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GROWTH AND DEVELOPMENTAL RESPONSES
OF HYBRID GERANIUMS TO
LIGHT AND TEMPERATURE

by

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ABSTRACT

GROWTH AND DEVELOPMENTAL RESPONSES OF HYBRID GERANIUMS TO LIGHT AND TEMPERATURE

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Vegetative and reproductive development of _Pelargonium hortorum_ - Bailey in response to: time, irradiance, day and night temperature, and supplemental lighting was studied. Flower development in response to supplemental light was found to be influenced by irradiance level, temperature and duration of irradiance, and age of the plants. Days to anthesis was more closely correlated with mean daily irradiance (r = 0.921) than with total cumulative irradiance (r = -0.863). A threshold irradiance was necessary for simultaneous reductions in days to flower and number of nodes in 'Ringo Scarlet'. A hypothesis for the high irradiance phenomenon is presented.

Prediction equations were developed for days to initiation, visible bud, and anthesis. Irradiance and day temperature were shown to have the greatest influence on flower initiation and development to visible bud, while temperature alone was most contributory from visible bud to anthesis. Three-dimensional response surface plots were developed to graphically represent the functions. Prediction equations were also developed for total plant height, leaf area, and shoot fresh and dry weight as functions of time, irradiance, and day and night temperatures.

Guidance Committee:

The paper format is adopted for this dissertation in accordance with departmental and university regulations. All sections are to be submitted to the _Journal of the American Society for Horticultural Science_ for publication.

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INTRODUCTION

Hybrid geraniums (_Pelargonium hortorum_ - Bailey) and zonal geraniums (_Pelargonium hortorum_ - Zonale) are among the most popular floriculture products in the world today. According to the USDA floriculture survey (71), nearly 65 million dollars worth of geraniums were produced in the United States in 1984, and a value of nearly 10 million dollars was produced in Michigan alone. Only Ohio and Pennsylvania exceed Michigan in the quantity of geraniums produced annually.

Since the first development of seed propagated geraniums (Nittany Lion Red) in the 1960's (30), continuous improvements in the cultivars and their earliness of flowering has occurred. The market for seed-propagated geraniums has been expanding steadily because of decreased costs of seed compared to the cost of cuttings, decreased loss as a result of diseases in stock plants and rooting beds, decreased plant size which yields increased production density, and increased garden performance. Separate markets are developing for seed and cutting-propagated geraniums. The zonals (cutting-propagated) are being used more as specimen and container plants while the hybrids (seed-propagated) are being used largely in ground beds and for large plantings.

Currently, many advances are being realized in the production of hybrid geraniums. The advent of the plug production system (small individual containers or cells attached together in one sheet), mechanical seeders, improved seed germination, supplemental lighting, and the application of the computer to control greenhouse conditions, all have resulted in many important advances in the way we produce hybrid geraniums. The usefulness of the computers is dependent on the amount of information available which defines the reproductive and vegetative responses to the greenhouse environment. It was the focus of this study to investigate the physiological responses of hybrid geraniums to light and temperature and to begin to develop functional models of these responses.

LITERATURE REVIEW:

This review of literature focuses on the influences of environmental factors, primarily light and temperature, on the vegetative and reproductive development of hybrid geraniums. Emphasis is given to information useful in developing a clearer understanding of the vegetative and reproductive responses to environmental factors at different stages of development. Information useful to the development of functional plant growth models is included with an eye toward application in computer-controlled greenhouses.

HISTORY OF PRODUCTION TECHNIQUES:

The introduction of the first popular seed geranium 'Nittany Lion Red', by Craig (30) started a revolution in the geranium industry. Many shifts in cultural practices and cultivars have occurred since this event. While the first cultivars took from 120 to 140 days to flower from sowing, improved cultivars and selections reduced the flowering time to 100 to 120 days (5). It was found that with the application of the growth regulator (2-chloroethyl) trimethylammonium chloride (cycocel), the plant size could be controlled and flowering enhanced by 5 to 7 days (24). The use of this growth regulator also allowed for increased plant densities in the greenhouse. In the early 1980's plug production, the use of supplemental lighting, and further improvements in cultivars made it possible to produce finished marketable plants in 80 to 100 days. The application of silver thiosulfate prior to the anthesis (59), has further increased the market quality of the hybrid geranium. Improved cultivars, including seed-propagated tetraploids (zonal types), increased use of supplemental lighting, and the use of computers (operating on models based on physiological responses) to control greenhouses will likely reduce the time to produce a quality product by an additional 20 to 30 days. This will mean significant increases in profit for producers, better performance to the consumers, and improved energy savings in this day of environmental concerns.

ENVIRONMENTAL INFLUENCES:

The two most important factors that are both highly influential and yet manageable at least to a certain extent, in the production of hybrid geraniums, are temperature and light. Temperature responses can be divided into day and night temperatures. Light responses fall into two physiological catagories, photosynthetic and photomorphogenic.

Photosynthetic responses deal largely with influences of irradiance levels on the growth and energy supply to the plant. The responses are usually associated with higher irradiance levels. In photosynthetic studies, Armitage (2, 6) has shown that the light compensation point in hybrid geraniums is temperature dependent. At a temperature of 20 ^{o}C, the light compensation point is near 46 μmols m^{-1} $^{-2}$, and at 32 ^{o}C, the light compensation point is at about 75 μmols m^{-1} $^{-2}$. The light saturation point is about 1100 μmols m^{-1} $^{-2}$ at 32 ^{o}C but about 700 μmols m^{-1} $^{-2}$ at temperatures below 15 °C. Thus, at low temperatures, less respiration and less photosynthesis are occurring.

Photomorphogenic responses are generally considered to be growth responses to the light environment and are nearly always independent of photosynthesis but are not easily seperated. However, they are somewhat dependent on photosynthetic products for the energies needed to perform the photomorphogenic responses. Photomorphogenic responses have been defined by Wareing and Phillips (74) as "the developmental strategies plants adopt when growing in the light." These responses have been associated but not always strictly related to the phytochrome system and are usually considered to occur at relatively low irradiance levels. However, a number of responses have been associated with high irradiance (43, 55). From studies using low irradiance, the geranium is considered a day-neutral plant (64). However, responses to extended periods of high levels of irradiance have resulted in earlier flowering with decreased numbers of nodes to the first flower (7, 25, 27, 28, 63).

Irradiance and Temperature Effects on Flowering

Early flowering responses of hybrid geraniums have been associated with the application of high levels of irradiation both supplementally in the greenhouse (2, 7, 8, 9, 25, 27, 35, 63, 70) and artificially in the growth chamber (2, 13, 77, 78). Photosynthetic photon flux (PPF) and cumulative photosynthetic photon flux (CPPF) in the 400-700 nm range have been related to the time from seeding to anthesis (7, 31, 35, 70). Craig and Walker (31) showed that flowering occurred naturally at a nearly constant total CPPF. They suggest the endogenous production of a hypothetical substance which influences floral initiation. The substance is independent of the photoperiod and the number of days from germination but dependent on cumulative solar energy and temperature. Using low levels of cumulative supplemental irradiation, Carpenter and Rodrequez (27) found no reduction in the time to flower from the first four weeks of lighting, but by extending the lighting an additional two weeks, a 20 to 30 day reduction in the time to flower was obtained. In addition, the number of nodes to the first flower was reduced by two to six. Likewise, Norton (63) produced flowering plants 3 weeks earlier by applying 67 days of supplemental irradiation to young plants. Armitage and Tsujita (7) indicated that high pressure sodium (HPS) light was more effective in reducing time to flower than low pressure sodium (LPS) light. They also found in their spring crop that CPPF was significantly correlated to days to flower. Their results indicated that an intensity by duration interaction may exist which is cultivar specific. In a study reported by Erickson et al. (35) 41 to 65 percent of the variability in days to flower was related to the CPPF. However, CPPF when measured from sowing to flowering may not be as important as the irradiation received prior to the visible bud stage. In the work of Armitage (2), the time to visible bud was negatively correlated to irradiance at a given temperature whereas after the visible bud stage irradiance was no longer significant but temperature was. Heins (45) has also demonstrated a greater influence of temperature than irradiance on the time from visible bud to flowering.

An early flowering potential has been observed when high irradiance was coupled with high temperatures. Mastalerz (56) produced flowers on the cultivar (Carefree White in 60 days using a growth chamber with flourescent light) at intensities of about 2000 foot-candles (approximately 350 $\mu mols^{-1} m^{-2}$) for 18 hours a day. Armitage (2) observed visible buds as early as 33 days after sowing, and flowering in nearly half the normal production time, 65 days, by applying continuous irradiation at a PPF of 375 $\mu mols^{-1} m^{-2}$ and at a temperature of 30 ^{o}C. Randolph and Law (77), in 1967, noticed macroscopic buds in 21 days on plants exposed to continuous high irradiance levels. White (78) has observed macroscopic buds 36 days after treatment on the cultivar Red Elite when irradiated at approximately 390 $\mu mols^{-1} m^{-2}$ and temperatures between 18 and 22.5 ^{o}C. Flowering occurred in the cultivar Cherry Diamond 29 days from sowing when supplemental irradiation was applied during the night hours and when daily high temperatures ranged from 30 ^{o}C to 37 ^{o}C and night lows were above 23 ^{o}C (13, 15).

To date no clear definitions or systematic studies of the factors which are involved in producing the early flowering responses in geraniums have been advanced. In many species high irradiance levels have been known to influence the induction of flowers. African violets

(*Saintpaulia*) (32, 53), *Rudbeckia* (62), snapdragon (*Antirrhinum*) (69), and roses (*Rosa hybrida L.*) (10, 28, 48, 61), all show increased flowering responses to treatments of high irradiance. Floral initiation has been observed under prolonged periods of high irradiance levels in *Anagallis arvensis L.* (65), *Rhododendron sp.* (Azalea) (18), and *Alstromeria* (44, 54).

In photomorphogenic studies of *Brassica campestris* (36), *Pharbitis nil.* (37, 68), and *Sinapsis alba.* (19), increased flowering responses were found to occur under treatments of high irradiance. Bodson et al. (19), studying the effects of high irradiance on *S. alba*, suggest that light sensing reactions in addition to photosynthesis are likely to contribute to the induction of flowers.

The phytochrome system and phytochrome intermediates have been implicated in high irradiance response (34, 72). In the early studies of photoinduction, Hamner (41) found that high irradiance levels, over long time periods, were necessary for expression of the flowering response in soybean (*Glycine max*). Conversely, in the long day plant, radish (*Raphanus sativus L.*), low light, crowding, and a high far-red to red ratio yielded increased flowering and decreased root development (75). Shading and decreases in irradiance have decreased flowering in geraniums and snapdragons (39, 69) as well as in Leucospermum (49).

In geraniums, some incidental observations suggest that flower induction may possibly be a high irradiance response (HIIR) (15). Reportedly (11), a grower in New York removed some of the upper foliage from vegetative young plants to allow the light to get down into the shoot tip of the plant. He claimed earlier and more uniform flowering from this practice. Riese (66) suggested that decreased plant size and spreading of the leaves, as a result of application of cycocel, allows increased light into apical meristem of the plant. He suggested that increased light to the center of the plant is the explanation for the increased earliness resulting from cycocel sprays. In a study of planting time and flowering response (3) little additional earliness was achieved from earlier sowings. Sowing as much as 7 weeks earlier resulted in only 2 weeks earlier flowering. Ambient radiation and daily irradiance periods increased toward spring so photosynthetic increases could be responsible for the accelerated development. Note that each cultivar aged as spring approached. Also, day temperatures became higher in the greenhouse as spring approached thus influencing growth rates.

Irradiance levels have been known to influence induction of flowers since the studies of Hamner (41). In *B. campestris* flowering was related to an interaction of the irradiance level and irradiance period (36). Maximum responses occurred when the irradiance levels were the highest and the irradiance period the longest. Schneider et al. (67) demonstrated that a minimum intensity of light during the long day was necessary to produce flowers *Hyoscyamus niger*. With increased intensity, there was an increased flowering response. In geraniums, the effects of varying levels of irradiation on growth and flowering have been studied by a number of researchers (2, 7, 8, 15, 25, 27, 63, 70). The effects on geraniums appear to be similar to effects observed for other species. In nearly all cases, the greatest responses were observed when the irradiance was the highest and the length of irradiance was the greatest.

Temperature is known to influence the response of many plants to inductive stimuli (12, 72). It is well established that photoperiodic responses can be temperature dependent. In *B. campestris* Cv. ceres, the most flowering occurred at 25 °C (36). The percentage of flowering increase with increases in both the intensity and the duration of the irradiance at that temperature. Murneek (62) studying the long-day plant *Rudbeckia bicolor*, concluded that high temperatures may substitute for long days in induction. In geraniums Tsujita (70), Armitage (6) and White (79) have all shown that higher temperatures can decrease time to flowering. Additional earlier flowering was obtained when the plants were irradiated continuously at high temperatures (2, 15, 77).

Duration of inductive conditions is of importance, too. Hamner (41) has shown that the duration of irradiance treatment is critical to changing the reproductive status of soybeans. In many photoperiod studies, it is documented that a sufficient duration or number of cycles (23, 67) of inductive conditions are necessary for floral initiation. In some plants, e.g. a cultivar of *B. campestris*, only one day of high irradiance is necessary for flowering (36, 72).

Other cultivars and species require several days (12) to induce flowering. Armitage (2) found in a limited study, that a treatment as short as nine days at high irradiance levels and high temperatures can result in more rapid flowering in geraniums. Previously, it was thought that four to six weeks of continuous lighting was necessary to influence the time to flower and in some cases the node number (8, 13, 25, 26, 48, 62).

Juvenility, which insures that a plant reaches a given stage before it is capable of responding to reproductive stimuli, exists in many herbaceous species. This condition, often called "ripeness-to-flower", is discussed in detail in the texts of Vince-Prue (72) and Bernier et al. (12). A reduction in the extent of the conditions necessary to induce flowering has frequently been observed due to aging (12, 19, 41).

The phenomenon of juvenility as it relates to flowering responses to high irradiance has also been studied in several other species. In *Pharabis nil* (37) the older the plants the more responsive they became. In *Sinapsis alba* (19) the number of long-day cycles required for induction is 6 to 7 cycles at an age of 15 days, 2 cycles at 30 days, and 1 cycle at 60 days. At 8 days, only a minimal response was observed. In a study of geraniums, by Armitage, (1) it was found that at least 6 leaves were necessary to induce flowering in the cultivar Sooner Red. In the short-day plant *Chrysanthemum morifolium*, different cultivars have been shown to vary in the time required to overcome the juvenile period (12). Also, in a specialized study of *Pisum sativum* (Garden Pea) the level of a genetically controlled inhibition of flowering was found to decrease as the plants aged (12).

Ripeness-to-flower may also be a factor in the responses of geraniums. It is thus apparent that any possible effects of age and responsiveness to treatment must be considered when examining flowering responses in geraniums.

Influences of Light and Temperature on Vegetative Developments

In addition to the reproductive responses to light and temperature, vegetative responses are known to influence height, leaf area, and fresh and dry weight.

Total plant height has been shown to be increased by limited PPF (39, 79), and to be decreased by applications of supplemental irradiation (25, 27, 70). Moderate night temperatures have been shown to increase plant height (1, 26, 35, 52, 57). Tsujita (70) obtained taller plants in the cultivar 'Encounter Red' at a NT of 17° C than at 13° C, and Konjoian and Tayama (52) obtained the tallest plants at night temperatures of 16° C. While shorter plants develop under higher and lower temperatures, earlier flowering occurrs at the higher temperatures. Carpenter and Carlson (26) produced the tallest plants with day temperatures of 22-24° C and low night temperatures.

White and Warrington (79), examining the effects of split-night-temperatures, found no differences in flowering, but in view of the other factors the range of temperatures studied in their work were not sufficient to show night temperature responses. In a comparison of 14 cultivars grown in Michigan (DT = 21 + 3°C) and in Georgia (DT = 26 + 3°C) (4), plants grown under the warmer days in Georgia averaged 4.3 cm taller. Merritt and Kohl (57) have shown that, in the cultivar 'Mustang', both soil temperature and irradiance period, as well as their interaction, had a significant influence on plant height during vegetative development. The tallest plants were produced under long irradiance periods (13 hr) with little or no influence of temperature. However, under short irradiance periods (9 hr), taller plants were produced in the cooler (18°C) temperatures. It appears that, under short days, mean daily irradiance became low, and, as a result, elongation was increased and flowering delayed.

Leaf area is influenced by a number of factors. White and Warrington (79) showed that in the absence of growth regulators, high light significantly decreased leaf area as did high DT and low NT. The lowest leaf area was obtained at DT = 20°C and NT = 20°C. CCC treated plants tended to show the same temperature responses, but the differences were not significant. Total leaf area increased over time in what appears to be a quadratic form in a study of Merritt and Kohl (57). In some instances, short irradiance periods (9 hr) also decreased leaf area. Armitage (2) demonstrated that increasing DT resulted in decreased leaf thickness and number of palisade layers. Specific leaf weight increased with increased PPF and decreased with increased temperature.

Thus, we see that the geranium leaves are very responsive to the environment in which they are developing. The partitioning of photosynthates during the organogenesis is apparently complex.

Leaf area has also been shown to be important to flower development. Armitage (1) suggests that a critical leaf area is necessary to produce flowers. This is similar to the hypothesis of this author (14). Accordingly high irradiance must be received by a plant of sufficient maturity before initiation of flowers can occur.

If one wishes to limit leaf area in geraniums, growth regulators have been shown to be very effective (60).

Fresh and dry weight appear to be greatly influenced by temperature. However, low irradiance levels have been reported to yield higher fresh weight (27, 39) than high irradiances. Supplemental irradiance has been shown in some cases to increase fresh weight where ambient light was limited (78). Specific leaf weight is reported to increase with increased irradiance (6).

White and Warrington (78) have shown a build-up of carbohydrates at low night tempertures in the form of sugars and starch throughout the plant. This build-up may account for some of the weight gain. Armitage et al. (2) found that, as temperatures increased, the specific leaf weight decreased as did leaf thickness. It is thought that the accumulation of carbohydrates increased at low DT, resulting in increased dry weight as described by White and Warrington (78). Short irradiance periods coupled with high temperatures have also resulted in decreases in shoot dry weight (77).

The observations of reproductive and vegetative responses to irradiance and temperature are thus spread over a wide range of experimental conditions and stages of development. It is apparent that irradiance and day and night temperatures are among the most influential factors involved in the responses. It has, then, been the focus of this study to examine systematically the influences of temperatures and light and to define the physiological responses to these factors (acting independently and interactively), and to produce functional models of these responses.

PLANT GROWTH MODELING:

Plant growth modeling can be said to have begun with Blackman (16) and the application of the compound interest law to plant growth. This was applicable to single factor studies under controlled conditions. However, in studies involving two or more factors, more sophisticated approaches of collecting data and defining responses are necessary. Gardiner et al. (38) demonstrated that the factorial approach of collecting data to define demonstrated responses is very efficient. The more elaborate the desired equation used to describe the response, the more levels of each variable are required (20). Over extensive regions, a high degree equation can be used to represent the full response surface. The fitting could require a very large number of experimental units using the factorial method. To cover the experimental region with a minimal number of treatments, Box and Hunter (21) and Gardner et al. (38) have developed a central composite design. In this design the number of treatments required is $2^k + 2k + 1$ for k factors. Thus, for 3 factors, 15 treatment combinations are required. Careful attention is needed in selecting the central location and the distance of the points from the origin. According to Box (20), some important considerations to be met when examining a composite design are: 1. The design should permit the errors of estimate of points on the fitted surface to be small. 2. The biases in the estimated coefficients, which may occur if the assumed equation were representationally inadequate, should be small. 3. Provisions should be made to estimate certain coefficients, or contributions of them, and those of higher order than in the assumed form of the equation fitted.

