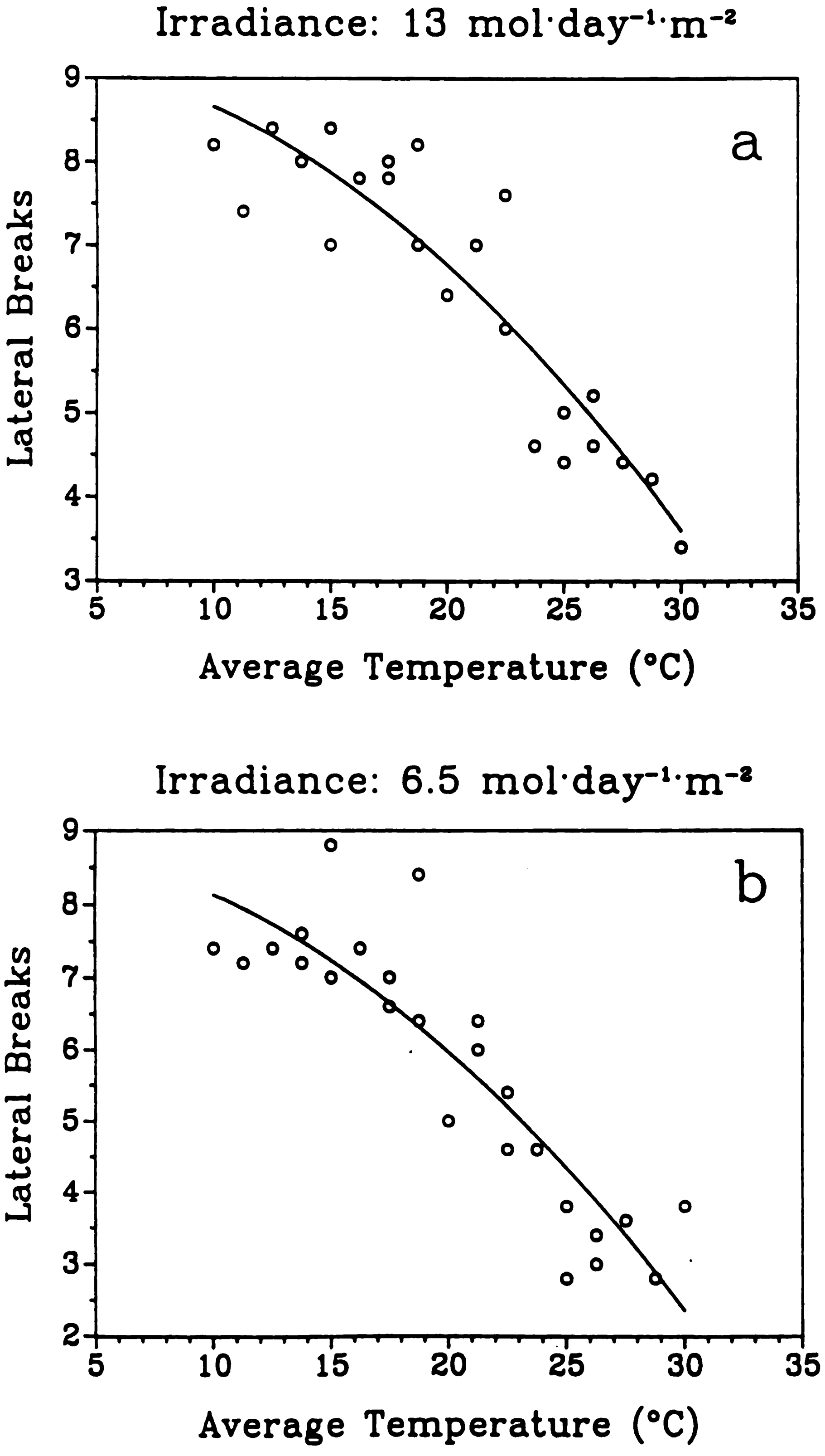

Irradiance: 13 mol·day⁻¹·m⁻²
a
Lateral Breaks
9
8
7
6
5
4
3
5
10
15
20
25
30
35
Average Temperature (°C)
Irradiance: 6.5 mol·day⁻¹·m⁻²
b
Lateral Breaks
9
8
7
6
5
4
3
2
5
10
15
20
25
30
35
Average Temperature (°C)

Figure 6

# SECTION II

# Quantifying Leaf Unfolding Rates, Leaf Number and Minimum Node Number in Petunia.

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Additional index words. *Petunia x hybrida* Vilm., day temperature, night temperature, average daily temperature, minimum leaf number.

Abstract. *Petunia x hybrida* 'Snow Cloud' plants were grown under 25 temperature combinations ranging from 10° to 30°C and at PPF levels of 100 or 200 micro-mol$\cdot$s$^{-1}\cdot$m$^{-2}$ (6.5 and

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13 $mol\cdot day^{-1}\cdot m^{-2}$, respectively). Leaf unfolding was a quadratic function of average temperature at 13 $mol\cdot day^{-1}\cdot m^{-2}$ and a linear function of average temperature at 6.5 $mol\cdot day^{-1}\cdot m^{-2}$. Plants initiated flowers after initiating a minimum of 13 leaves on the mainstem and unfolded an average of 18.8 leaves on the mainstem by flowering of the first bud.

Leaf unfolding rate has long been used to determine rate of development for several crops (Blaney et al., 1967; Leopold and Guernsey, 1953; McKinney and Sando, 1944; Wilkins and Roberts, 1969). In the floriculture industry, the use of leaf unfolding rates are used to time Easter lilies (Blaney et al., 1967; Wilkins and Roberts, 1969). Leaf unfolding can be used in the production of Petunia x hybrida and other floricultural crops if the number of leaves the plant will produce is known along with the rate of leaf unfolding (Collins and Wilson, 1974).

Accurate timing of petunia and other bedding plant species has become increasingly important in recent years to reduce production time because of rising production costs. Commercial producers are seeking to produce crops in the least amount of time to reduce overhead costs of the crop and to allow for the possibility of double or triple cropping production space while still maintaining the standard of quality needed for their market. The purpose of this experiment was to determine if leaf unfolding could be developed into a method of timing petunias and increasing commercial production efficiency.

Petunia seeds of the cultivar 'Snow Cloud' were sown in No. 406 plug trays (plug size:1.5 X 1.5 X 2.0 cm, 3.0 ml by volume) containing a commercial peat-lite mix (Michigan Peat Co., Sandusky, MI). Plug trays were covered with clear polyethylene and placed under constant light at 200 micro-mol$\cdot s^{-1} \cdot m^{-2}$ (17.3 mol$\cdot day^{-1} \cdot m^{-2}$) and a 23°C constant temperature. The polyethylene was removed after 5 days and the plug trays were placed on capillary matting. Ten days after sowing, the seedlings were transplanted into 9 cm pots (345 ml by volume) filled with the same commercial peat-lite mix. Plants were irrigated as necessary to prevent water stress and fertilized with 10.7 mM nitrogen and 3.18 mM potassium from $CaNO_3$ and $KNO_3$ at each irrigation.

The seedlings were placed in 1 of 5 walk in 5.85 $m^2$ growth chambers maintained at either a constant 10°, 15°, 20°, 25° or 30°C air temperature. Seedlings were placed at a spacing of 123.5 plants $m^{-2}$. Each chamber was maintained at an 18 hour photoperiod and divided to provide photosynthetic photon flux (PPF) levels of 100 or 200 micro-mol$\cdot s^{-1} \cdot m^{-2}$ (6.5 and 13 mol$\cdot day^{-1} \cdot m^{-2}$, respectively). Plants were moved among growth chambers to supply a factorial combination of 5 day temperatures (DT), 5 night temperatures (NT) and 2 PPF levels. Changes between NT and DT corresponded with the change in photoperiod.

Leaf temperatures were measured with a Sensortek BAT-12R meter and Omega copper-constanstan thermocouple. The difference between temperature set points and leaf temperature was less than 1.5°C; temperature set points were used for data analysis. PPF was provided by a mixture of cool-white fluorescent and incandescent bulbs (input wattage 90:10, respectively) and PPF levels were adjusted by raising the lamps to maintain the proper PPF at the canopy top. PPF levels were determined with a LI-COR LI-185A meter and LI-190SB quantum sensor.