Box and Hunter (21) have further proposed designs which provide constant variance of the estimated coefficients at points equidistant from the center of the experimental region. In this design, the reliability of the estimated response at any point $X_1 .....X_k$ depends on the distance of the points from the center and not on the direction. They are thus termed rotatable designs. They are not affected by rotation with respect to the origin. They are geometrically very similar to the composite design except that the points along the axes are required to be at $+ 2^{k/4}$ units out. This is 1.68 with 3 variables, and 1.414 with 2 variables.

In both the central composite design and the rotatable design, the coding is the same and the central unit can be replicated to find the standard error. Thus the error will have $N^1 - 1$ degrees of freedom where N is the number of replications at the central unit.

Davies (33) has presented an application of the central composite design in industrial experiments. He indicated that the central composite design is among the most efficient in determining the independent and interactive effects of the dependent variables. Hill and Hunter (46) presented a useful review of the use of response surface methods with special emphasis on their application and methodology. In their review, the versatility and application to a number of interacting experimental conditions was clear. Box and Youle (22) have further extended the application and the exploration of the response surface techniques. These researchers showed that studying the form of the developed empirical surfaces can shed light on the process and can make possible development of a theory of the process.

Hinchen (47) depicted graphically the application of multiple regression equations as they apply in production chemistry. Much emphasis was placed on the expected yields under a given set of conditions. Kissell and Marshall (51) studied the multi-factor resonses of cake quality in response to the ratios of the basic ingredients and effectively modeled results using the response surface techniques.

In biological response surface techniques, using the central composite design, calf nutrition was studied by Chandler et al. (29). They developed complex response surface models to a number of interacting nutritional factors. In plant sciences, the nutritional influence of copper, iron, and molybedenum on the growth of lettuce has been effectively studied using the response surface technique (40). Metcalf et al. (58) used the multiple regression and response surface techniques to define and predict the survival and root growth of wheat and barley from freezing and drought stress.

In floriculture, Hammer and Langhans (42) used response surface techniques to study the effects of irradiance, root temperature, day length, and air day and night temperature in controlled environmental growth chambers on _Helianthus annuns_ and _Zinnia elegans_. Fresh and dry weight of shoots and roots, and total dry weight for _H. annuns_ were successfully modeled using response surfaces. No significant model could be fitted to the _Z. elegans_ data. Armitage et al. (6) fitted response surfaces to time-to-flower, dry weight, leaf areas, vegetative height, and chlorophyll and anthocyanin contents in Tagets patula, using variables of irradiance and day and night temperatures. Karlsson (50) modeling the growth of _Chrysanthemum morifolium_, effectively used the central composite design and response surface techniques to develop a functional relationship between irradiance and day and night temperatures on the time to flower, shoot length, flower size, and dry weight. In this work, a discussion of the classical and functional approaches to plant growth modeling is presented. Strong emphasis is made on the partitioning of the photosynthetic products to different plant parts as expressed in the dry weight models.

It is thus clear that the use of the central composite design, multiple regression techniques, and response surfaces, are well-suited to the study of growth responses of hybrid geraniums to irradiance and day and night temperatures.

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SECTION I

THE EFFECTS OF DAILY SUPPLEMENTAL IRRADIANCE PERIOD AND IRRADIANCE LEVELS ON DAYS TO FLOWER AND NODE NUMBER IN HYBRID GERANIUMS

ABSTRACT:

Supplemental lighting of greenhouse-grown hybrid geraniums (*Pelargoium hortorum* - Bailey 'Ringo Scarlet') using high pressure sodium lamps reduced time to anthesis. Irradiances (Photosynthetic Photon Flux PPF in the 400-700 nm range) of 45 $\mu\text{mols}^{-1}\ \text{m}^{-2}$ or higher decreased time to anthesis when supplied for 18 or more hours a day or as a 4 or 12 hr night break. Supplemental irradiance treatments of 65 $\mu\text{mols}^{-1}\ \text{m}^{-2}$ for 14, 28, and 42 days given to 10-day-old plants reduced time to anthesis by 9.6, 43.2, and 50.4 days, respectively. When supplied to 40-day-old plants the time to anthesis was reduced by 22.8, 25.4, and 26.5 days respectively. When the application of supplemental light was delayed, equal delays in the flowering response were observed. Mean daily cumulative photosynthetic photon flux (CPPF) provided a better correlation to days to flower than did total CPPF. Ninety-three percent of the variation in days to anthesis and 87% of the variation in node numbers could be described as functions of mean daily CPPF. A threshold irradiance response which was observed at a PPF of 45 $\mu\text{mols}^{-1}\ \text{m}^{-2}$ (3.9 moles d^{-1}) reduced days to anthesis and node numbers simultaneously. Ninety-five percent of the variation in node numbers was correlated in a linear function with days to flower.

INTRODUCTION:

Under natural winter-spring conditions, hybrid geraniums (Pelargonium hortorum - Bailey) flower in 100 to 140 days (2, 3) and require large quantities of heat and greenhouse space. Early flowering in response to supplemental irradiation has been reported (1, 9, 14, 17). However, many growers supplying supplemental light have experienced only limited success in reducing the time to flower.

Reports in the literature provide little explanation of these failures. According to Post (15), photoperiod is not a significant factor in geranium flowering. Craig and Walker (11) suggested that cumulative solar energy was a major environmental factor controlling flowering in this crop. They (11) suggested that a nearly constant quantity of accumulated solar energy was necessary for flowering. Erickson et al. (12) recently reported that 41% to 65% of the variability in days to anthesis was related to cumulative irradiance. According to Armitage (4), the time to visible bud was negatively correlated with irradiance at a given temperature. After the visible bud stage, irradiance was less effective than temperature in influencing time to flower. Carpenter and Rodrequez (9), found that the time to anthesis was not affected by the first four weeks of supplemental light. A six-week period of supplemental light reduced time to anthesis by 20 to 30 days and reduced the number of nodes produced before the first flower. Similarly in the northwestern United States, Norton (14) produced flowering plants three weeks earlier by applying 67 days of supplemental irradiation.

Since supplemental irradiation has been shown to cause earlier flowering in hybrid geraniums and only limited systematic studies of the response have been reported, it was decided to study and to quantify the conditions necessary for flowering. It is the expectation that this information will lead to more efficient production techniques.

MATERIALS AND METHODS

CULTURAL PRACTICES:

Similar cultural practices were used in three experiments on the cultivar Sprinter Scarlet. A peat-lite medium composed (by volume) of 50% fibrous peat, 25% vermiculite, and 25% perlite was used both as germination and growing medium. Seeds were planted in the medium and covered to a depth of 0.5 cm, then germinated at $22^{o} + 2^{o}$ C. Plants were watered as needed using a water soluble fertilizer (20N - 8.7P - 16.7K) to provide 200 mgl^{-1} nitrogen at each watering. Greenhouse temperatures were maintained at 17 + 2 C nights (1800 to 0800 hours) and 21 + 2 C days (0800 to 1800 hours). From May through September ambient light was reduced to about 65% of incident radiation by means of white washing the greenhouse.

SUPPLEMENTAL LIGHTING:

All supplemental lighting was provided using 400 and 1000 watt high pressure sodium lamps. Treatment Photosynthetic Photon Flux in the 400 to 700 nm range (irradiance, PPF) were measured using a Li-Cor (Lincoln, Nebraska) Lambda Li-190s quantum sensor. Ambient daily cumulative irradiance (CPPF) was recorded using a Kysor intigrator recorder. Treatment irradiances were checked and adjusted every 14 days by changing the height and location of the lamps over the plants. The supplemental irradiance periods varied with the treatments in each experiment.

EXPERIMENT 1:

The effect of supplemental light duration on flowering in young seedlings was studied. On November 17, ten-day-old seedlings were transplanted into 6 cm square plastic containers and immediately placed in the greenhouse under continuous (24 hours/day) supplemental irradiation of 65 + 8 μmols^{-1} m^{-2} for periods of 14, 28, and 42 days. Control plants recieved no supplemental light. At the end of each treatment period, 32 plants were randomly selected and placed on an unlighted adjacent bench. After all treatments were completed, the plants were potted into 10-cm clay pots, randomized, and grown to flowering under ambient greenhouse conditions. The days to anthesis, defined as the opening of the first floret, were recorded.

EXPERIMENT 2:

In experiment 2, the effect of supplemental light duration on flowering of older plants was studied. Fifteen-day-old seedlings from an October 7 sowing were transplanted to clay pots, 10-cm in diameter, and grown under ambient greenhouse conditions. When the plants were 40 days old, treatments of 14, 28, and 42 days of continuous (24 hours/day) supplemental irradiance (PPF = 65 + 8 μmols^{-1} m^{-2}) were started. Other treatments were started when the plants were 54 and 68 days old and were continued until anthesis. Control plants were lighted: 1) from 3 days after transplanting to anthesis, 2) from 40 days old to anthesis, or 3) not at all. All groups consisted of single plants replicated 8 times. Days to anthesis, the number of lateral branches 1 cm long or longer, and the number of visible buds per plant were recorded at the time when all plants had reached anthesis.

EXPERIMENT 3:

A third experiment, designed to study the effects of quantity, intensity and duration of the daily supplemental irradiance, was started on August 16. Seventeen-day-old seedlings which had been planted directly into 4-cm square plastic containers were placed in the greenhouse under 42 combinations of supplemental light differing in irradiance levels and daily irradiance periods (Table 3). The treatments were arranged factorially in a split-plot design. The main plot consisted of 6 supplemental irradiance period treatments: 1) 4 hours of lighting from 0000 to 0400 hours, 2) 12 hours during the night from 1900 to 0700 hours, 3) day extension to 15 hours of light from 0700 to 2200 hours, 4) 18 hours from 0700 to 0100 hours, 5) 21 hours from 0700 to 0400 hours, and 6) continuous supplemental lighting, 24 hours/day. In the split of the main plot, plants were arranged within each treatment at different locations under the lamps to provide PPF of 15, 30, 45, 60, 75 and 90 μmols $^{-1}$ m^{-2}. The greenhouse ambient light lasted from approximately 0700 to 2100 hours. The unlighted control plants received less than 3 μmols $^{-1}$ m^{-2} of the supplemental irradiation as scattered light 24 hours/day. After 33 days of treatment, the plants were removed from the supplemental light and potted into 10-cm square plastic pots, and grown under ambient greenhouse light. The daily CPPF, date of anthesis and the number of nodes on each plant from seed emergence to first anthesis were recorded. The total crop CPPF was determined by summing the daily ambient CPPFs and the daily supplemental CPPFs from seed to anthesis.

RESULTS AND DISCUSSION:

Continuous supplemental irradiation applied to 10-day-old seedlings (Experiment 1) for a period of 14 days reduced the average time to anthesis by 9.6 days (Figure 1), while the 28 and 42 day treatments reduced the time to anthesis by 43.2 and 50.4 days respectively. While large reduction in time to anthesis occurred from lighting during the 14 to 28 day treatment period, only small decreases in time to anthesis occurred from the last 14 days of supplemental irradiation. These results, which are similar to those obtained by others (4, 5, 6, 8, 9), raise a number of questions: Is an accumulation of radiant energy necessary for flower induction as suggested by Craig and Walker (11)? Is a certain minimum average daily CPPF necessary as was suggested by Ericksan et al. (12)? Were the young plants at first in a juvenile state, i.e. unable to respond to the irradiation, until they matured sufficiently during the treatments? Is there a high irradiance response in which a certain duration of irradiance is required before initiation occurs?

In addition to the questions, above results provide other information. The smaller reductions in time to anthesis that occurred from the first two weeks of irradiation, as well as those differences that occurred between 28 and 42 days of treatment, may reflect the additional growth mainly due to increased photosynthetic activity. The differences between 14 and 28 days of supplemental lighting may be due to both increased photosynthetic activity and to a high irradiance induction-like response in plants that are sufficiently mature to respond to the irradiance stimuli.

In Experiment 2, time to anthesis was reduced by all supplemental light treatments given to forty-day-old plants when compared with the unlighted control plants. However, time to anthesis was longer than for the continuously lighted control plants (Table 1). None of the responses to the duration of supplemental light were significantly different, i.e., in 40-day-old plants 14 days of supplemental irradiation was as effective as 42 days. The small differences between 14, 28, and 42 day treatments may have been due to increased photosynthetic activity during the longer light treatments.

On plants that were irradiated at the age of 54 and 68 days, delays in anthesis were approximately equal to the number of days before the supplemental irradiation began. It is noteworthy that the plants lighted from 18 days old to anthesis (lighted control) flowered an average of 46.4 days earlier than the unlighted control, and 20.3 days earlier than all plants irradiated 22 days later. Significant differences in days to anthesis existed between plants given supplemental irradiation at 40, 54, and 68 days of age, but no significant differences were found between plants irradiated at 68 days and the unlighted control. It is likely that, with sufficient ambient light, at 68 days, flower initiation had already occurred when the supplemental light treatment was started. Floral initiation of the meristem was found to occur in spring crops at about this age in the work of Miranda (13).

Few small differences occurred in the time span from the beginning of supplemental lighting to anthesis. Only plants lighted while very young (18 days old) or for a short period of time (14 days) took significantly longer to reach anthesis. The data indicate that flower initiation may be occurring during the period immediately following application of supplemental irradiation. This flowering response may require a sufficient duration of high irradiance on plants that have completed a juvenile phase. It is possible that the induction may result from the increased photosynthesis or from a high irradiance photomorphogenic induction, altered by the supplemental irradiation treatments. On plants irradiated for 28 or more days (Table 1), an increase in lateral branches was observed. The number of buds per plant were not significantly increased unless the irradiance treatments began early, before forty days, and continued to first anthesis. Shorter term irradiation (14 to 42 days) decreased the time to anthesis and did not significantly increase lateral branching.

Comparing the results of the light treatments applied to old (40 days old, Exp. 2) and young (10 days old, Exp. 1) plants, it appears that the older plants are more responsive to the supplemental irradiation treatments. This is not surprising since the sensitivity of other herbaceous species to inductive stimuli can increase with increasing age. In the short-day plant *Chrysanthemum morifolium*, different cultivars have been shown to vary in the time required to grow out of the juvenile phase. In one study with *Pisum sativum* (garden pea) the level of genetically controlled flowering inhibiton was found to decrease as the plants aged (7). This ripeness-to-flower may also be a factor in the responses of geraniums to high irradiance levels.

In the study of the effects of responses to supplemental irradiance levels and daily irradiance period (Exp. 3), plants treated with daily irradiance periods greater than 15 hours flowered in less time and with fewer nodes when supplemental irradiance levels exceeded 45 $\mu mols^{-1}$ m^{-2} (Table 2). Plants in the control group flowered in an average of 138 days with an average of 19.4 leaves preceeding the first inflorescence. Plants receiving high levels of irradiation flowered an average of 78 days earlier and the number of nodes to first inflorescence was reduced by an average of 10.9. No reduction in days to flower or node number was observed at any irradiance level when the daily supplemental irradiance period was only 15 hours. Significant decreases in days to anthesis and node number were observed when the supplemental irradiance levels were greater than 45 $\mu mols^{-1}$ m^{-2} and the irradiance period was 18 hours or longer, or when there was a night interruption. Four and 12 hours of supplemental irradiation as a night interruption, were as effective as the 18 hours, 21 hours, or continuous (24 hours/day) irradiance periods.

Many treatments providing the same quantity of supplemental irradiation at different irradiance levels and daily periods yielded different results. Plants in treatment No. 1 received 42.8 mol M^{-2} of supplemental irradiation over the duration of the treatment and flowered in an average of 131.0 days having 10.0 nodes to anthesis. Treatment 36 also received 42.8 molM^{-2} of supplemental irradiation and flowered in 82.3 days with an average of only 8.5 nodes. Treatments 2 and 28, 3 and 30, 17 and 24 and 22 and 24, also received the same quantities of supplemental CPPF over the same period but showed wide differences in both days to flower and node number. These results indicate that the quantity of accumulated CPPF is not as important as the incident irradiance level and daily irradiance period. Irradiance periods longer than 15 hours were not effective in reducing time to anthesis.

Plots of the data demonstrating relationships between total CPPF, mean daily CPPF and days to flower or node number are presented in Figure 2. Since the plots appear non-linear the logarithmic, squared, and cubed transformation of the CPPF terms were submitted to a step-wise addition multiple linear regression analysis. Equations which most significantly define the relationships are presented in Table 3. A positive linear relationship of days to anthesis with total CPPF accounted for 74% of the variability in days to anthesis and 59% of the variability in the number of nodes to anthesis: these correlations indicate that the slower flowering treatments were exposed to a greater quantity of CPFF, while plants that were induced to flower earlier flowered with less total CPFF. Correlations to the mean daily CPFF yielded coefficients of determination as high as 93.4% and 84.8% for regression equations which included logarithmic and linear terms. These relationships yielded negative correlations indicating that with increased mean daily CPFF there is a decrease in the days to flower. It thus appears from the results that mean dailv CPFF may be a better predictor of flowering response than the total CPFF.

In correlating the days from sowing to anthesis (Y) with the number of nodes to flower (X), a correlation coefficient of 0.974 was obtained for the linear relationship $Y = 3.6 + 7.62\ X$. The high positive correlation indicates that early flowering may be associated with morphogenic resonses producing early floral initiation and less nodes to first anthesis. The greater number of nodes is associated with later flowering and apparently later floral initiation despite the greater amount of accumulated radiant energy.

The intensity of supplemental irradiation significantly influences the days and nodes to anthesis (Table 4). Linear and quartic terms are significant in relation to days to anthesis. Linear, quadratic and cubic and quartic terms are significant in relation to node number. Plots of the means related to the level of supplemental irradiance are presented in Figure 3. The plots demonstrate the simultaneous decrease in days to flower and node number with increased supplemental irradiation. Note that the greatest reduction in both days to flower and node number occur around a critical level, or threshold, of 45 μmols $^{-1}$ m^{-2}, in the fall crop. Again, the close relationship of days to anthesis and node number is observed in the simultaneous shift of both responses to the increased supplemental irradiance.

SUMMARY AND CONCLUSIONS:

The number of lateral branches increased when supplemental irradiation was provided for 28 or more days. The number of buds per plants was increased when lighting began at a young age and continued until anthesis. Supplemental irradiances above 20 µmols $^{-1}$ m $^{-2}$ in combination with photoperiods longer than 15 hours were effective in reducing the time to anthesis in these experiments.

The quantity of light received by the crop was not as important as the daily irradiance. Mean daily CPPF provided a better estimator of days to anthesis than the crop total CPPF. The number of days to anthesis was highly correlated (r = 0.937) to the number of nodes. A critical supplemental irradiance of 45 µmols $^{-1}$ m $^{-2}$ was observed when supplied for 15 or more hours daily. The decreased node numbers and accelerated flowering response to supplemental irradiance, extended high irradiance periods, and night interruption treatments, raise the question that a photomorphogenic response, by definition of Wareing and Phillips (16), may be occurring. This may be a high irradiance induction response which occurs in plants when they are sufficiently ripe-to-flower, or a response to added photosynthates produced by the added light. Based on field observation and other unreported experimental data, the length of the juvenile phase, the critical irradiance, and the duration of high irradiance, may vary in each cultivar thus giving differences in days to anthesis of cultivars selected for commercial production. It is possible that wide differences may exist in cultivars not selected for spring production or rejected by breeders as not being desirable under current production practices.

It is apparent that when supplemental irradiation is applied to geraniums which are sufficiently mature to flower and high enough irradiance levels are present for long daily irradiance periods, consistent reductions in the time to anthesis and node number can be expected.

Table 1. Effects of age and duration of supplemental irradiation ($65 \mu mol s^{-1} m^{-2}$) on days to anthesis, lateral branching, and total bud count in Pelargonium hortorum - Bailey 'Sprinter Scarlet'.