Data were collected at time of transplant and every five days thereafter until the plants flowered. The experiment was terminated 120 days after sowing the seed. Data collected included the number of unfolded leaves on the mainstem excluding any leaves that formed on lateral side shoots, and the node number at which flowering occurred. A leaf was considered unfolded when it had attained a minimum width of 0.5 cm. Multiple linear regression analysis was used to determine the relationship between temperature and leaf unfolding. Equations were developed for each PPF level and used to create isopleth plots for leaf unfolding at different night and day temperature combinations.

Leaf unfolding rate (Figure 1) was a function of average daily temperature, although the rates were not the same for each PPF level. At 10° and 30°, plants at both irradiances had similar leaf unfolding rates, but at an irradiance of 13 $mol \cdot day^{-1} \cdot m^{-2}$, plants unfolded leaves at a faster rate for the mid range temperatures. At 20° constant temperature, plants unfolded leaves 21.6% faster at 13 $mol \cdot day^{-1} \cdot m^{-2}$ than at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$.

The number of nodes to first flower was influenced by PPF level and temperature (Table 1). All plants grown at 10° constant temperature and those grown at 15° nights and 10° days at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ did not flower within 120 days from sowing. Plants in the remaining treatments initiated flower buds when they attained a minimum of 13 nodes on the mainstem. All plants formed the same number of nodes before initiation except those grown at a constant 30° temperature, and those grown at 20° nights and 30° days at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$. These plants produced up to 6 additional nodes before initiation.

Unlike Easter lily or chrysanthemum, petunia initiates flowers axilarily while the terminal meristem remains vegetative. As a result, additional leaves unfold above the flower bud as it develops. All plants unfolded an average of 18.8 leaves by anthesis except those grown at a constant 30° temperature, and those grown at 20° nights and 30° days at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ (Table 2). These plants unfolded as many as 6 additional leaves before anthesis.

Increased light intensity accelerated growth rate in peas (Vince, 1964). This acceleration occurred at all stages of leaf development: initiation of the leaf primordia, enlargement and maturation. Similar results were obtained with lettuce (Verkerk and Spitter, 1973). Little difference in leaf unfolding was found between temperatures in the range 9° NT and 17° DT to 17° NT and 25° DT for lettuce grown in the greenhouse under low light conditions of winter. However, leaf unfolding increased as the light level was increased. This increase led to the conclusion that light was the more important factor in determining leaf unfolding in lettuce.

Heins et al. (1982) reported that increased growth rate of Easter lilies at high irradiances could be explained by the resulting increase in leaf temperature at the higher irradiance. Irradiance had no effect on leaf unfolding rate which was later determined to be a linear function of average daily temperature (Karlsson et al., 1988). The difference between leaf temperature and temperature setpoints in this study was less than 1.5°. We therefore concluded that the increased rate of leaf unfolding in petunia was due to the increased PPF as seen in lettuce (Verkerk and Spitter, 1973).

Minimum node number before initiation has been detected in other plants. Armitage (1984) reported 15 nodes were required before flower buds were initiated in the seed geranium cultivar 'Sooner Red'. Explanations were offered for minimum node number before initiation (Holdsworth, 1956;

Kester, 1976). The first was that the plant morphologically must initiate a set number of leaf primordia and obtain a degree of anatomical maturity. Secondly, it was suggested that vegetative growth represented unfolding of parts already present in the embryo. Lastly, photoperiodic or other floral induction simply takes time.

High temperatures and low light levels induced flower bud abortion in the plants used in this study (Table 3). When bud abortion was taken into account, plants grown at 20° nights and 30° days at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ initiated their first bud at the same node as the other plants, but the plants grown at 30° constant temperature at either PPF did not. These plants may have initiated between the 13th and 15th node like the rest, but these buds aborted before reaching the visible bud stage and were not detected.

The increase in leaf number on the mainstem of plants grown at a constant 30° and those grown at 20° nights and 30° days at 6.5 $mol \cdot day^{-1} \cdot m^{-2}$ can likewise be attributed to flower bud abortion. Since the terminal meristem remains vegetative, it continues to produce leaves while the plant produces and aborts several flower buds. When the plant develops a flower, additional leaves have formed.