Age at lighting	Duration of lighting	Days from sowing to anthesis	Days from lighting to anthesis	Lateral branches per plant	Buds per plant
-	0 days	135.2	-	7.3	2.8
18	to anthesis	88.8	70.9	10.8	9.1
40	14 days	112.4	72.4	7.5	3.9
40	28 days	109.9	69.9	11.4	4.6
40	42 days	108.8	68.8	11.4	4.9
54	to anthesis	122.5	68.5	11.3	4.6
68	to anthesis	134.5	66.6	13.0	4.0
H. S. D.[z]	-	8.1	5.2	4.0	2.5

z Tukey's w test (honestly signifigant difference), $\alpha=0.05$.

Table 2. Effects of PPF and irradiance period on the number of nodes and days to flower in <u>Pelargonium</u> <u>hortorum</u> - Bailey 'Sprinter Scarlet'.

	Supplemental treatments				To Anthesis			
	Irradiance		MD	T	T	MD		
No.	period[q]	PPF[r]	CPPF[s]	CPPF[t]	CPPF[u]	CPPF[v]	Days	Nodes
1	24	15	1.30	42.8(a)[y]	1431.1	10.99	131.0	18.0
2	24	30	2.59	85.5(b)	1501.0	13.18	130.6	18.8
3	24	45	3.89	128.2(c)	1298.4	16.12	81.2	10.2
4	24	60	5.18	170.9	1353.2	16.70	84.2	11.6
5	24	75	6.48	213.8	1292.3	19.48	67.0	10.0
6	24	90	7.78	256.7	1313.1	21.01	62.6	9.4
7	21	15	1.14	37.6	1476.7	10.01	150.0	20.4
8	21	30	2.27	74.9	1545.0	10.91	145.6	20.0
9	21	45	3.40	112.3	1358.7	14.74	94.2	12.2
10	21	60	4.53	149.6	1419.7	15.11	95.8	12.0
11	21	75	5.67	187.1	1431.1	16.21	90.0	12.6
12	21	90	6.81	224.6	1416.5	17.70	85.2	11.8
13	18	15	0.98	32.2	1424.4	10.77	134.8	18.6
14	18	30	1.94	64.1	1450.9	11.38	128.0	16.8
15	18	45	2.92	96.3	1313.4	14.46	95.4	13.4
16	18	60	3.89	128.2	1338.0	15.33	91.8	12.4
17	18	75	4.86	160.4(d)	1387.2	16.00	88.2	11.4
18	18	90	5.84	192.6	1226.7	19.64	63.4	9.4
19	15	15	0.81	26.8	1483.9	10.22	147.8	20.0
20	15	30	1.62	53.4	1458.8	10.84	134.8	18.2
21	15	45	2.43	80.2	1529.3	10.52	146.0	20.2
22	15	60	3.24	106.9(e)	1552.6	11.01	142.2	18.8
23	15	75	4.05	133.7	1591.6	12.00	137.6	18.0
24	15	90	4.86	160.4(d)	1635.1	12.29	145.4	16.6
25	12[w]	15	0.65	21.4	1376.9	11.13	125.0	17.0
26	12	30	1.30	42.4	1409.1	11.24	126.2	15.4
27	12	45	1.95	64.2	1295.8	14.00	93.8	11.6
28	12	60	2.59	85.5(b)	1320.4	14.25	94.8	12.8
29	12	75	3.24	106.9(e)	1246.7	15.91	82.8	10.2
30	12	90	3.89	128.2(c)	1211.6	17.23	70.8	9.8
31	4[x]	15	0.22	7.2	1446.2	9.75	150.4	23.8
32	4	30	0.43	14.3	1420.0	10.21	140.2	19.8
33	4	45	0.65	21.4	1278.3	12.63	104.8	13.2
34	4	60	0.86	28.5	1163.3	14.40	82.8	11.2
35	4	75	1.08	35.6	1173.1	14.57	81.2	11.2
36	4	90	1.30	42.8(a)	987.6	12.00	82.3	8.5
Ambient control					1394.3	10.22	138.0	19.4
H.S.D.[z]					300.2	4.48	42.8	6.7

Table 2. (continued)

q Period of irradiance expressed in hours.
r Intensity of irradiance expressed in Photosynthetic Photon Flux (PPF) in the 400-700 nm range, umols^{-1}m^{-2}.
s Mean daily cumulative photosynthetic photon flux in mm^{-2} over the crop life.
t Total cumulative photosynthetically active radiation in mm^{-2} over the life of the crop.
u Summation of ambient and supplemental irradiation.
v Daily average of the ambient and supplemental irradiation.
w Treatment during the ambient night period.
x Treatment as night break (0000-0400 hrs).
y Letters in paranthesis indicate pairs of treatments of the same quantity of supplemental irradiation but at different times and intensities.
z Honestly significant difference determined using Tukey's procedure $\alpha = 0.05$

Table 3. Prediction equations for days and nodes to flower in *Pelargonium hortorum* - Bailey 'Sprinter Scarlet' comparing mean daily and total cumulative photosynthetic photon flux as predictive variables.

Dependent variable	Independent variable	Prediction equation[Z]	Regression statistics		
			F-ratio	sign.[Y]	R^2
days	MD CPPF[X]	243.4-9.8(X)	1030.2	***	.848
days	MD CPPF	843.6+16.6(X)-855.6(logX)	1282.2	***	.934
days	T CPPF[W]	-148.4+0.1866(X)	536.9	***	.744
days	T CPPF	$-20.7+6.7E-5(X^2)$	556.8	***	.753
nodes	MD CPPF	32.1-1.27(X)	473.2	***	.721
nodes	MD CPPF	-62.8-47.7(logX)	679.1	***	.788
nodes	T CPPF	-17.3+0.0233(X)	262.0	***	.589
nodes	T CPPF	$1.4+8.39E-6(X^2)$	269.0	***	.595

Z Equations were developed through step-wise addition regression analysis, including lenear, quadratic, cubic and $\log_{10}$ trensformed terms.

Y Significance of the regression equation; ***, $\alpha = 0.001$.

X MD CPPF = mean daily cumulative photosynthetic photon flux.

W T CPPF = total cumulative photosynthetic photon flux during the life of the crop.

Table 4. Analysis of variance for the influence of supplemental irradiance on days and nodes to flower in *Pelargonium hortorum* - Bailey 'Sprinter Scarlet'.

Variable	Source	Degrees of freedom	F-ratio	Significance^Z
Days				
	Between Levels	6	34.3	***
	Linear	1	186.4	***
	Quadratic	1	1.0	n.s.
	Cubic	1	3.8	n.s.
	Quartic	1	5.4	*
	Within levels	147		
Nodes				
	Between Levels	6	31.2	***
	Linear	1	90.0	***
	Quadratic	1	5.8	**
	Cubic	1	3.9	*
	Quartic	1	7.4	**
	Within levels	147		

Z significance of the variable and it's trends; n.s. = not significant, * α= 0.05, ** α= 0.01, *** α= 0.001.

Figure 1. Days to anthesis in *Pelargonium hortorum* - Bailey 'Sprinter Scarlet' when supplementally irradiated with high pressure sodium lights at a PPF of 65±8 μmol $s^{-1}m^{-2}$ continuously for different durations.

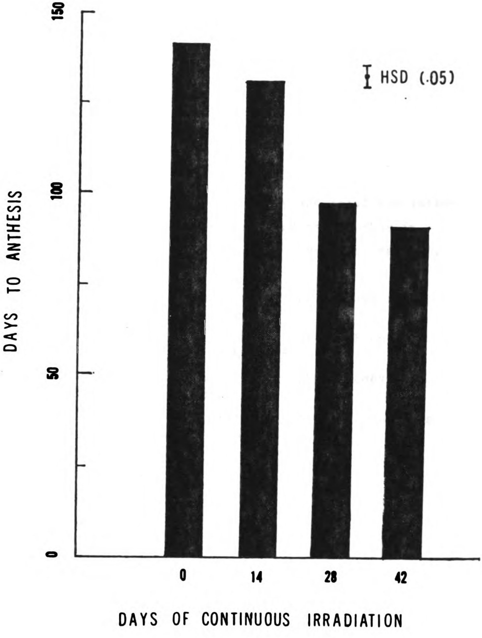

150
100
50
0
DAYS TO ANTHESIS
HSD (.05)
0
14
28
42
DAYS OF CONTINUOUS IRRADIATION

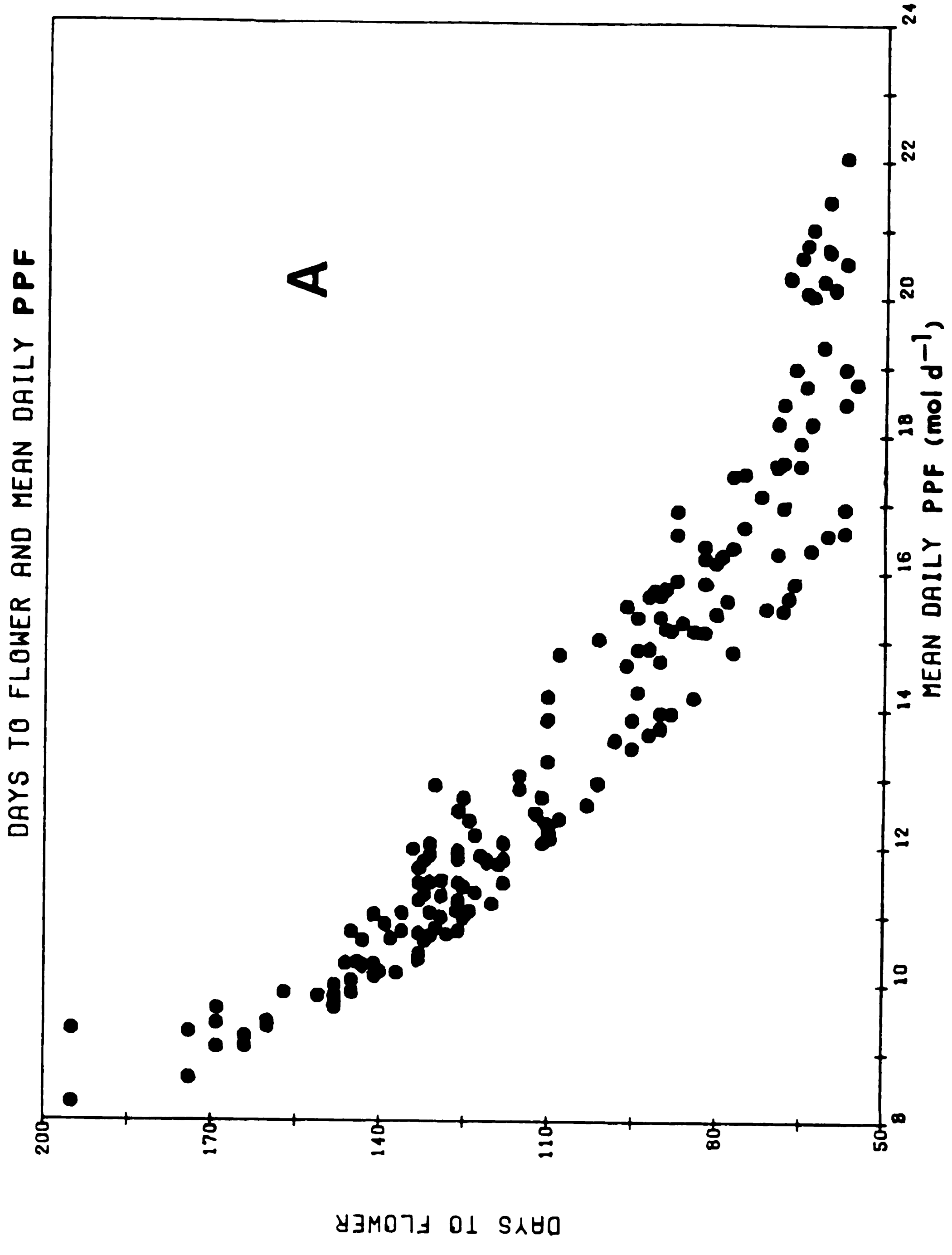
Figure 2. The relationship of mean daily and total cumulative PPF to the days to anthesis and node number in Pelargonium hortorum - Bailey 'Sprinter Scarlet'.

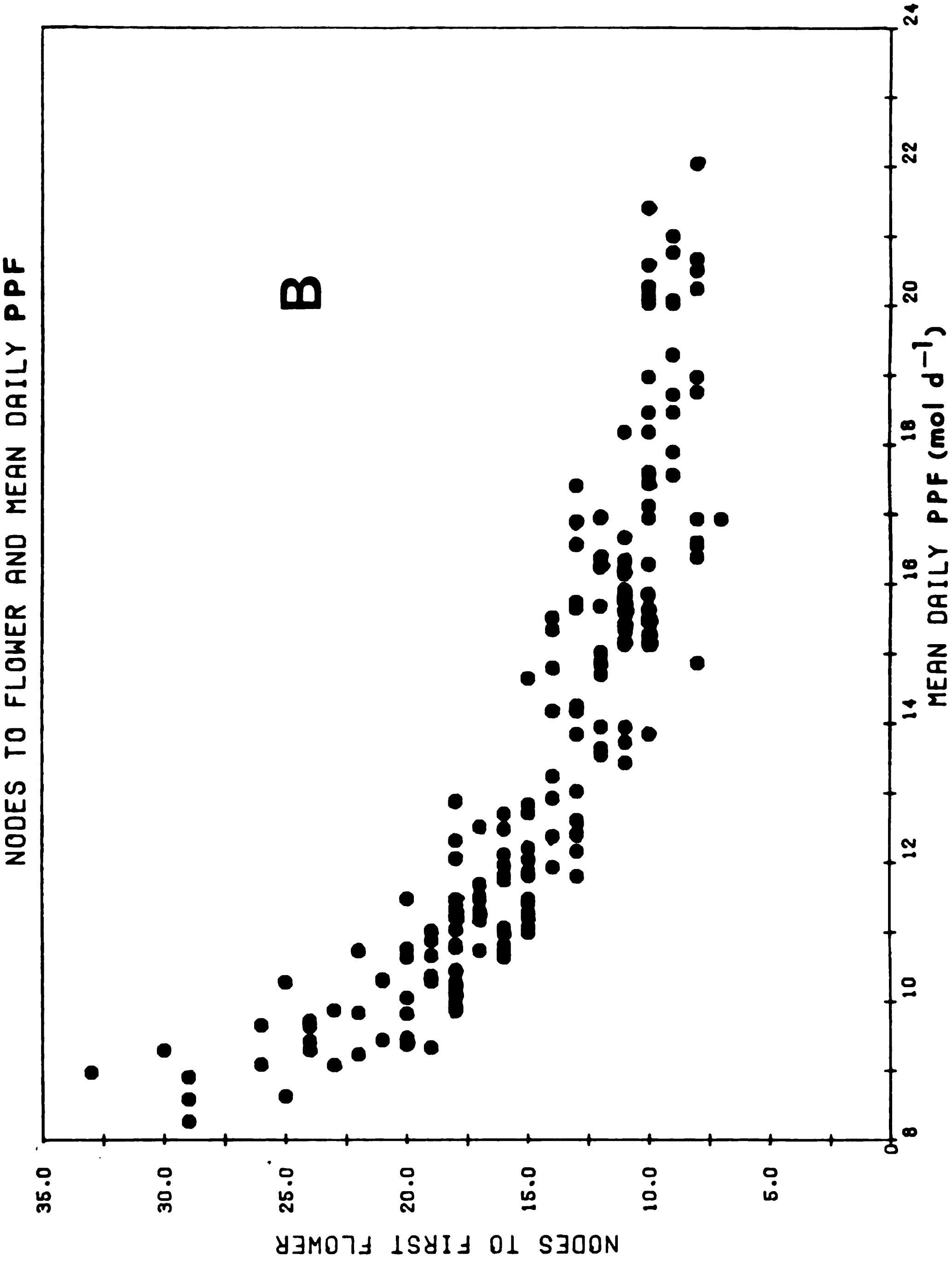
(A) The effect of mean daily PPF on days to anthesis in each plant.

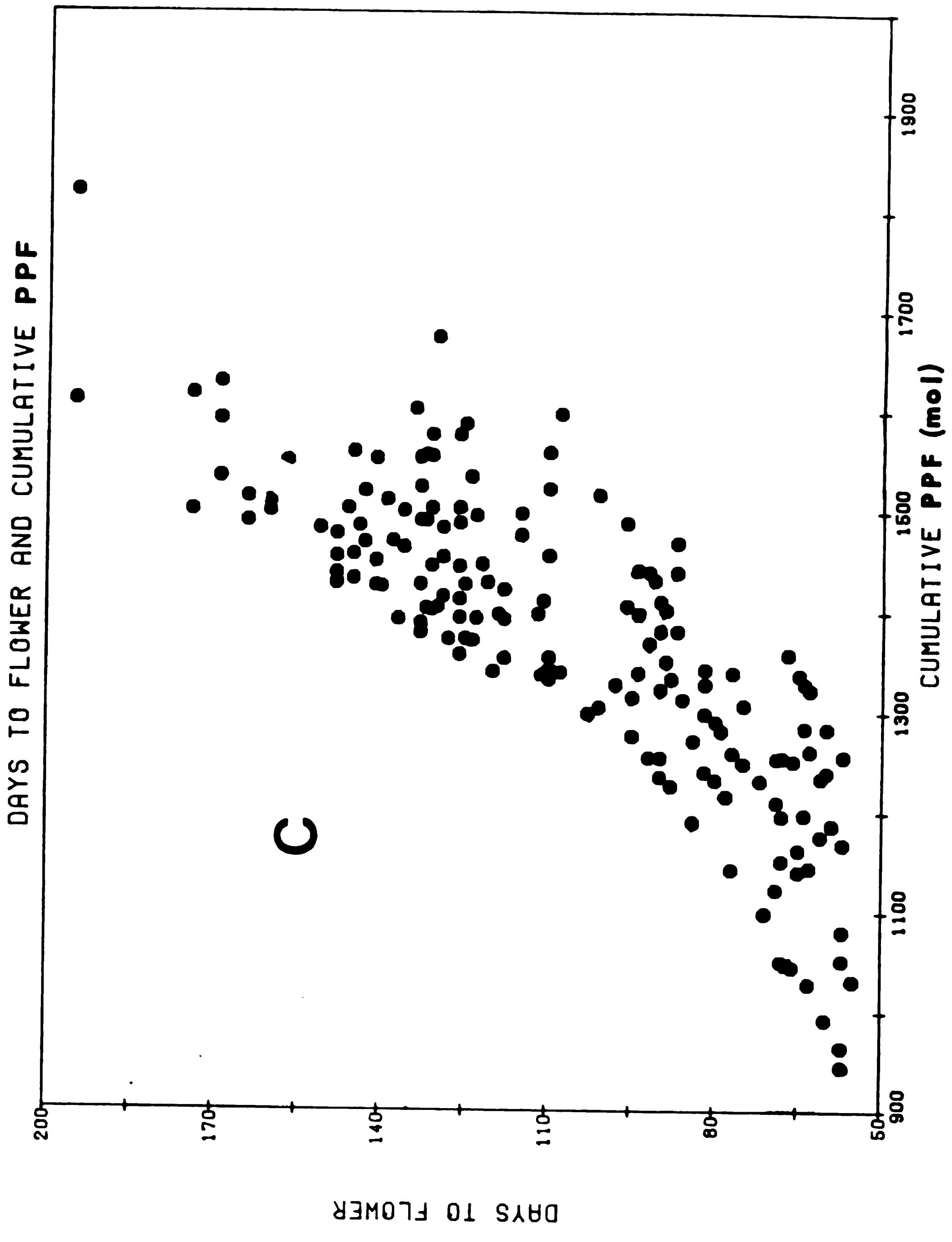
(B) The effect of total cumulative PPF on days to anthesis in each plant.

(C) The effect of mean daily PPF on nodes to anthesis in each plant.

(D) The effect of total cumulative PPF on nodes to anthesis in each plant.


DAYS TO FLOWER AND MEAN DAILY PPF
A
DAYS TO FLOWER
200
170
140
110
80
50
8
10
12
14
16
18
20
22
24
MEAN DAILY PPF (mol d^{-1})


NODES TO FLOWER AND MEAN DAILY PPF
B
NODES TO FIRST FLOWER
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0
8
10
12
14
16
18
20
22
24
MEAN DAILY PPF (mol d^{-1})



DAYS TO FLOWER AND CUMULATIVE PPF

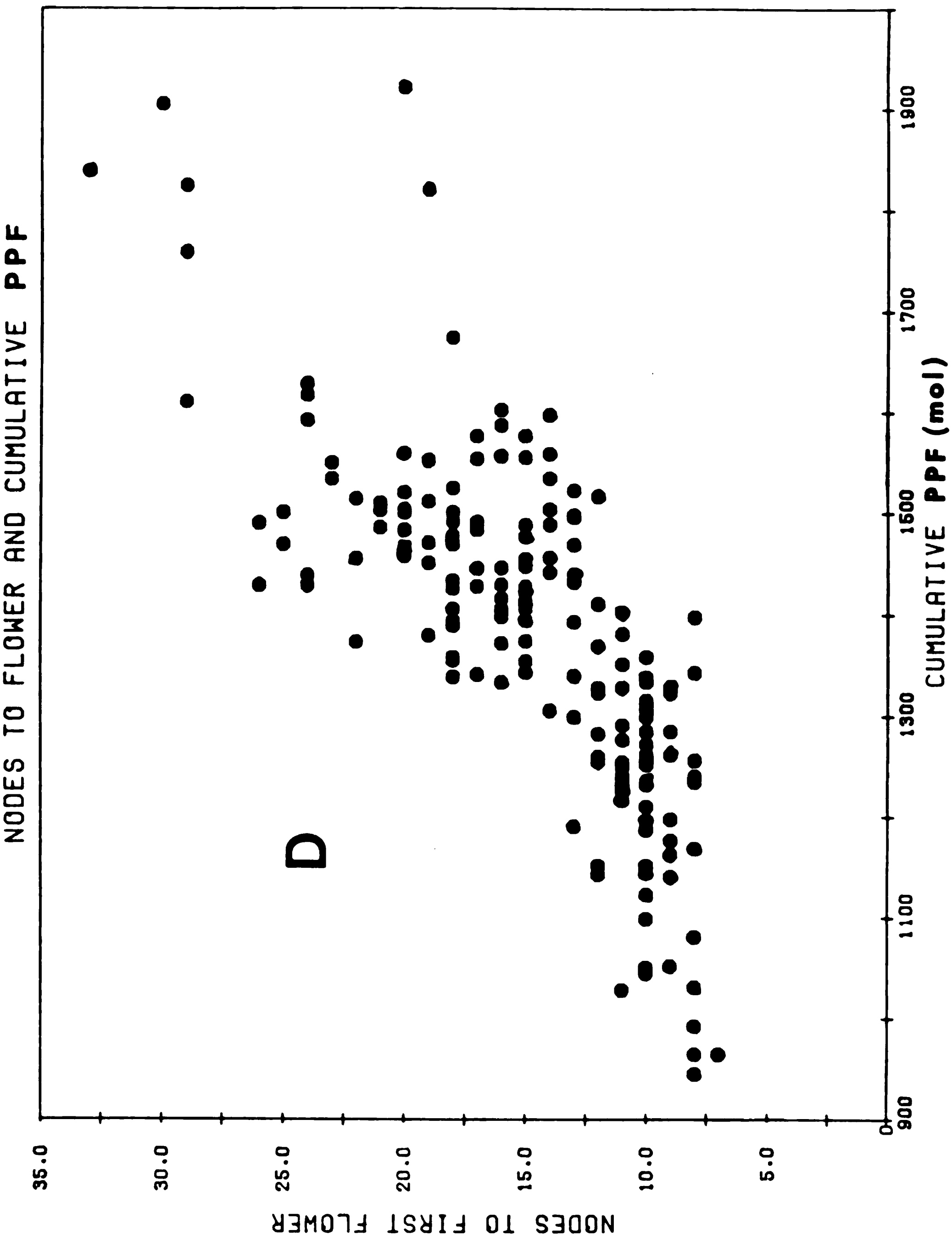
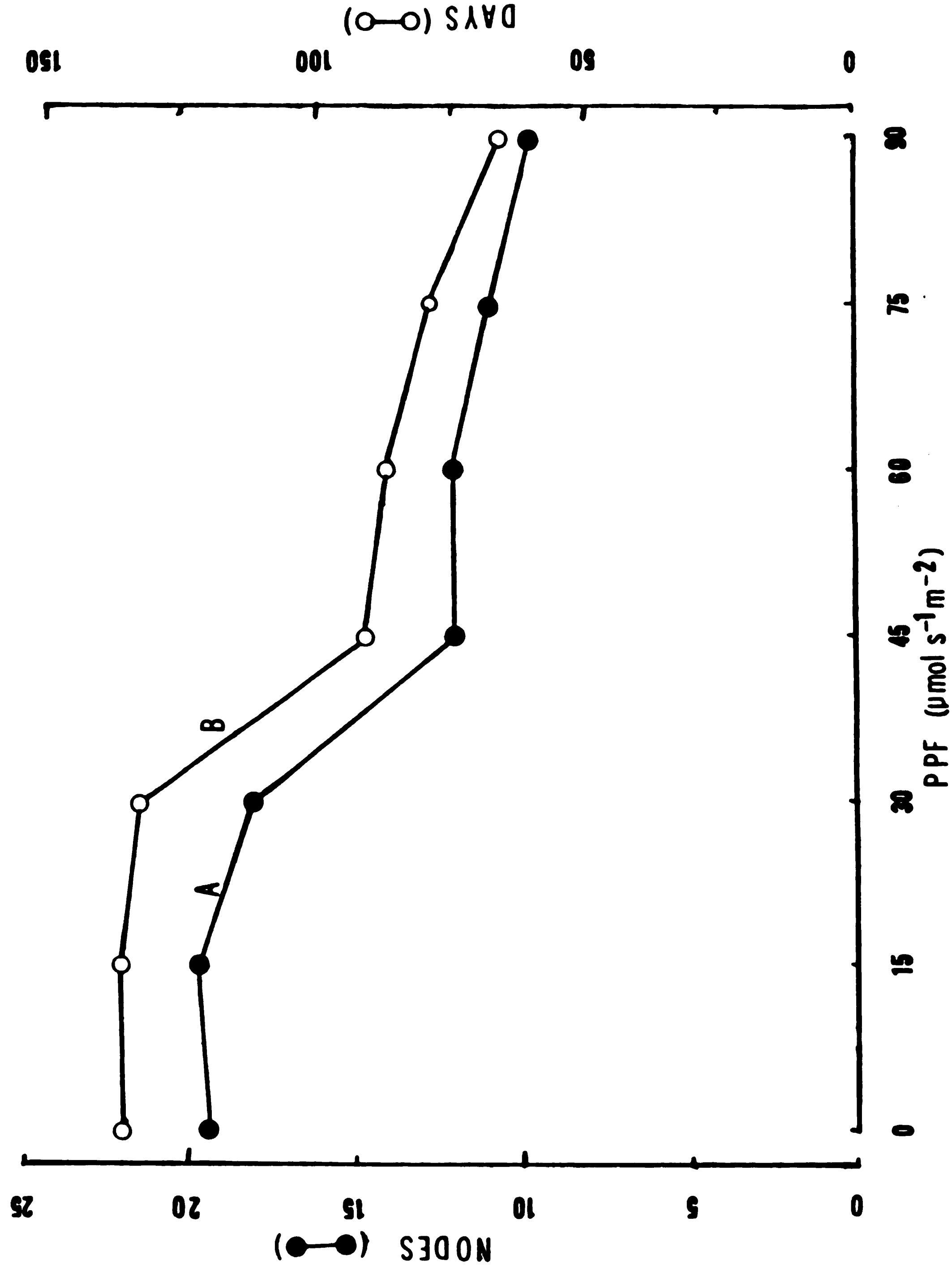

NODES TO FLOWER AND CUMULATIVE PPF
D
NODES TO FIRST FLOWER
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0
CUMULATIVE PPF (mol)
900
1100
1300
1500
1700
1900

Figure 3. Effects of continuous supplemental high pressure sodium irradiation on the node number (A), and days to anthesis (B) in Pelargonium hortorum - Bailey 'Sprinter Scarlet' when applied for 18 or more hours a day.


DAYS (○—○)
0
50
100
150
NODES (●—●)
0
5
10
15
20
25
PPF (μmol s⁻¹m⁻²)
0
15
30
45
60
75
90
A
B

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SECTION II

EFFECTS OF HIGH IRRADIANCE AND TEMPERATURE ON EARLY FLOWERING IN HYBRID GERANIUMS

ABSTRACT:

Treatments of hybrid geraniums (Pelargonium hortorum - Bailey) in growth chamber with short periods of continuous irradiation and temperature decreased the days and number of nodes produced from sowing to anthesis. A non-inductive juvenile phase from germination to between the 4th and 5th leaf was identified in the cv. Ringo Scarlet. Continuous (24 hours/day) irradiances (Photosynthetic Photon Flux, PPF) providing at least 10.4 mol d^{-1} (120 $\mu mols^{-1}$ m^{-2}) was effective in reducing the days and nodes from sowing to anthesis when applied for 12 or more days at $30^{o}C$. When PPF was higher, shorter durations of treatment were required for early induction. Temperature increased from $20^{o}C$ to $30^{o}C$ decreased the time of continuous irradiance treatment necessary for early induction. Under high irradiances (240 $\mu mols^{-1}$ m^{-2}) and high temperatures ($30^{o}C$) early induction responses occurred in 83% of the population from 9 days of treatment. An earlier induction response was indicated due to the simultaneous decrease in node numbers and days to anthesis. An hypothesis to describe a possible high irradiance induction response is presented.

INTRODUCTION:

Finding methods to decrease the normal time to flower (100 - 140 days) in hybrid geraniums (*Pelargonium hortorum* - Bailey) has been a goal of many floriculturalists for some time.

Early flowering of geraniums has been observed with the application of high levels of supplemental irradiation under greenhouse (1, 3, 6, 9, 11, 14, 18, 23) and growth chamber (6, 26, 27) conditions. High irradiance coupled with moderate to high temperatures have been shown to accelerate flowering (2, 27). Armitage (2) observed visible buds in 33 days after sowing on plants exposed to continuous irradiation at 375 $\mu mols^{-1}$ m^{-2} and 30^{o} C, they flowered in 65 days, nearly half the normal production time. Randolf and Law (27), obtained macroscopic buds in 21 days on plants exposed to high (about 375 $\mu mols^{-1}$ m^{-2}) levels of continuous irradiance. White (26) observed macroscopic buds on the cv. Red Elite 36 days after beginning irradiation with approximately 390 $\mu mols^{-1}$ m^{-2} at 18 to 22.5 C. Anthesis occurred in 29 days from sowing in the cv. Cherry Diamond when plants were grown at 30^{o} to 37^{o} C days with supplemental irradiation applied at 80 $\mu mols^{-1}$ n^{-2} during the night hours (5).

High irradiance levels have been known to influence the induction of flowers in many species, for example; African Violets (*Saintpaulia*) (10), Rudbeckia (17), Snapdragon (*Antirrhinum*) (22), and Roses (*Rosa hybrida*), (4, 5, 14). Increased floral induction has been observed under prolonged periods of high irradiance in *Anagallis arvensis* L. (Pimpenal) (19), *Rhododendron sp*. (Azalea) (7), and *Alstromeria* (Peruvian Lily) (14).

In geraniums, no clear definition of the factors involved in early flowering has been advanced. Many varying observations of the potential for early flowering have been reported. For reliable application to production it was necessary that the factors which yield the early flowering be defined. Understanding the response would be useful, not only in accelerating geranium production but also in studies of the physiology of flowering. It was the purpose of this study to examine those factors which were thought to influence initiation of flowering in hybrid geraniums.

MATERIALS AND METHODS

CULTURAL PRACTICES:

Three experiments were conducted, and similar cultural practices were used in all of them. A peat-lite medium composed (by volume) of 50% fibrous peat, 25% vermiculite, and 25% perlite was used both as a germination and a transplant medium. Seeds were sown, covered to a depth of 0.5 cm and germinated at 22^{o} + 2^{o} C. Plants were watered as needed in a constant liquid feed program using a water soluble fertilizer (20N - 8.7P - 16.7K) to provide 200 μgl^{-1} nitrogen at each watering. Greenhouse temperatures were maintained at 17^{o} + 2^{o} C night and 21^{o} + 2^{o} C days.

GROWTH CHAMBER CONDITIONS:

All light and temperature treatments were performed in growth chambers. Lighting was from cool-white fluorescent lamps only. The irradiance at the upper surface of the plant was measured at the beginning of each treatment and checked weekly. It varied by not more than + 12% of the indicated irradiance levels. Temperature was maintained at the specified treatment conditions and checked daily varying not more than + 2^{o} C.

EXPERIMENT 1:

The duration of continuous light treatment was studied using mature winter-grown vegetative plants of the cultivar Ringo Dolly. On December 14, four treatments of eight plants each began. The plants were grown in 6-cm square plastic containers and averaged 4.3 leaves at treatment. An irradiance of 240 $\mu mols^{-1}$ m^{-1} was maintained continuously (24 hours/day) for 3, 6, and 12 days. An untreated control remained in the greenhouse. After treatment, the plants were grown under greenhouse conditions. Time to anthesis and the number of nodes to the first inflorescence were recorded and the data was subjected to an analysis of variance.

EXPERIMENT 2:

The effect of temperature and duration of irradiation were investigated using the cultivar JackPot. Continuous irradiance of 240 µmols $^{-1}$ m^{-2} was applied to mature winter grown plants in combination with temperatures of 20°, 25°, and 30° C (+ 1° C) for 3, 6, and 12 days. Seventy-seven-day-old plants having 10 nodes each were selected at random for treatments which started on December 14. Five replications were grown and treated in 5-cm square plastic containers. Days to anthesis and node number to first anthesis were recorded and an analysis of variance performed.

EXPERIMENT 3:

The interactive effects of plant age, irradiance, and the duration of light treatment were investigated in a 3 x 3 x 5 factorial arrangement of treatments. Plants were selected for treatment from a September 30th sowing of the cultivar Sprinter Scarlet into 5 x 7 x 9 cm plastic containers, treatments of six plants each at the age of 18, 24, and 30 days were subjected to irradiance levels of 60, 120, and 240 µmols $^{-1}$ m^{-2} for periods of 0, 3, 6, 9, and 12 days. At the beginning of the treatment the 18-day-old plants averaged 2.0 expanded leaves while the 24 and 30-day-old plants averaged 3.3 and 4.6 leaves respectively. The number of nodes that emerged during treatment and the number to anthesis were recorded along with the date of the beginning of anthesis. An analysis of variance was performed.

RESULTS AND DISCUSSION:

The age of the plants at treatment and the interaction of irradiance and temperature, and the duration of continuous exposure to the treatments all appear to influence the inductive response.

Duration of Light and Temperature:

Continuous irradiation of the plants with 240 $\mu mols^{-1}\ m^{-2}$ for 12 days at 30°C decreased the time to anthesis by an average of 51.6 days, and the number of nodes before the first inflorescence by an average of 14.1 (Exp. 1, Fig. 1). Three or 6 days of treatment had no significant effect on flowering, compared to the control. In experiment 2 (Tab. 1), similar results were observed from 12 days of treatment, at 25° or 30°C. Seventeen percent of the population did flower earlier from only 6 days of irradiance (240 $\mu mols^{-1}\ m^{-2}$) and temperature (30°C) treatments. In Experiment 3 (Fig. 2 and 3) 50% of the 30-day-old plants responded to only 6 days of irradiance and temperature treatment at 240 $\mu mols^{-1}\ m^{-2}$.

The results reported here are in agreement with previous observations where flowering time and numbers of nodes to first inflorescence were decreased in plants exposed to high irradiance levels over extended periods (2, 9, 11, 18, 23). Armitage (2) reported that 9 days of continuous high irradiance (375 $\mu mols^{-1}\ m^{-2}$) was effective in decreasing the time to flower. This data is in agreement with his; they show that the higher levels of irradiation supplied to mature plants at higher temperatures required shorter irradiance periods for early induction. Carpenter and Rodrequez (9), Tsujita (23), and Norton (18) found 28 to 42 days of continuous light was necessary to yield a significant reduction in the time to anthesis. Age of the plants at treatment as well as the temperature and irradiance levels appear to have influenced the results previously reported.

In traditional photomorphogenic studies, it is well documented that a given duration or number of cycles (13, 24) of inductive conditions are necessary for floral initiation. In one cultivar of *Brassica campestris* (turnip rape), only one day of high irradiance is necessary to induce flowering (12).

Age:

The data indicate that sufficient plant development is necessary in geranium seedlings before inductive responses to high irradiance and temperature can occur. Results from Experiment 3 are presented in Figure 2 and 3. Eighteen-day-old plants, having an average of 2.0 leaves expanded to at least 0.75 cm in diameter, did not respond to any combination of treatments. In 24-day-old plants, averaging 3.3 expanded leaves at treatment, 17, 50 and 83 percent of the population flowered earlier from 6, 9, and 12 days of treatment with 240 μmols^{-1} m^{-2}. The 30-day-old plants, averaging 4.6 expanded leaves at treatment, showed early flowering of 50, 83 and 100 percent of the population from 6, 9 and 12 days of treatment at irradiance of the 240 μmols^{-1} m^{-2}. As treatment continued, the 24-day-old plants developed sufficiently and responded like the older plants. In all cases, node numbers to first anthesis followed a pattern similar to days to anthesis (Figure 3).

The average rates of new leaf emergence in experiment 3 were 0.28, 0.35, and 0.39 leaves per day at the low, medium and high irradiance levels. The 30-day-old plants, averaging 4.6 leaves each at the beginning of the irradiance treatments, were the most responsive to treatments. Nine days of treatment at 240 μmols^{-1} m^{-2} were sufficient to yield early flowering in a 50% of the population of the 24-day-old plants. When treated for 12 days at 240 μmols^{-1} m^{-2}, 100% of the population showed decreased days to flower and node numbers. Experiment 1 and 2 were performed on older plants and in each case 9 or more days were needed to yield a response. Thus, growth past an average of 4.6 leaves was of minimal additional benefit in increasing the responsiveness in the cultivars studied.

The phenomenon of juvenility in flowering responses to high irradiance has been reported in other species. In *Pharabitis nil* (21), the older the plants, the more responsive they became to light. In *Sinapsis alba* the number of long-day cycles required for induction was 6 to 7 at 15-days-old, 2 at 30-days-old, and 1 at 60-days-old. It is note worthy that in the 8-days-old plants only a minimal response was observed (8). In a study of hybrid geraniums by Armitage (1) it was found that the first 6 to 8 leaves may be necessary to influence flowers in the cultivar Sooner Red.

Ripeness-to-flower is important in the cultivars reported here. It appears that an average of 4.6 leaves or more are necessary in 'Sprinter Scarlet'. However in some cultivars currently being studied, flowers differentiated after the third plastchron (6). Thus, the extent of juvenility is likely cultivar-dependent and probably contributes to the relative earliness of each cultivar.

TEMPERATURE:

Results from the study of the effects of temperature and duration of irradiance treatments on winter grown 77-day-old plants (Experiment 2, Table 1) indicate that interactions were significant for both days to anthesis and number of nodes from sowing to the first inflorescence. Early flowering and reduction of node number occurred in 50% of the population with as few as 6 days of treatment at 30^{o} C, and with 12 days of treatment all the plants flowered earlier. At 25^{o} C all plants of the population treated for 12 days flowered earlier and node numbers were again significantly decreased. At 20^{o} C, only 20% of the population flowered earlier and with less nodes from the 12 day treatment. It is suggested that if the 20^{o} C treatment were maintained for a longer period of time, a response to the high irradiance may have occurred in a greater percentage of the population. The rate of induction was slower at cooler temperatures.