Isopleth plots were developed from equations describing leaf unfolding rates for various night and day temperatures at an 18 hour photoperiod (Figure 2). Different night and day temperature combinations can be selected from the plots when the the necessary leaf unfolding rate is known for petunias between the stages of transplant and flower. The plants will produce an average of 18.8 leaves when reaching anthesis under an 18 hour photoperiod except at the highest temperatures (Table 2). However, extreme temperatures such as those that would induce bud abortion are not used in commercial production and can be dismissed.

Petunias must form a minimum of 13 nodes before initiating a flower and will form an average of 18.8 leaves by anthesis when grown at an 18 hour photoperiod. Leaf unfolding rates were found to be an average temperature response within a given PPF level. This information can be used by the commercial grower as an aid in timing the crop if adequate growing practices are used, since other factors such as water availability and nutrition can affect plant responses to irradiance and temperature. Under normal conditions, leaf unfolding provides a good indication of stage of development for petunia.

## Literature Cited

Armitage, A. M. 1984. Effect of leaf number, leaf position and node number on flowering time in hybrid geranium. J. Amer. Soc. Hort. Sci. 109(2):233-236.

Blaney, L. T., A. N. Roberts, and P. Lin. 1967. Timing Easter lilies. Flor. Rev. 140:19.

Collins, W. J. and J. H. Wilson. 1974. Node of flowering as an index of plant development. Ann. Bot. 38:175-180.

Heins, R. D., H. B. Pemberton, and H. F. Wilkins. 1982. The influence of light on lily (Lilium longiflorum Thunb.). I. Influence of light intensity on plant development. J. Amer. Soc. Hort. Sci. 107(2):330-335.

Holdsworth, M. 1956. The concept of minimum leaf number. J. Exp. Bot. 7(21):395-409.

Karlsson, M. G., R. D. Heins, and J. E. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113(1):70-74.

Kester, D. E. 1976. The relationship of juvenility to plant propagation. Proc. Int. Plant Prop. Soc. 26:71-84.

Leopold, A. C. and F. S. Guernsey. 1953. Flower initiation in 'Alaska' pea. I. Evidence as to the role of auxin. Am. J. Bot. 40:46-50.

McKinney, H. H. and W. J. Sando. 1944. Earliness and seasonal growth habit in wheat. J. Heredity 24:169-179.

Verkerk, K. and Spitter, C. J. Th. 1973. Effects of light and temperature on lettuce seedlings. Neth. J. Agric. Sci. 21:102-109.

Vince, D. 1964. Photomorphogenesis in plant stems. Biol. Rev. 39:506-536.

Wilkins, H.F. and A. N. Roberts. 1969. Leaf counting- A new concept in timing Easter lilies. Minn. State Flor. Bul. 18(6):10-13.

Table 1. Mean number of nodes required on the mainstem to initiate the first flower for *Petunia x hybrida* 'Snow Cloud'.

| Night Temperature (°C) | Day Temperature (°C) 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|
| 13 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | NF | 14.6 | 13.6 | 14.2 | 13.4 |
| 15 | 14.2 | 13.8 | 14.6 | 14.0 | 13.2 |
| 20 | 14.6 | 14.0 | 13.4 | 14.6 | 14.6 |
| 25 | 14.0 | 14.4 | 13.6 | 14.2 | 14.8 |
| 30 | 13.8 | 13.6 | 14.0 | 13.2 | 17.8 |
| 6.5 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | NF | 14.6 | 14.2 | 14.0 | 15.4 |
| 15 | NF | 15.0 | 15.0 | 14.2 | 14.6 |
| 20 | 15.0 | 15.0 | 14.6 | 14.2 | 16.0 |
| 25 | 14.8 | 14.2 | 14.0 | 14.6 | 15.4 |
| 30 | 14.2 | 14.6 | 14.6 | 14.8 | 18.4 |

| Significance | |
|---|---|
| NT | * |
| DT | *** |
| Irradiance | *** |
| NT X DT | *** |
| NT X Irradiance | NS |
| DT X Irradiance | NS |
| NT X DT X Irradiance | NS |

---

[NS, *, ***] Nonsignificant, significant at the 5% and .1% levels, respectively.

[NF] Did not flower over the course of the experiment.