Many photomorphogenic responses are influenced by temperature. In *Brassica campestris* 'Ceres', the greatest flowering response occurred at 25^{o} C (12). The percentage of flowering increased with increases in both irradiance and duration of irradiance. Murneek (17), studying the long day plant, *Rudbeckis bicolor*, concluded that high temperatures may be substituted for long days in induction. In geraniums, Armitage (2) has obtained results similar to those reported here. Observations of White (26) also indicate a very significant effect of temperature. Flowering in the cv. Cherry Diamond was obtained in 29 days, but only when high temperatures (23-37 °C) were present throughout the vegetative and reproductive phases (6).

It is apparent that at irradiance levels of 240 µmols^{-1} m^{-2} temperature and duration interact under continuous irradiation to influence floral induction. With higher temperatures and longer durations of continuous irradiance, increased flowering responses were observed in the cv. JackPot. Additional field observations indicate that cultivars may vary considerably in their responsiveness to temperatures and durations of irradiance. This interaction of temperature and duration of irradiance may also be of importance under natural conditions. In geranium production an earlier sowing provides only a small change in the time of flowering compared to a later sowing (2). It can be speculated for hybrid geraniums that flower initiation may not occur until a developed plant is exposed to enough long periods of high irradiance for a sufficient number of nearly consecutive days. The number of days may be reduced when the temperatures are higher. Additional study of this hypothesis would be helpful in growing spring geranium crops.

IRRADIANCE LEVELS:

The effects of different irradiance levels on the inductive responses to continuous irradiation at 30 °C were studied in combination with the duration of treatment and age of plants (Exp. 3). The results are presented in Figures 2 and 3 and Table 2. Irradiance levels had a strong influence on both time to anthesis and number of nodes to the first inflorescence (Table 2). Significant interaction of irradiance with the age of the plants and duration of treatment is evident in the data.

The age of the plants at the beginning of treatment had a great effect on the responses to the irradiance levels. Eighteen-day-old plants showed no significant response to the irradiance treatments. In 24-day-old plants, irradiances of 240 μmols m^{-1} $^{-2}$ reduced time and nodes to first inflorescence in 17, 50 and 100 percent of the treatment populations from 6, 9, and 12 days of treatment. In 30-day-old plants 3, 6, 9, and 12 days of irradiance of 240 μmols m^{-1} $^{-2}$ reduced days and nodes to anthesis in 17, 50, 83, and 100 percent of the population. Increased age at the beginning of treatment reduced the duration of treatment required for induction. In 30-day-old plants an irradiance of 120 μmols m^{-1} $^{-2}$ for 6, 9, and 12 days induced earlier flowering in 33, 50, and 50 percent of the population, but in 24-day-old plants flowering time and nodes were decreased only by the 12 day exposure to the 120 μmols m^{-1} $^{-2}$. No responses were observed in treatments at 60 μmols m^{-1} $^{-2}$, regardless of the age of the plants or the duration of treatment. Generally, at lower irradiances and with younger plants, longer periods of treatments were required.

The mean daily cumulative PPF has been highly correlated to the days to flower in the previous section (I) of this dissertation. The dependency of geraniums on irradiance levels for induction and/or development of flower primordia is apparent. Converting the treatment levels into mean daily cumulative Photosynthetic Photon Flux (CPPF), 120 $\mu mols^{-1}\ m^{-2}$ of continuous irradiation provides 10.4 mol d^{-1} and 240 $\mu mols^{-1}\ m^{-2}$ provides 20.4 mol d^{-1}. In literature "critical irradiance" levels for flower induction have been reported. Erickson et al. (11) proposed that a mean dialy CPPF of above 9.0 was necessary for accelerated anthesis when supplemental light was applied. The data of Tsujita (23) indicated that a mean daily CPPF of near 10 was required to induce flowers when supplemental light was supplied. It is interesting here to note that with continuous irradiance treatments for as short as 9 days at 10.4 mol d^{-1} applied to 30-day-old plants, decreased node numbers and time to anthesis occurred in 50% of the population. A response to a threshold or "critical irradiance" level is apparent.

SUMMARY AND CONCLUSIONS:

The work presented here, coupled with field observation and information in the literature, has led to a number of conclusions about flowering in hybrid geraniums.

1. Reproductive responses to high irradiance was dependent on the age or maturity of the plants. Plants were not responsive until they passed through a juvenile phase which in the cv. Ringo Scarlet lasted through about the fourth leaf.

2. Irradiance levels influenced induction. Continuous irradiances of 240 μmols m^{-1} $^{-2}$ decreased days and number of nodes from sowing to anthesis when applied for 9 days at 30 ^{o}C. Lower irradiances, 120 μmols m^{-1} $^{-2}$, were effective when the plants were treated for a duration of 12 or more days.

3. Temperature also influenced induction. Days and number of nodes from sowing to anthesis were decreased from continuous treatment with temperatures of 30 ^{o}C and irradiances of 120 μmols m^{-1} $^{-2}$. Lower temperatures were effective at higher irradiances or when given for longer durations.

4. Treatment duration was dependent on the irradiance level and temperature as well as the maturity of the plants. On 30-day-old plants durations as short as 6 days resulted in some decrease in the number of days and nodes to anthesis. Consistent early induction was obtained from 12 days on continuous irradiation with 240 μmols m^{-1} $^{-2}$. Decreased temperatures or irradiance levels increased the

duration of treatment necessary for early induction.

5. Cultivars differed in response. Although this aspect was not studied here, field observations indicate cultivar differences in the length of the juvenile phase, the minimum irradiance needed for induction, and the duration of the irradiance.

Large reduction in node numbers were associated with small changes in the rates of leaf emergence, thus, flowering responses to irradiance levels are the likely result of inductive responses in addition to accelerated growth rates.

HYPOTHESIS:

Since high irradiance levels were required to obtain early flowering in a large percentage of the population, since the response was not simply a growth response, and since the number of nodes decreased along with earlier flowering, it appears that the response may be called photomorphogenic as defined by Wareing and Phillips (25) and is high irradiance and temperature dependent. Photosynthesis may also play a significant role in the response. This response might best be termed a HIGH IRRADIANCE INDUCTION RESPONSE (HIIR). Further investigation, may show that the high irradiance is necessary over a given daily period and for a given number of consecutive days. If this were the case, a more descriptive term might be "photon-flux-periodism" or simply "flux-periodism" in which a given irradiance could be necessary for a given daily interval and for a certain series of days to provide for induction and/or differentiation of flowers. This phenomenon if more thoroughly explored mav assist in defining why a number of plants demonstrate a given irradiance requirement for flowering (5, 17, 19). Further identifying and understanding this phenomenon may also help explain why shaded portions of many plants, having relatively independent meristematic regions, produce less flowers than those in full sun, and why many long day plants require sufficient daily duration of high irradiance to flower. The long day requirement may be a protraction of a high irradiance requirement in these species.

The present and future observations made require an orderly explanation of the phenomena surrounding flowering in hybrid geraniums. A reasonable hypothesis for the early flowering response in hybrid geraniums, based on present literature, field observations, and the data presented here might take the following form.

A high irradiance induction response exists in hybrid geraniums. A cultivar dependent juvenile phase must be passed before floral induction in the meristem is possible. A cultivar dependent series of nearly consecutive days of sufficiently high irradiance and temperature over a long enough daily period (flux period) are necessary to provide both the photomorphogenic stimuli and the photosynthates necessary for floral initiation and/or development. Shaded and winter grown plants seldom receive sufficient flux-periods to induce flowers, especially to meri

upor

decl

vega

meristematic regions or leaves subtending those regions. Upon removal of the reproductive stimuli a gradual depletion of the flowering growth will occur until only vegetative growth remains.

Table 1. Effect of temperature and duration of continuous irradiation (240 µmol s^{-1} m^{-2}) on the days and nodes to anthesis in *Pelargonium hortorum* - Bailey 'Jackpot'.

Temperature °C	Duration days	Days to anthesis from sowing	Days to anthesis from treatment	Early anthesis[Z]	Nodes to anthesis from sowing	Nodes to anthesis from treatment	Early induction[Y]
20	3	182.6	105.6	0	27.0	16.4	0
20	6	185.6	108.6	0	25.8	15.2	0
20	12	175.2	98.2	20	24.8	14.2	20
25	3	180.2	103.2	0	26.6	16.0	0
25	6	184.2	107.2	0	26.6	16.0	0
25	12	127.6	50.6	100	19.2	8.6	100
30	3	183.6	106.6	0	27.2	16.6	0
30	6	155.0	78.0	40	21.6	11.0	40
30	12	124.6	47.6	100	19.4	8.8	100
H.S.D.[Y]		26.5	26.5		5.5	5.5	

Z Percent of the population showing early anthesis by flowering in 55 days or less from the beginning of treatment.

Y Percent of the treatment population reaching anthesis with the emergence of 12 or less nodes from the beginning of treatment.

X Tukey's w test (honestly significant difference), = 0.05.

Table 2. Analysis of variance for the effects of age, irradiance, and duration of treatment on days and nodes to flower in *Pelargonium hortorum* - Bailey 'Sprinter scarlet'.

Factor	Degrees of Freedom	Nodes		Days	
		F	Sig. F[Z]	F	Sig. F
Age	2	19.01	***	11.26	***
Irradiance	2	31.86	***	26.29	***
Duration	4	15.19	***	8.49	***
Age x Irr.	4	5.76	***	4.77	***
Age x Dur.	8	6.14	***	4.71	***
Irr. x Dur.	8	7.80	***	5.17	***
Age x Irr. x Dur.	16	2.08	**	1.67	n.s.

[Z] Significance of the factor or the interaction of factors; n.s. = not significant, ** α= 0.01 , *** α= 0.001

Figure 1. Effects of duration of continuous irradiance (240 umol $s^{-1}m^{-2}$) on days and node number from treatment to anthesis at 30°C in *Pelargonium hortorum* - Bailey 'Ringo Dolly".

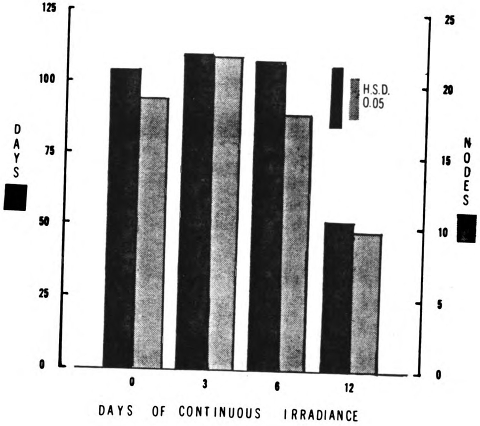
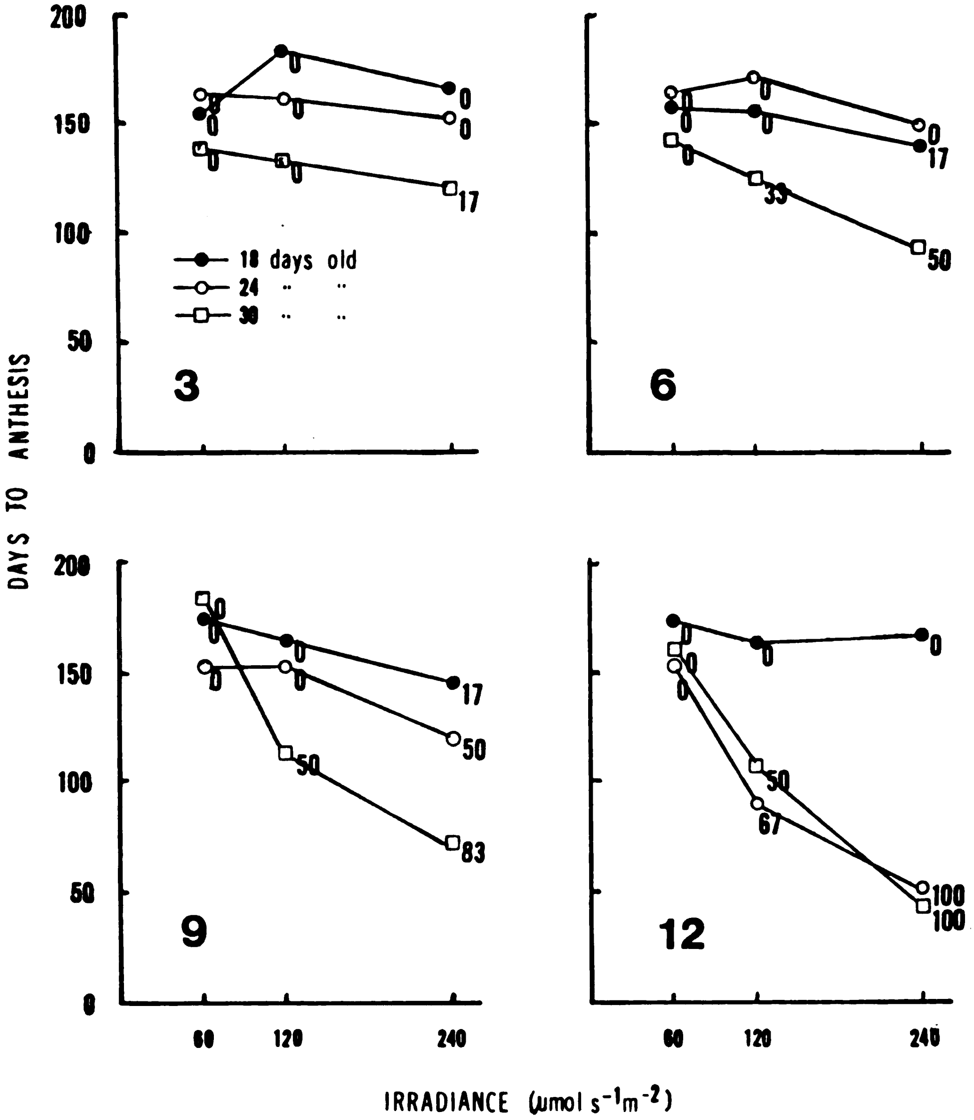

125
100
75
50
25
0
DAYS
25
20
15
10
5
0
NODES
H.S.D.
0.05
0
3
6
12
DAYS OF CONTINUOUS IRRADIANCE

Figure 2. Mean effects of irradiance, plant age, and duration of treatment at 30°C on days from treatment to anthesis and percent early induction[Z] in *Pelargonium* *hortorum* - Bailey 'Sprinter Scarlet'.

(A) 3 days of continuous irradiance.
(B) 6 days of continuous irradiance.
(C) 9 days of continuous irradiance.
(D) 12 days of continuous irradiance.

Z number adjacent to plotted means indicate the percentage of the treatment population to reach anthesis in 55 days or less from the beginning of treatment.


DAYS TO ANTHESIS
200
150
100
50
0
18 days old
24 " "
30 " "
3
6
9
12
60
120
240
IRRADIANCE (μmol s-1m-2)
0
0
0
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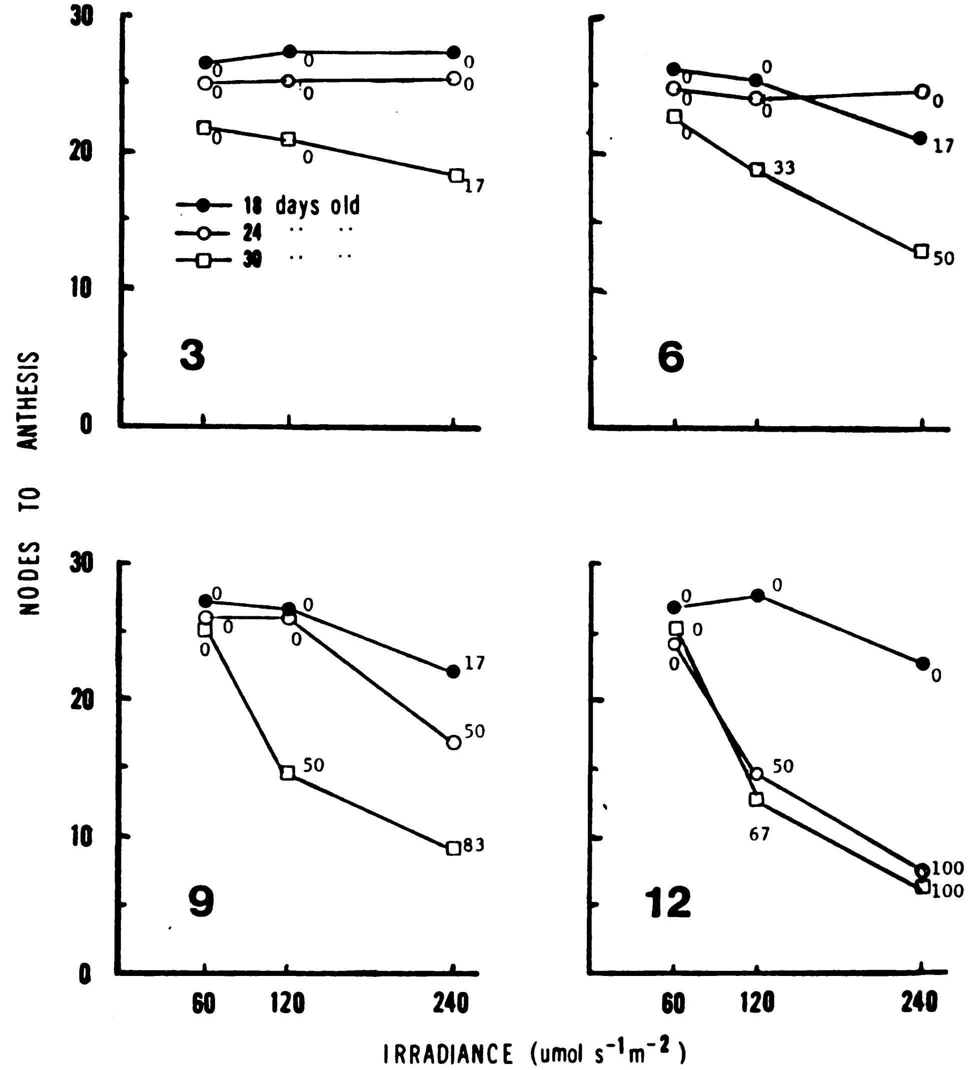
0
0
0
0
17
0
0
0
0
17
33
50
0
0
0
0
0
17
50
50
83
0
0
0
0
0
50
67
100
100

Figure 3. Mean effects of irradiance, plant age, and duration of treatment at 30°C on nodes from treatment to anthesis and percent early induction[z] in *Pelargonium hortorum* - Bailey 'Sprinter Scarlet'.

(A) 3 days of continuous irradiance.
(B) 6 days of continuous irradiance.
(C) 9 days of continuous irradiance.
(D) 12 days of continuous irradiance.

[z] number adjacent to plotted means indicate the percentage of the treatment population to reach anthesis with the emergence of 12 or less nodes from the beginning of treatment.


30
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10
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NODES TO ANTHESIS
18 days old
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30 .. ..
3
6
9
12
0
17
33
50
83
67
100
60
120
240
IRRADIANCE (umol s^{-1}m^{-2})

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SECTION III

MODELING REPRODUCTIVE DEVELOPMENT IN HYBRID GERANIUMS

ABSTRACT:

Functional relationships relating reproductive responses to irradiance and day and night temperatures in hybrid geraniums (Pelargonium hortorum - Bailey cv. 'Ringo Scarlet') were developed. Predictors for time from sowing to the primary stages of initiation, visible bud and anthesis, were formulated using multiple linear regression analysis. Predictors of the interval between the primary stages were fit to the differences of the means. Eighty-one percent of the variation in days to initiation and visible bud and up to 55% of the variation of days to anthesis were accounted for by functions including the variables: irradiance, day temperature, and night temperature. The relative influence of these variables changed with advances in stage of development. Irradiance was most significant at the time of floral initiation and remained influential through differentiation to visible bud. In the early stages of growth increased day temperature accelerated the rate of initiation and bud development. However, day temperature was most influential in the development from visible bud to anthesis. Night temperature effects were comparatively small at all stages. No single function could effectively predict the reproductive developmental responses without consideration of plant age or stage of development. A schematic representation of the relative influence of irradiance and day and night temperatures at stages of development is presented. A "Critical Irradiance" level was necessary to accelerate flower initiation and bud

development. Cuboid presentations of response surface models graphically represented the four-dimensional dynamics of the models.