Table 2. Mean number of leaves formed on the mainstem at anthesis in <u>Petunia x hybrida</u> 'Snow Cloud'.

| Night Temperature (°C) | Day Temperature (°C) | | | | |
|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 |
| 13 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | NF | 17.6 | 18.4 | 19.6 | 19.2 |
| 15 | 17.6 | 18.2 | 19.6 | 19.0 | 19.8 |
| 20 | 18.2 | 17.8 | 18.6 | 19.6 | 19.0 |
| 25 | 18.2 | 19.4 | 19.2 | 19.4 | 19.4 |
| 30 | 18.0 | 18.2 | 18.4 | 17.8 | 23.0 |
| 6.5 mol·day$^{-1}$·m$^{-2}$ | | | | | |
| 10 | NF | 18.0 | 18.4 | 18.4 | 19.2 |
| 15 | NF | 18.2 | 18.4 | 18.4 | 19.0 |
| 20 | 18.4 | 18.8 | 18.8 | 18.4 | 20.2 |
| 25 | 18.2 | 19.0 | 19.0 | 18.8 | 18.6 |
| 30 | 17.8 | 18.8 | 18.6 | 18.6 | 23.4 |

| Significance | |
|---|---|
| NT | *** |
| DT | *** |
| Irradiance | *** |
| NT X DT | *** |
| NT X Irradiance | NS |
| DT X Irradiance | NS |
| NT X DT X Irradiance | NS |

NS, *** Nonsignificant and significant at the .1% level, respectively.

NF Did not flower over the course of the experiment.

Table 3. Mean number of buds aborted by <u>Petunia x hybrida</u> 'Snow Cloud' at an irradiance of 6.5 mol·day$^{-1}$·m$^{-2}$.

| Night Temp (°C) | Day Temp (°C) | Aborted Buds |
|---|---|---|
| 10 | 30 | 0.4 ± 0.5[z] |
| 15 | 30 | 0.4 ± 0.9 |
| 20 | 30 | 1.2 ± 1.1 |
| 25 | 30 | 0.3 ± 0.5 |
| 30 | 30 | 2.0 ± 1.9 |

[z] Mean ± SE.

Figure 1. Rate of leaf unfolding of Petunia x hybrida 'Snow Cloud' in response to average daily temperature between 10° and 30°C from 10 days after sowing to anthesis for:

a) 13 $mol \cdot day^{-1} \cdot m^{-2}$

(Leaves per Day = $-0.2737+(0.05059*AVG)-(0.000722*AVG^2)$)

$r^2=.922$

b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$

(Leaves per Day = $-0.09315+(0.02322*AVG)$)