INTRODUCTION:

In the production of hybrid geraniums, new technological developments give rise to a need for development of functional whole-plant models. The developments include: the recognition of a high degree of flowering responsiveness to light and temperature, the availability of interactive computing facilities used in greenhouse environmental control, and the widespread use of supplemental lighting in crop production. Functionally defined relationships can be useful in crop production to predict responses and find optimum production conditions. The functions can also provide clearer definitions of both separate and interacting influences on physiological responses.

In floriculture crops, predictive models which simulate both separate and simultaneous changes in light and temperature inputs are limited (1, 22). In hybrid seed propagated geraniums, differences have been observed in the reproductive responses to: irradiance (photosynthetic photon flux) reported as PPF, measured in the 400-700 nm range) (5, 6, 10, 12, 16, 17, 18, 27, 33), day temperature (DT) (10, 11, 20, 33), and night temperature (NT) (15, 23, 31, 33). Although many useful findings and temperature recommendations for production have been reported (13, 18, 27, 30) little information is available on the simultaneous influences of light and of day and night temperatures. In addition stage of development has often confounded the interpretation of the data (15, 16, 17, 18, 27, 30). Recent work (3, 11, 12, 20, 34) indicates that plant maturity and the stage of reproductive development must be considered in studying the responses of geraniums to environmental factors.

It was the purpose of this study to develop representative functional models of reproductive responses to irradiance and day and night temperature during the different stages of development in hybrid geraniums.

MATERIALS AND METHODS:

Similar culture practices were used in all phases of the experiment. A peat-lite medium composed (by volume) of 50% fibrous peat, 25% vermiculite, and 25% perlite was used both as a germination and growing medium. Seeds of the cultivar 'Ringo Scarlet' were sown into 5 cm square plastic pots covered to a depth of 0.5 cm, and germinated at 22° + 2° C. Plants were watered as needed with a constant liquid feed program using a water soluble fertilizer (20N - 8.7P - 16.7K) to provide 200 mg/l nitrogen at each watering. A day-night cycle of 14 and 10 hours was used. Greenhouse temperatures were set at 17° + 2° C night and 21° + 2° C days. Ten days after emergence the plants were transferred to the growth chamber treatments. Lighting was provided using cool white fluorescent lamps. The irradiances at the upper surface of the leaf canopy were measured weekly using a Li-Cor (Lincoln Nebraska) Li-185B meter and Li-190SB quantum sensor (measuring in the 400-700 nm range). The distance from the lamps was adjusted weekly to maintain the desired levels of irradiance. Temperature was checked daily and varied by not more than +2° C. When plants were 37 days old, a spray application of 1500 mg/l of (2-chloroethyl) trimethylammonium chloride, chlormequat (CCC), was made to simulate current production practices. At the age of 49 days, the plants were repotted into 9-cm square plastic pots and grown pot-to-pot to simulate production spacing.

A 3-factor, 5-level central composite design was used (Table 1). The ranges for the 3 factors were 50 - 450 $\mu mols\ m^{-1}\ {}^{-2}$ for PPF and 10-30 ^{o}C for day temperature (DT), (14 hours) and 10-30 ^{o}C for night temperatures (NT) (10 hours).

Data were collected on 9 plants at seven day intervals beginning with day 36 and extending to day 78 with additional samplings when all 9 plants reached visible bud and anthesis. On treatments 1 and 2, two week sampling intervals were used because of the slow growth rate. Dates of visible bud and anthesis were recorded. Visible bud was defined as the day when buds reached a diameter of 0.5 cm or larger. Anthesis was the day when a single petal began to reflex to a horizontal position. Leaf area, fresh weight, dry weight and plant height to the surface of the uppermost leaf were recorded and are presented in another section. Apical meristems were preserved in FAA (50% ethyl alcohol, 10% formaldehyde, 5% glacial acetic acid and 35% distilled water), dehydrated with tertiary butyl alcohol and infiltrated with paraffin (21). At a later date the meristems were dissected and examined under a microscope for evidence of reproductive differentiation. Reproductive differentiation, i.e. flower, initiation, was considered to have occurred if development reached stage 3 as described by Wetzstein and Armitage (31).

An analysis of variance, polynomial analysis, and multiple regression analysis were performed using the 'Oneway' and 'Regression' subroutines of SPSS (26), (Tables 1 through 9). Linear, and linear-interaction terms along with squared and cubic terms of irradiance and day and night temperature were regressed on days to initiation, visible bud and anthesis. Comparison of the simplest and the most complex equations for each response was made. Step-wise addition of all factors with a significant (0.05) impact on the descriptiveness of the equation, in the presence of the previously added factors, provided the simplest function. A second equation was developed that included linear terms forced into the function, followed by step-wise addition of the remaining significant (0.05) terms. In a third equation, all terms were forced into the equation.

Three dimensional surface and contour plots (Figure 1 through 3) were developed using the 'Surface II' plotting system (28). Equations with linear terms forced-in were used to develop the contoured surfaces. To unitize the surface plots, the height of each surface was adjusted to a percentage of the surface with the greatest range. A schematic representation of the relative influence of the treatment at each stage was developed considering the simple correlations of each variable at each stage (Figure 4).

RESULTS AND DISCUSSION:

PPF levels were most influential on reproductive development at all stages. Linear, quadratic, and cubic terms (Table 3) most effectively describe variations in response to PPF levels.

Day temperature variations produced significant linear and quadratic initiation responses. In extending the treatments to visible bud, only linear functions were significant. To anthesis, linear, quadratic as well as cubic DT terms were again significant. These changes in responsiveness to DT during stages of growth are in support of the findings of Heins (20) and Armitage (1).

Responses to night temperature were minimal compared with DT and PPF. When treatments are extended to anthesis, the highest significance of NT was observed.

In the regression analysis, PPF factors were significantly negatively correlated with days to initiation and visible bud and less highly correlated to anthesis (Table 4 through 6). NT as a linear function is not significantly correlated with days to initiation, visible bud, or anthesis. NT interactions with PPF or DT yielded significant correlations. Many significant responses to changes in NT are reported in the literature (13, 23, 30). In view of these reports it was decided that, despite the low significance of linear NT in the treatments used, the variable would be submitted as one of the predictive factors. The apparent description of some responses to NT is presented in Figures 1 through 4. Future work may more closely define these NT responses.

Regression coefficients and their significance in the presence of other terms indicate the relative importance of each variable at their respective stages of development (Table 4 through 9). Although equations with all terms forced in provided the highest correlation with the data, equations with only linear terms forced in appear to provide nearly as complete a definition of the response without an overfit model. Equations with only significant terms added into the model had fewer terms but were less traditional in that higher order terms were included in the absence of the lower order terms.

Primary prediction equations for the time from sowing to initiation, visible bud and anthesis were determined from raw data. Secondary equations, describing responses between the primary stages were fitted to the interval between the primary predictors using differences in treatment means. They thus describe the physiological responses for the intervals between the primary stages. The responses are presented in Figure 4. As a result, the predictors can be fitted together to form a unit which covers sequentially all developmental stages.

Up to 81% of the variation in days to initiation and to visible bud, and 50% to anthesis are accounted for in the primary predictors. Up to 97% of the variation of the mean difference from initiation to visible bud and up to 78% from visible bud to anthesis are accounted for in the secondary predictors containing all factors. In predicting the time from initiation, through visible bud, to anthesis. Up to 93% of the variance of the mean difference is accounted for. This decrease in accountability is likely the result of physiologically different responses at different stages.

The precision of these predictors appears to be within the ranges presented by other authors. Erickson et al. (18), under greenhouse conditions, achieved 41 to 64% correlation of days to anthesis with cumulative PPF. Armitage (1) found up to 99% description of photosynthetic rates in geraniums as a quadratic polynomial of PPF when held at a constant temperature. Ninety-three percent of the variation in days from sowing to flower was described as a function of mean daily PPF (10). And up to 97% of the variation in days from visible bud to anthesis was described using a second-order function of temperature under a given light condition (1).

Predicted values deviate by less than 10% from the observed means (Table 10). Limited and uniform distribution of the residuals for the initiation and anthesis predictors indicate adequacy of the equations. For anthesis, the equation underestimates at PPF 50 and 250 when temperatures are low and overestimates for PPF levels around 150 and above 350 when temperatures are high. However, over the full range of treatments, the anthesis predictor estimates close to the observed responses. The models, thus, can be considered to be a reliable representation of the responses to light and temperature for the cultivar 'Ringo Scarlet' when grown under constant environmental conditions.

In comparing the predicted values for anthesis to the data in the literature, the model predicts values within 0 to 9 days of the reported results for similar cultivars. Tsujita (30) flowered plants of the cultivar 'Encounter Red' in 103 days at DT = 22^{o}, NT = 17^{o}, and ambient light (averaged about 175 $\mu mols^{-1}\ m^{-2}$ on a 14 hour basis). The model predicts 101 days. With ambient plus supplemental light (245 $\mu mols^{-1}\ m^{-2}$), flowering occurred in 89 days. The model predicts 93 days. Miranda (25), had a Feb. 23 sowing of 'Ringo Scarlet' grown at DT = 22^{o} and NT = 17^{o} with an estimated mean PPF, on a 14 hour basis, of near 175 $\mu mols^{-1}\ m^{-2}$ which flowered in 95 days (predicted 96). With NT variations, Konjoian and Tayama (23) observed a 17-day increase in the time to flower from an 11 ^{o}C drop in NT. The model predicts only a 9 day increase. White and Warrington (33) have demonstrated no effect of NT at higher PPF levels; this is in approximate agreement with the model. Differences in DT can explain the differences observed in a recent comparison of cultivars grown in Michigan and Georgia (4). Many comparisons of the data indicate a close correlation of the predicted values and observed trends. Thus these models closely represent what happens in many similar cultivars in response to a wide range of environmental combinations.

Day temperature was significantly negatively correlated to reproductive development at all stages. In the interval between visible bud and anthesis, the highest simple correlation to any of the variables was realized (r = -

0.6180). Also very important is the effect of high DT on initiation. It appears that increasing temperature at or near the time of initiation has the greatest influence on reproductive development, especially when light levels are low. The influence of DT on initiation is also reflected in the visible bud and anthesis data. It appears that the developmental influence of DT, relative to NT and irradiance, increases to initiation and then decreases until visible bud. After visible bud, DT becomes very important. With increased irradiance levels, the influence of DT decreases for all stages except visible bud to anthesis. Interactions of DT with PPF and NT are discussed later.

Variations in irradiance were negatively correlated to the rate of reproductive development (Table 4 through 9). The highest simple correlation was in the interval from initiation to visible bud ($r = -0.5864$). Time from sowing to initiation was nearly as highly correlated ($r = -0.5192$). These findings correspond to those previously observed (5, 20). The importance of high irradiance during early stages of development have been reported (12).

The influence of irradiance can most accurately be described in functions which include both lower and higher order terms. The equations presented in Tables 6 through 11 emphasize the impact of PPF on the responses, while Figures 1 through 4 clearly depict the degree of response to each of the primary stages. In development to visible bud an irradiance threshold is apparent in the rapid drop in days around the irradiance of 200 $\mu mols^{-1}\ m^{-2}$ (Figure 4, B and D). However, limited data from sowing to initiation did not yield a function which reflects the presence of a distinct threshold for that stage. The author suspects that more detailed studies of initiation may demonstrate an irradiance threshold response in the interval from sowing to initiation and after the juvenile phase has been passed. The "critical irradiance" appears to fall in the PPF range from 150 to 250 μmols m^{-2} $^{-1}$ and it is suspected that the critical irradiance level is cultivar dependent. The data of Tsujita (30) indicates that a critical cumulative PPF, equivalent to a 14-hour daily irradiance of near 200 μmols^{-1} m^{-2}, is necessary to achieve flowering at DT = 22^{o} and NT = 17^{o}. Erickson et al. (18) suggest that a mean daily PPF of greater than 9.0 mol d^{-1} (175 μmols^{-1} m^{-2} for 14 hours) is necessary for earlier induction. In previous work, irradiance treatments have been confounded by daily variations in PPF for periods before and after the critical induction period. The present work provides data from controlled, simulated conditions, separated by developmental stages, and yields a clearer definition of the responses during each stage.

Comparing the apparent threshold PPF levels for reproductive development with a photosynthetic curve for geraniums (5), we see that irradiance levels for initiation are much lower than light saturation levels. According to Armitage (5) the light saturation point is near a PPF of 1000 μmols^{-1} m^{-2} and the compensation point is near 70 μmols^{-1} m^{-2} at 25^{o} C.

Irradiance alone does not fully explain the variance in reproductive responses. Temperature influences the degree of response. NT increases result in decreases in time to visible bud and anthesis at low DT but has little effect when DT is high. One can speculate that in this C-3 plant, photosynthetic products are likely fully metabolized at higher DT leaving little reserves for night growth. When DT is low, photosynthates may accumulate during the day, and during the night growth may continue. Thus, the effect of the following NT may be important. The models demonstrate a greater response to NT after cool days. White and Warrington (34) found no significant impact on soluble sugars and carbohydrates or on the rate of reproductive development from varying NT when irradiance and DT were high. In the work of Carpenter and Carlson (15), NT showed a strong influence under moderate day temperatures (22-24 ^{o}C) and high irradiance (PPF of approximately 475 μmols $^{-1}$ m $^{-2}$).

Day temperatures have a large influence on the reproductive response to the initiation and to the visible bud stages (Figures 1 and 2). Increased DT greatly increases the rate of initiation at all irradiance levels, but at lower irradiances the increase per degree is much greater. The responses that occur prior to visible bud are reflected and accumulate in the visible bud and anthesis responses. However, in the interval from visible bud to anthesis, no apparent interaction of light and temperature exist, while DT had the greatest influence on the rate of development.

Night temperature was less significant than day temperature or PPF in influencing reproductive responses. In separating out NT effects, little influence was observed over the broad range and combination of treatments studied here. The interactions discussed previously indicate that if DT is near optimum, NT may be reduced to low levels without greatly affecting the rate of reproductive development to the visible bud stage. After visible bud, the relative influence of the NT becomes greater. If DT is suboptimal for the irradiance, increases in NT have a greater effect. Thus, the cooler the DT under high light, the greater the effect of NT. These suggestions are in line with the observations of White and Warrington (33).

Figure 5 provides a schematic overview of the relative reproductive developmental influences of each of the three factors studied. Note that both day and night temperature are equally influential during germination (stage A). During the vegatative juvenile phase (B) the influence of PPF rises. At that stage, the growth rate becomes important in developing sufficient leaves (3) to respond to the high irradiance. Photosynthates produced are subject to metabolism and thus the influence of temperature remains high. Once juvenility is passed and the mature phases begin, shifts in responsiveness occur, apparently irrespective of photosynthetic needs. During the inductive phase (C) irradiance levels become very critical. The need for high irradiance persists to visible bud. This author has observed, in a number of marginally inductive light conditions, that very young buds fail to fully develop in low irradiance. The aborted buds often remain on the stem, while vegetative growth continues. In the flowering stage (D), the impact of light greatly declines while DT and NT appear to be much more influential. When light is limited during the flowering stage, flowering occurs but quality is reduced. In the stages subsequent to first anthesis (E), the author suspects a continued need of high irradiance for continued reproductive development in any given active meristem. After continued periods of growth in the shade, geraniums continue to develop leaves but cease to flower until high irradiance is present (19). It is apparent that a survival strategy exists. In the continued development of the meristem, a balance of vegetative and reproductive growth must exist. This balance is controlled in response to the day and night temperatures and the light received by the plant.

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SUMMARY AND CONCLUSION:

The functional relationships found in these experiments represent responses of a single cultivar to controlled environmental conditions. These responses closely agree with reported data from greenhouse studies with similar cultivars. The models are thus considered to be reasonably representative of responses in the field and for similar cultivars. The functions are useful in distinguishing physiological changes and the influence of each of the environmental parameters over the developmental stages. Irradiance appears to be required at or above a critical level before floral initiation occurs.

Day temperatures interact with irradiance to accelerate initiation and development to visible bud. From visible bud to anthesis temperature alone was of greatest significance. A "critical irradiance" appears to be necessary for induction and may be necessary through to visible bud. All the developmental stages are accelerated by increasing temperatures up to about 28 ^{o}C. Night temperature appears to be important only when irradiance is high and DT is low.

From the data presented here it can be concluded that:

1. A single functional relationship describing reproductive development cannot be employed. Consideration must be given to the stage of development.

2. Separate functions which represent stages of development can predict the observed responses.

3. Graphic representation of the functions can readily be used to examine the physiological responses and observe the effects of single and interacting factors.

4. The relative influences of irradiance and day and night temperature vary with the stages of development (Figure 5). A more thorough examination of the juvenile and initiation stages should be made to more clearly describe the responses.

5. Irradiance and DT, alone, and interacting, are very influential in reproductive development. NT appears to have less effect under most conditions. More extensive studies of NT relative to DT are necessary to define the impact of NT on reproductive development.

Table 1. Influence of PPF, day and night temperature on the reproductive development of *Pelargonium hortorum* - Bailey 'Ringo Scarlet'.

Treatment number	Treatment Environment			Average No. of Days to		
	PPF[u]	DT[v]	NT[w]	initiation[x]	visible bud[y]	anthesis[z]
1	50	20	20	93.0	154.9	190.4
2	150	15	15	80.5	112.2	155.0
3	150	25	15	56.0	71.4	91.4
4	150	15	25	72.8	117.2	141.9
5	150	25	25	53.8	72.8	88.6
6	250	20	20	61.5	75.6	114.8
7	250	10	20	74.5	93.6	130.1
8	250	30	20	43.2	59.7	78.2
9	250	20	10	61.1	80.0	121.7
10	250	20	30	-	72.7	118.8
11	350	15	15	58.3	87.4	134.6
12	350	25	15	44.3	64.2	82.2
13	350	15	25	69.0	78.8	120.4
14	350	25	25	47.8	69.2	80.3
15	450	20	20	50.2	65.3	113.4

u photosynthetic photon flux in the 400-700 nm range.
v day temperatures °C
w night temperatures °C
x as observable under 10X disecting scope
y first observed with a diameter of near 0.5 cm
z first emergence of a single petal of one floret

Table 2. Average effects of PPF, day and night temperature on the reproductive development of <u>Pelargonium</u> <u>hortorum</u> - Bailey 'Ringo Scarlet' over all treatments and interactions.

Treatment Environment	Average number of days to		
	Initiation	Visible Bud	Anthesis
PPF[Z]			
50	93.0	154.9	190.4
150	63.8	88.7	110.0
250	62.1	73.7	109.7
350	55.4	73.9	97.7
450	50.2	65.3	113.4
DT[Y]			
10	74.5	93.6	130.1
15	70.0	96.6	137.2
20	62.2	79.4	114.1
25	51.0	69.5	85.4
30	43.2	59.7	78.2
NT[X]			
10	62.2	79.6	121.7
15	59.5	81.7	106.3
20	64.5	86.0	114.4
25	64.5	79.6	100.2
30	60.0	63.7	118.8

[Z] photosynthetic photon flux in the 400-700 nm range.

[Y] day temperature in °C.

[X] night temperature in °C.

Table 3. Significance of the ploynomial contrasts of PPF, and day and night temperature on reproductive responses in *Pelargonium hortorum* - Bailey 'Ringo Scarlet'.