$r^2=.947$

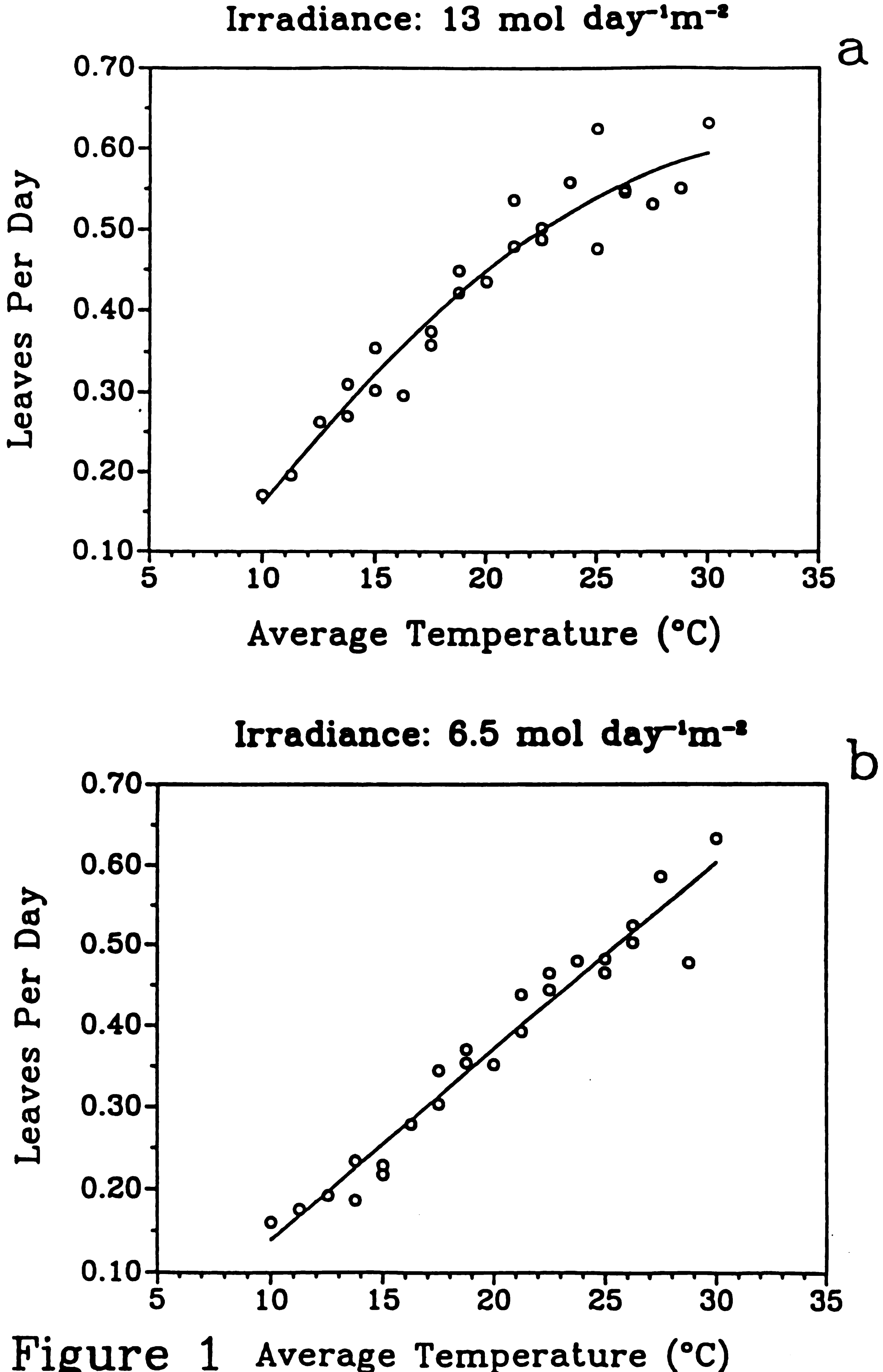
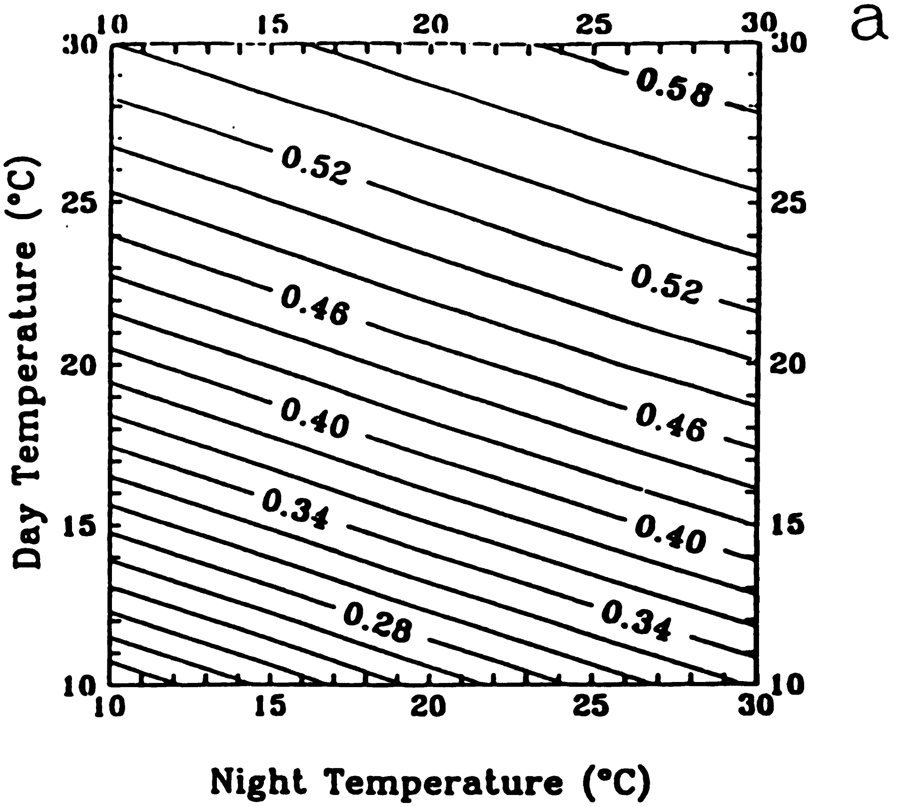