Environmental Factor	Response Significance^Z		
	initiation	visible bud	anthesis
PPF			
Between Levels	***	***	***
Linear	***	***	***
Qudratic	**	***	***
Cubic	**	***	**
Deviations	*	*	***
Day Temperature			
Between Levels	***	***	***
Linear	***	***	***
Quadratic	*	n.s.	*
Cubic	n.s.	n.s.	***
Deviations	n.s.	n.s.	n.s.
Night Temperature			
Between Levels	n.s.	n.s.	n.s.
Linear	n.s.	n.s.	n.s.
Quadratic	n.s.	n.s.	n.s.
Cubic	n.s	n.s.	n.s.
Deviations	n.s.	n.s.	n.s.

Z significance of the factor in describing the developmental response; *α=0.05, **α= 0.01, ***α= 0.001, n.s. = not significant

Y Photosynthetic photon flux in the 400-700 nm range.

Table 4. Predictions for days from sowing to floral initiation in <u>Pelargonium hortorum</u> - Bailey 'Ringo Scarlet'

Environmental variables	Simple r	All terms forced[Z] coefficient	sign.[W]	Linear terms forced[Y] coefficient	sign.	Step-wise addition[X] coefficient	sign.
Constant		215.044	***	161.174	***	142.996	***
PPF	-.519	-0.653	***	-0.617	***	-55.511	***
DT	-.614	5.507	n.s.	-0.231	n.s.	-	-
NT	.028	-16.795	**	-1.424	***	-	-
PPF x DT	-.773	2.213E-3	n.s.	-	-	2.900E-3	*
PPF x NT	-.403	5.897E-3	***	5.867E-3	***	5.462E-3	***
DT x NT	-.441	-9.186E-3	n.s.	-	-	-	-
$(PPF)^2$	-.452	1.570E-3	***	1.642E-3	***	1.630E-3	***
$(DT)^2$	-.629	-370.960E-3	*	-39.119E-3	*	-44.722E-3	***
$(NT)^2$	.013	929.300E-3	***	-	-	-36.086E-3	***
$(PPF)^3$	-.402	-1.767E-6	***	-1.885E-6	***	-1.885E-6	***
$(DT)^3$	-.627	5.960E-3	n.s	-	-	-	-
$(NT)^3$	-.002	-17.581E-3	**	-	-	-	-
R^2		.8278		.8052		.8060	
F-ratio		45.66		70.25		83.16	
Significance[V]		***		***		***	

Z all variables were forced into the prediction equation

Y only simple linear variables wer forced in with the remainder added step-wise if significant at α= 0.05.

X all variables were added step-wise if significant, α= 0.05.

W significance of the variable in the presence of the other variables in the equation; n.s. = not significant, * α= 0.05, ** α= 0.01, *** α= 0.001.

V significance of the regression equation containing the listed coefficients.

Table 5. Prediction equations for days from sowing to visible bud in *Pelargonium hortorum* - Bailey 'Ringo Scarlet".

Environmental variables	Simple r	All terms forced		Linear terms forced		Step-wise addition	
		coefficient	sign.	coefficient	sign.	coefficient	sign.
Constant		265.280	***	218.715	***	314.368	***
PPF	-.519	-1.543	***	-1.566	***	-1.544	***
DT	-.614	12.306	*	12.514	*	-5.269	***
NT	.028	-6.843	n.s.	-0.143	n.s.	-	-
PPF x DT	-.773	13.569E-3	***	13.248	***	12.454E-3	***
PPF x NT	-.403	-1.731E-3	n.s.	-	-	-	-
DT x NT	-.441	59.119E-3	n.s	-	-	-	-
(PPF)^2	-.452	4.186E-3	***	4.154E-3	***	4.166E-3	***
(DT)^2	-.629	-1.022	***	-0.964	***	-	-
(NT)^2	-.013	-3.110	n.s.	-	-	-	-
(PPF)^3	-.402	-4.440E-6	***	-4.398E-6	***	-4.453E-6	***
(DT)^3	-.627	17.154E-3	***	16.204E-3	**	-	-
(NT)^3	-.002	-5.149E-3	n.s.	-	-	-	-
R^2		.8130		.8098		.7939	
F-ratio		61.216		92.04		135.59	
Significance		***		***		***	

Table 6. Prediction equations for days from sowing to anthesis in *Pelargonium hortorum* - Bailey 'Ringo Scarlet'.

Environmental variables	Simple r	All terms forced coefficient	All terms forced sign.	Linear terms forced coefficient	Linear terms forced sign.	Step-wise addition coefficient	Step-wise addition sign.
Constant		1.033	n.s.	21.753	n.s.	264.088	***
PPF	-.255	-1.243	***	-1.150	***	-1.104	***
DT	-.571	46.481	***	49.865	***	-	-
NT	-.049	6.338	n.s.	-0.416	n.s.	-	-
PPF x DT	-.510	6.538E-3	n.s.	-	-	-	-
PPF x NT	-.240	0.272E-3	n.s.	-	-	-	-
DT x NT	-.438	0.111	n.s.	-	-	-	-
$(PPF)^2$	-.177	3.406E-3	***	3.629E-3	***	3.477E-3	***
$(DT)^2$	-.581	-2.722	***	-2.694	***	-94.994E-3	***
$(NT)^2$	-.047	-0.487	n.s.	-	-	-	-
$(PPF)^3$	-.126	-3.414E-6	***	-3.718E-6	***	-3.565E-6	**
$(DT)^3$	-.574	43.228E-3	***	42.733E-3	***	-	-
$(NT)^3$	-.044	8.271E-3	n.s.	-	-	-	-
R^2	.5557			.5486		.4952	
F-ratio	21.89			37.32		53.46	
Significance	***			***		***	

Table 7. Prediction equations for days from initiation to visible bud in *Pelargonium hortorum* -Bailey 'Ringo Scarlet'.

Environmental variables	Simple r	All terms forced		Linear terms forced		Step-wise addition	
		coefficient	sign.	coefficent	sign.	coefficeint	sign.
Constant		60.866	n.s.	149.269	***	153.294	***
PPF	-.586	-0.910	n.s.	-0.989	***	-0.989	***
DT	-.281	12.665	n.s.	-2.813	*	-2.813	***
NT	.083	-1.077	n.s.	0.201	n.s.	-	-
PPF x DT	-.602	8.525	n.s.	8.525E-3	*	8.525E-3	***
PPF x NT	-.474	-6.025E-3	n.s	-	-	-	-
DT x NT	.137	8.500E-3	n.s	-	-	-	-
$(PPF)^2$	-.455	2.875E-3	n.s.	2.793E-3	**	2.793E-3	***
$(DT)^2$	-.310	-855.167E-3	n.s.	-	-	-	-
$(NT)^2$	.065	74.833E-3	n.s.	-	-	-	-
$(PPF)^3$	-.371	-3.054E-6	n.s.	-3.054E-6	*	-3.054E-6	***
$(DT)^3$	-.323	14.700E-3	n.s.	-	-	-	-
$(NT)^3$	.048	-0.300E-3	n.s.	-	-	-	-
R^2		.9710		.9786		.8717	
F-ratio		5.603		9.65		12.23	
Significance		n.s.		**		***	

Table 8. Prediction equations for days from visible bud to anthesis in *Pelargonium hortorum* - Bailey 'Ringo Scarlet'.

Environmental variables	Simple r	All terms forced		Linear terms forced		Step-wise addition	
		coefficient	sign.	coefficient	sign.	coefficient	sign.
Constant		-120.065	n.s.	65.480	**	43.599	***
PPF	.157	0.152	n.s.	18.635E-3	n.s.	-	-
DT	-.618	17.212	n.s.	-1.468	*	-	-
NT	-.189	13.665	n.s.	-0.450	n.s.	-	-
PPF x NT	-.212	-4.500E-3	n.s.	-	-	-	-
PPF x DT	.032	-0.050E-3	n.s.	-	-	-	-
DT x NT	-.545	0.113	n.s.	-	-	-	-
$(PPF)^2$	.190	0.499E-3	n.s.	-	-	-	-
$(DT)^2$	-.661	-0.973	n.s.	-	-	-	-
$(NT)^2$	-.152	0.973	n.s.	-	-	-	-
$(PPF)^3$	.214	0.858E-6	n.s.	-	-	-	-
$(DT)^3$	-.680	15.133E-3	n.s.	-	-	-1.230E-3	**
$(NT)^3$	-.109	17.866E-3	n.s.	-	-	-	-
R^2		.7830		.4420		.4620	
F-Ratio		0.601		2.903		11.18	
Significance		n.s.		n.s.		**	

Table 9. Prediction equations for days from initiation to anthesis in *Pelargonium hortorum* - Bailey 'Ringo Scarlet'.

Environmental variables	Simple r	All terms forced		Linear terms forced		Step-wise addition	
		coefficient	sign.	coefficient	sign.	coefficient	sign.
Constant		-54.040	n.s.	153.210	***	89.123	***
PPF	-.290	-0.757	n.s.	-0.389	*	-	-
DT	-.605	29.922	n.s.	-2.149	**	-	-
NT	-.084	11.467	n.s.	-0.299	n.s.	-	-
PPF x DT	-.553	4.025E-3	n.s.	-	-	-	-
PPF x NT	-.310	-6.075E-3	n.s.	-	-	-10.306E-6	*
DT x NT	-.468	0.122	n.s.	-	-	-	-
$(PPF)^2$	-.182	2.424E-3	n.s.	0.673E-3	*	-	-
$(DT)^2$	-.653	-1.829	n.s.	-	-	-	-
$(NT)^2$	-.074	-0.829	n.s.	-	-	-	-
$(PPF)^3$	-.108	-2.196E-6	n.s.	-	-	0.738E-6	*
$(DT)^3$	-.673	29.833E-3	n.s.	-	-	-1.660E-3	**
$(NT)^3$	-.059	16.233E-3	n.s.	-	-	1.788E-3	*
R^2		.9358		.6655		.6996	
F-ratio		2.42		4.97		5.821	
Significance		n.s.		*		**	

Table 10. The difference in observed (Y) and predicted ($\hat{Y}$) reproductive responses of <u>Pelargonium</u> <u>hortorum</u> - Bailey 'Ringo Scarlet'.

Treatment Environment			$(Y - \hat{Y})^W$		
PPF	DT^Y	NT^X	initiation	visible bud	anthesis
50	20	20	-1.6	-0.2	-8.0
150	15	15	-0.3	4.5	6.8
150	25	15	3.7	-0.9	3.0
150	15	25	2.0	-3.9	10.4
150	25	25	1.5	0.9	5.7
250	20	20	-0.8	0.1	-2.5
250	10	20	0.2	-0.3	-7.0
250	30	20	-4.3	-0.1	-3.1
250	20	10	-0.9	-2.7	-3.7
250	20	30	-	-0.7	-10.1
350	15	15	3.0	-0.9	5.3
350	25	15	1.7	3.1	3.1
350	15	25	-1.3	1.3	9.4
350	25	25	4.5	-1.8	4.8
450	20	20	-1.9	-0.2	4.8

Z Photosynthetic photon flux in the 400-700 nm range.
Y day temperature in °C.
X night temperature in °C.
W differences from the observed (Y) and predicted ($\hat{Y}$) values using the function with the linear terms forced in.

Figure 1. Predicted days to initiation for *Pelargonium hortorum* - Bailey 'Ringo Scarlet' as effected by PPF, day and night temperature.

★ DT = 15°C NT = 15°C
● DT = 20°C NT = 20°C
▲ DT = 25°C NT = 25°C

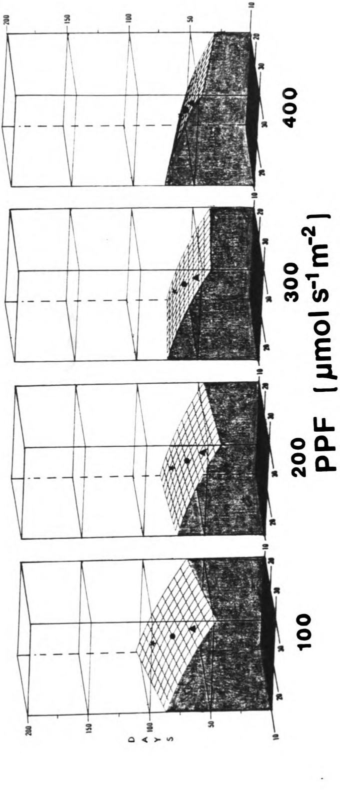

DAYS
200
150
100
50
10
20
30
100
200
300
400
PPF (µmol s-1 m-2)

Figure 2. Predicted days to visible bud for *Pelargonium hortorum* - Bailey 'Ringo Scarlet' as effected by PPF, day and night temperature.

★ DT = 15°C NT = 15°C
● DT = 20°C NT = 20°C
▲ DY = 25°C NT = 25°C

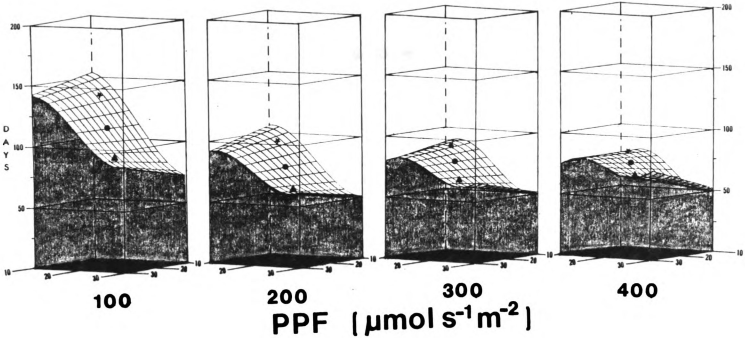

200
150
100
50
10
DAYS
20
30
30
20
100
200
300
400
PPF (µmol s-1 m-2)

Figure 3. Predicted days to anthesis for *Pelargonium hortorum* - Bailey 'Ringo Scarlet' as effected by PPF, day and night temperature.

★ DT = 15°C NT = 15°C
● DT = 20°C NT = 20°C
▲ DT = 25°C NT = 25°C

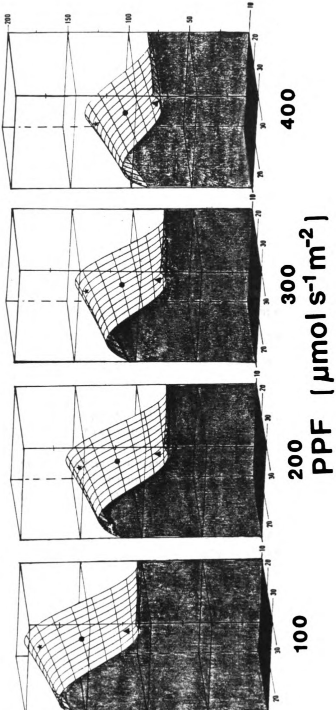
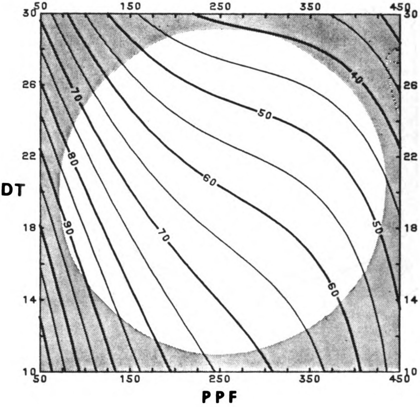

DAYS
200
150
100
50
10
20
30
30
20
10
100
200
300
400
PPF (μmol s-1m-2)

Figure 4. Predicted reproductive responses at night temperature 16°C[Z] for Pelargonium hortorum - Bailey as effected by irradiance, and day temperature at different stages of development.

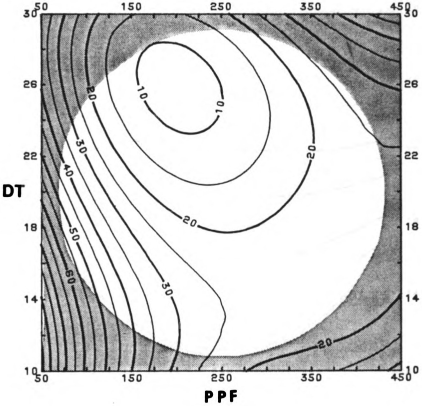
(A) Days from sowing to floral initiation.
(B) Days from initiation to visible bud.
(C) Days from visible bud to anthesis.
(D) Days from sowing to visible bud.
(E) Days from initiation to anthesis.
(F) Days from sowing to anthesis.

[Z] The shaded areas represent predictions outside the range of the experiment at night temperature 16°C in the central composite design.

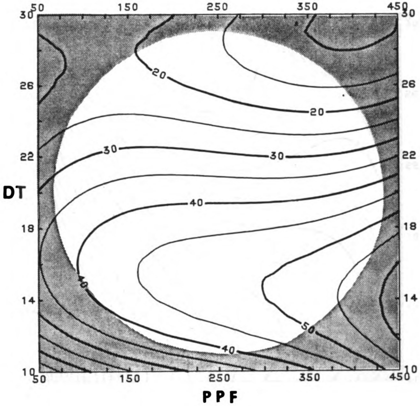
A. Days from sowing to floral initiation.



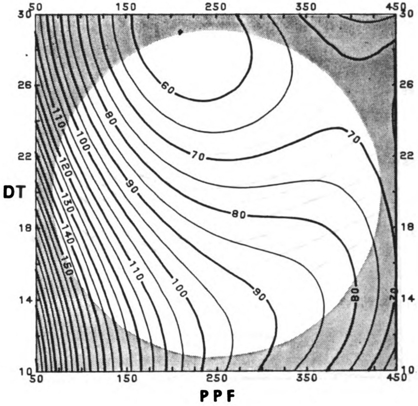
B. Days from initiation to visible bud.



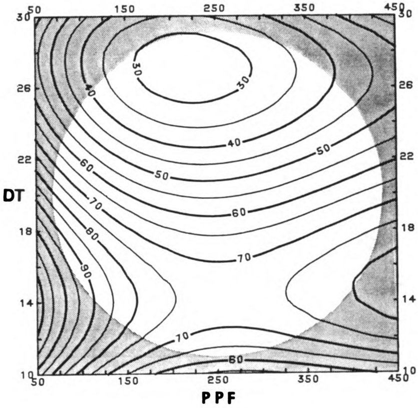
C. Days from visible bud to anthesis.