Irradiance: 13 mol day⁻¹m⁻²
a
Leaves Per Day
0.70
0.60
0.50
0.40
0.30
0.20
0.10
5
10
15
20
25
30
35
Average Temperature (°C)
Irradiance: 6.5 mol day⁻¹m⁻²
b
Leaves Per Day
0.70
0.60
0.50
0.40
0.30
0.20
0.10
5
10
15
20
25
30
35
Average Temperature (°C)

Figure 1

Figure 2. Isopleth plots of leaves unfolded between 10 days after sowing and anthesis for varying combinations of night and day temperature between 10° and 30°C for Petunia x hybrida 'Snow Cloud' at a) 13 $mol \cdot day^{-1} \cdot m^{-2}$ and b) 6.5 $mol \cdot day^{-1} \cdot m^{-2}$.

Irradiance: 13 mol·day$^{-1}$·m$^{-2}$



Irradiance: 6.5 mol·day$^{-1}$·m$^{-2}$

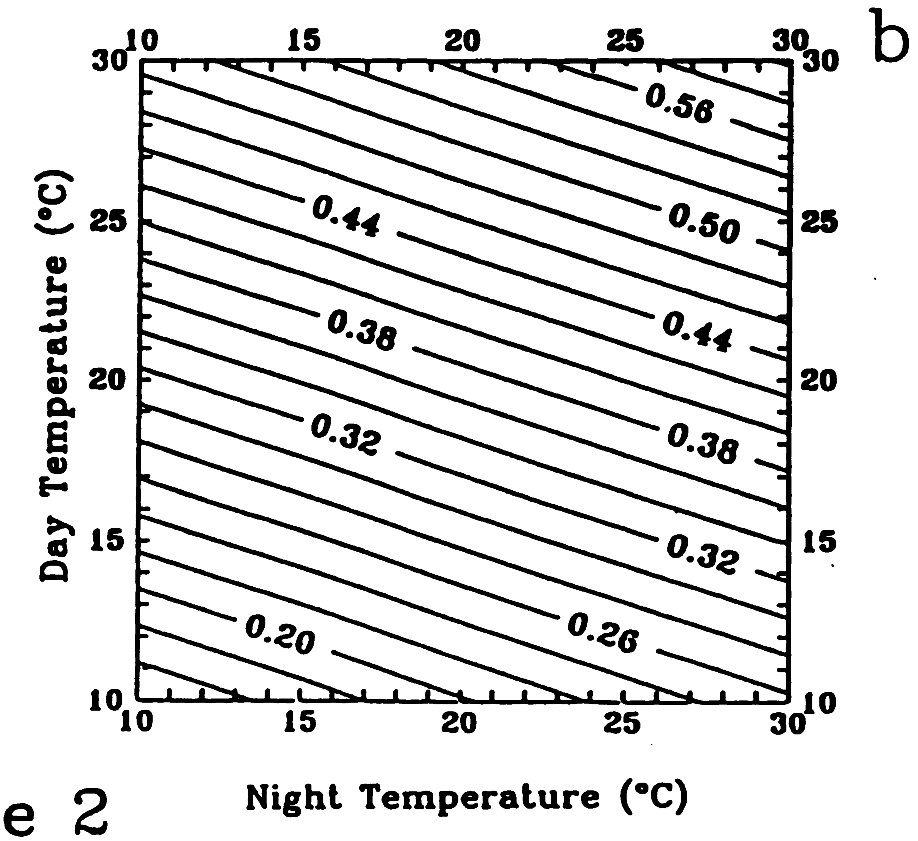


Figure 2