D. Days from sowing to visible bud.



E. Days from initiation to anthesis.



F. Days from sowing to anthesis.

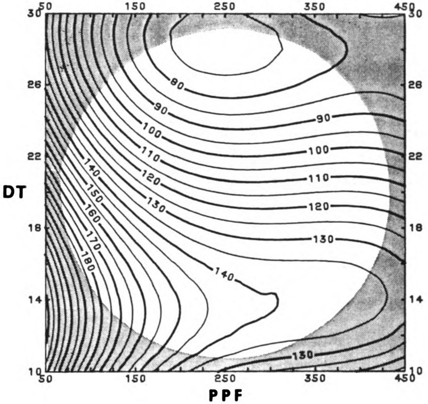
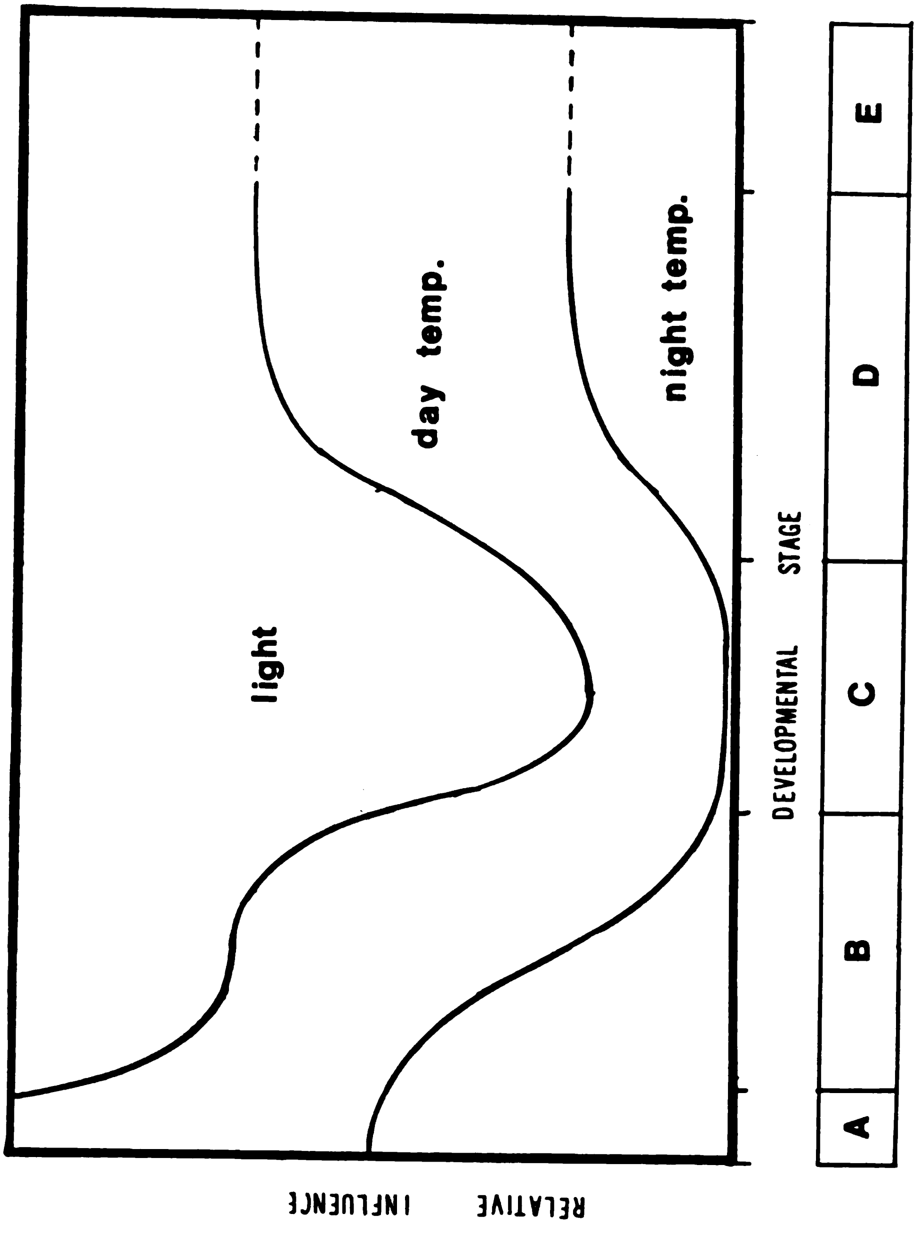


Figure 5. The relative influence of light, day and night temperatures on reproductive development at different stages of development in _Pelargonium_ _hortorum_ - Bailey 'Ringo Scarlet'.

(A) Germination.
(B) Vegetative (juvenile) phase.
(C) Initiation to visible bud phase.
(D) Visible bud to first anthesis phase.
(E) Equilibrium phase.


RELATIVE INFLUENCE
DEVELOPMENTAL STAGE
light
day temp.
night temp.
A
B
C
D
E

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SECTION IV

MODELING VEGETATIVE DEVELOPMENT IN HYBRID GERANIUMS

ABSTRACT:

Mathematical equations describing vegetative growth of hybrid geraniums (Pelargonium hortorum - Bailey) in response to irradiance and day and night temperatures over time were developed using response surface techniques. A central composite design employing irradiances (photosynthetic photon flux, PPF) from 50 to 450 μmols^{-1} m^{-2} and day and night temperatures ranging from 10° to 30°C, with samplings of plants from 36 days old to anthesis, provided data to develop predictons for total plant height, leaf area, shoot fresh and dry weight.

Up to 57% of the variance in plant height and leaf area, 55% in shoot fresh weight, and 47% in dry weight could be explained using a function of time, irradiance, with day and night temperatures. Only 10.6% of the variance in percent dry weight could be described using these variables.

Height was greatest at 20 C day and night temperatures. Leaf area was greatest with high day and low night temperatures. Fresh weight was most strongly influenced by night temperature. However, the greatest fresh weight occurred from the interaction of high night temperatures and low day temperatures. Low day temperatures over time yielded the greatest dry weight.

Height, leaf area, and fresh and dry weight increased with increasing irradiance up to 150 μmols^{-1} m^{-2}. Cuboid presentations of the response surface models graphically represent the five dimensions of the model.

INTRODUCTION:

In computerized greenhouse crop production, precise definition of developmental responses to separate and interacting environmental conditions has become increasingly important. The need to optimize greenhouse crop environments while minimizing inputs of total energy and other resources require functional definitions of responses to environmental factors. Modern computing facilities allow the constant monitoring and control of the greenhouse environment. By using predictive models and these facilities we can continuously and simultaneously monitor and alter the environment to assist in producing the desired product in a given time. However, there are few useful predictive models for floriculture crops which simulate both separate and simultaneous changes in responses to input variables (1, 13, 14).

In hybrid geraniums (Pelargonium hortorum - Bailey) many differences have been observed in vegetative responses to irradiance (5, 7, 9, 11, 12, 13), day temperature (4, 13, 22) and night temperature (8, 15, 20, 21, 22). With the ability to induce early flowering using high irradiance treatments (6), the need to predict the time and conditions required to produce a plant of a given marketable size is apparent. Vegetative growth models are useful to predict the size of a plant at a given age and to determine container size and plant production density necessary to obtain the desired product in the time allowed.

The purpose of this study was to develop representative functional relationships for hybrid geraniums by describing vegetative developmental responses to environmental factors over time. These models may be useful in predicting responses to the production environment.

MATERIALS AND METHODS

Similar culture practices were used in all phases of the experiment. A peat-lite medium composed (by volume) of 50% fibrous peat, 25% vermiculite, and 25% perlite was used both as a germination and growing medium. Seeds of the cultivar 'Ringo Scarlet' were sown into 5-cm square plastic pots covered to a depth of 0.5 cm, and germinated at 22^{o} + 2^{o}C. Plants were watered as needed with a constant liquid feed program using a water soluble fertilizer (20N - 8.7p - 16.7K) to provide 200 mg/l nitrogen at each watering. A day-night cycle of 14 and 10 hours was used. Greenhouse temperatures were maintained at 17^{o} + 2^{o}C night and 21^{o} + 2^{o}C days. Ten days after emergence the plants were transferred to the growth chamber treatments. Lighting was provided using cool white fluorescent lamps. The irradiances at the upper surface of the leaf canopy were measured weekly using a Li-Cor (Lincoln Nebraska) Li-185B meter and Li-190SB quantum sensor (measuring in the 400-700 nm range). The distance from the lamps was adjusted weekly to maintain the desired levels of irradiance. Temperature was checked daily and varied by not more than $+2^{o}$C. When plants were 37 days old, a spray application of 1500 mg/l of (2-chloroethyl) trimethylammonium chloride, chlormequat (CCC), was made to simulate current production practices. At the age of 49 days, the plants were repotted into 9-cm square plastic pots and grown pot-to-pot to simulate production spacing.

A 3-factor, 5-level central composite design was used (Table 1). The ranges for the 3 factors were 50 - 450 μmols m^{-1} $^{-2}$ for PPF and 10-30 ^{o}C for day (DT) and night temperatures (NT).

Data were collected on 9 plants in each treatment at seven-day intervals beginning with day 36 and extending to day 78, with additional samplings when the plants reached visible bud and anthesis. On treatments 1 and 2 two week sampling intervals were used because of the slow growth rate. Dates of visible bud and anthesis were recorded. Visible bud was defined as the day when buds reached a diameter of 0.5 cm or larger. Anthesis was defined as the day when a single petal began to reflex to a horizontal position. Leaf area, shoot fresh weight, dry weight and plant height to the surface of the uppermost leaf were recorded and are presented in another section.

An analysis of variance, polynomial analysis, and multiple regression analysis were performed using the 'Oneway' and 'Regression' subroutines of SPSS (18). The results are reported in Table 1 through 9. Linear, and linear interaction terms along with squared and cubic terms of irradiance and day and night temperature were regressed on days to initiation, visible bud, and anthesis. Comparison of the simplest and the most complex equations for each response was made. Step-wise addition of all factors with a significant (0.05) impact on the descriptiveness of the equation, in the presence of the previously added factors, provided the simplest function. A second equation was developed that included linear terms forced into the function, followed by step-wise addition of the remaining significant (0.05) terms. In a third equation, all terms were forced into the equation.

Three-dimensional surface and contour plots (Figure 1 through 3) were developed using the 'Surface II' plotting system (19). Equations with linear terms forced in were used to develop the contoured surfaces. To unitize the surface plots, the relative height of each surface was adjusted to a percentage of the surface with the greatest range.

RESULTS AND DISCUSSION

PLANT HEIGHT:

Plant height is the product of two forms of environmental responses: reproductive responses determining the node number at which flowers are initiated (5), and vegetative responses determining the size of the cells and organs. This study is focused primarily on defining the vegetative development, however some influence of the environment on the reproductive development enters into these results.

Looking at simple linear correlations, aside from time, PPF showed the greatest simple correlation to plant height while NT had the lowest (Table 4). Averages over all sampling times (Table 2) indicate that the tallest plants are produced at 20 ^{o}C day and night and a PPF of 150 $\mu mols^{-1}$ m^{-2}. Both high and low day and night temperatures and high irradiance produced the shortest plants. Significant linear, quadratic and cubic responses to PPF are present (Table 3). Responses to DT are best described using quadratic and cubic terms and to NT using quadratic terms. Over time, height changes are best described as a linear function of time. However, at the median ages, some slowing of growth occurred and thus higher order terms are necessary. A leveling-off of the rate of increase in plant height occurred at the time when the majority of the plants were in the early stages of reproductive development. At this time, meristems subtending the reproductive apex became dominant and resumed vegetative elongation. This has also been suggested in the work of Merritt and Kohl (16).

Prediction equations which account for up to 57% of the variation in plant height (Table 4) produce a dome shaped (Figure 1) response surface because of the prevalence of positive linear, negative quadratic, and cubic terms. The interaction of irradiance and DT was negatively correlated to height and had a significant influence on the accuracy of the equation in describing the response.

In observing the description of the response as presented in the prediction equations (Table 4 and Figure 1), height increased to a PPF of about 225 μmols $^{-1}$ m^{-2} and then decreased as irradiance increased. The steepness of the dome-shaped response to both DT and NT became greater as the irradiance increased. This interaction of PPF with temperature indicates that as irradiance increased above 225 μmols $^{-1}$ m^{-2} both low and high temperatures produce shorter plants, while little effect is observed in the intermediate temperature regions. Also at higher DT, flower initiation occurs at a lower node number.

Night temperatures have been shown by many to influence plant height (3, 8, 10, 15, 16, 20). Tsujita (20) obtained taller plants in the cv. Encounter Red at a NT of 17 ^{o}C than at 13 ^{o}C. Konjoian and Tayama (15) produced the tallest plants at night temperatures of 16 ^{o}C. At higher and lower temperatures, the plants were shorter. Earlier flowering occurred only at the higher temperatures. Carpenter and Carlson (8) produced the tallest plants with day temperatures near 22-24 ^{o}C and 10 ^{o}C night temperatures. No differences because of night temperatures were observed by White and Warrington (22) in studying the effects of split night temperatures. The range of temperatures studied in that work was however not sufficient in the presence of the other factors to show a NT response. Low PPF has been shown to cause increases in total plant height in a number of studies (11, 12, 20). Also, application of supplemental irradiation has been shown to decrease plant height (7, 9, 20). In general, these observations correspond to those used in the model presented here (Table 4).

While no data was taken, total plant height appears to be influenced by petiole elongation until the canopy becomes dense, and after that by shoot elongation and an increase in internode length.

Overall, limiting plant height can be achieved by reducing either day or night temperatures below 18 °C. Raising day temperatures above 24 °C will reduce plant height as a result of decreasing node numbers and causing earlier onset of reproductive development. When rapid reproductive development is desired, higher temperatures may best be employed to decrease plant height while decreasing the nodes to the first flower and producing smaller plants. Where time is not a factor and short plants are desired, one can choose to reduce temperatures and reduce height.

Growth regulators and limited water supplies remain an important tool in height control of geranium. It is apparent that with the often excessive height development in intermediate temperature regions, and the need to keep crop timing on schedule, growth regulators may remain the single most effective means of height control. Repeated applications of chlormequat (CCC) can effectively be used to manage plant height (17). It is suggested that if the model predicts excessive height for a given growth regime, then height may be more easily controlled by growth regulator than by water, temperature, or irradiance manipulation. Thus the application of the height predictor may be effectively used to predict when growth regulators are needed.

LEAF AREA:

Prediction equations describing up to 57% of the variance in leaf area were developed (Table 5). In comparing the linear influences, time provided the greatest simple effects, while both PPF and NT exceeded DT. DT and NT interactions also were influential. The greatest leaf area is produced at irradiances of 150 μmols m^{-1} $^{-2}$ with a DT of 25 °C and a NT of 15° or 20 °C (Table 1). Averaging the main effects (Table 2) of temperature appear to present an inaccurate representation of the simple effects because of the strong interactions over the range of treatments studied.

Over time, linear and higher-order terms are significant in describing the development of the leaf canopy. A general slowing in the development of the leaf area corresponded to the time of reproductive development in each treatment. This response is similar to that observed for height. For a time, the plant is initiating and developing floral primordia instead of leaf primorida.

A PPF of around 150 µmols m^{-1} $^{-2}$ produces the greatest leaf area. At PPFs below 150 µmols $m^{-1\ -2}$, leaf areas decrease, but, as irradiance increases above 150 µmols $m^{-1\ -2}$ leaf areas also decrease.

The effects of temperature on leaf area are more complex. Linear and cubic terms are most effective in describing DT responses. While linear terms are most effective in describing simple NT responses (Table 3), the interrelationship of DT with NT is more important in influencing the leaf area. At high DT, NT responses have a negative slope, while at low DT, NT responses yield a positive slope. Thus, NT responses rotate while moving up on the DT axis. Similarly, DT responses yield a negative slope at low NT and a positive slope at high NT. In the cuboid representations (Figure 2) it can be seen that rotation for DT is greater than for NT. The rotations are less at low irradiances. It may be that, if DT is sufficient for the plants to metabolize photosynthetic assimilates, the leaf area is not increased by increased night temperature and in fact it is decreased. If DT is not high enough for the plants to metabolize the photosynthetic assimilates, then increases in NT produce an increase in leaf area. Thus, DT increases produced increased leaf area at low NT, while DT increases resulted in decreased leaf area at high NT.

White and Warrington (22) showed that in the absence of growth regulators high light significantly decreased leaf area as did high DT and low NT. These data agree with the trends of the model. In a study of Merritt and Kohl (16), total leaf area increased in what appears to be a quadratic form, over time. They also found that short irradiance periods (9 hrs) decreased leaf area in some instances. Leaf area has been shown to be important to flower development. Armitage (2) suggests that a critical leaf area is necessary to produce flowers. This is similar to the hypothesis, described in Section III of this dissertation, where it is shown that high irradiance must be received by the plant after a juvenile phase is passed so that initiation of flowers can occur.

FRESH WEIGHT:

Up to 55 percent of the variance in fresh weight can be explained using factors of time, irradiance, and day and night temperatures. Time had the highest simple correlation to fresh weight (Table 6). NT had a simple negative correlation. DT alone did not appear to influence fresh weight. However, DT interacting with NT served to explain some of the variance in the regression analysis.

Over time, fresh weight increased in a quadratic manner. No leveling-off in the initiation to visible bud stage was apparent as with height and leaf area. From these data it can be implied that fresh weight continues to increase because of the development of reproductive organs during that phase.

Irradiances below 150 $\mu mols^{-1}\ m^{-2}$ produced the lowest average fresh weights (Table 2). Linear, quadratic and cubic terms are necessary to describe the response to PPF. At PPFs above 150 $\mu mols^{-1}\ m^{-2}$ little additional increase in fresh weight occurred. The greatest fresh weight was observed at an irradiance of 150 $\mu mols^{-1}\ m^{-2}$. This agrees with observations for leaf area and plant height. When irradiances are low, it appears that the plant produces more light harvesting facilities and therefore greater fresh weight increases. In the literature, lower irradiance levels have been reported to yield higher fresh weight (9, 10). Supplemental irradiance has been shown in some cases to increase fresh weight where ambient light was limited (11). Specific leaf weight is reported to increase with increased irradiance (4).

Night temperatures have a significant impact on fresh weight. Decreased night temperatures yield decreased fresh weight, but over time, the accumulation of fresh weight at low temperatures appears to result in final plant weights near those achieved at a higher NT. White and Warrington (22) have shown a build-up of carbohydrates in the form of sugars and starch throughout the plant at low night temperatures. This build-up may account for the weight gain. Armitage (1) found that, as temperatures increased, the specific leaf weight decreased as did the leaf thickness.

Day temperature interacted with NT. As NT increased, fresh weight increased at a greater rate at low DT than at high DT. High NT and low DT yielded the highest fresh weight in young plants; however, in older plants the interaction is less, presumably because of the build-up of unused photosynthates and of lower respiration rates.

DRY WEIGHT:

Only 45 percent of the variance in dry weight can be explained using factors of time, irradiance, and day and night temperature. Time had the highest simple correlation with dry weight (Table 8). PPF was negatively correlated with dry weight. DT showed some influence over time and NT appeared to have little impact.

Over time, dry weight increases could be explained using linear and quadratic terms (Table 3). No leveling-off of dry weight during the induction to visible bud stage was observed. The interaction of DT over time shows that, as time progressed, the build-up of dry weight was greater at low DT than at high DT.

Irradiance responses appear to require terms up to and including the cubic term. Irradiances below 150 μmols m^{-1} $^{-2}$ yielded reduced dry weights. The model predicts losses in dry weight for irradiances below 100 μmols m^{-1} $^{-2}$ and day temperatures below 22 ^{o}C with NT of 16 ^{o}C or higher. Armitage (1) indicated that the light compensation point at DT of 25 ^{o}C is 68 μmols m^{-1} $^{-2}$. Thus, a loss of stored carbohydrates would be expected at lower irradiances.

Apparently, as temperature increases respiration increases, at the expense of accumulation of photosynthetic products, resulting in a decrease in the rate of dry weight gain at high DT. The hinged rising-plane response (Figure 4) indicates that build up of dry weight is greater at low DT than at high DT regardless of NT.

The accumulation of carbohydrates, as described by White and Warrington (22), is increased at low DT. Short irradiance periods coupled with high temperatures have resulted in lower shoot dry weight (16). It is suggested that under long irradiance periods increases in dry weight can be expected.

NT in this study had little effect on dry weight. In a more detailed study focusing on the effects of NT over a smaller range of treatment combinations, some effects may be observed. NT was found to have a great influence on the shoot fresh weight while it had little effect on shoot dry weight. It is suggested that the total dry matter remains relatively stable but the partitioning within the shoots, of the photosynthetic assimilates, may change as a result of changes in NT. While the total dry weight is about the same over all night temperatures used, the fresh weight is higher at high NT, and plants are taller at moderate NT and have greater leaf areas at low NT.

DRY WEIGHT TO FRESH WEIGHT RATIO:

Low irradiances and high DT yielded the lowest percent dry weight (Table 1). Linear and quadratic responses to PPF and time were found (Table 2), while linear responses to DT were also present. No significant responses to NT could be identified. Some changes could be correlated to irradiance (r = 0.1845) and DT (r = -0.1466). Only a limited portion of the variance ($r^2 = 0.1064$) could be defined in the multiple linear regression analysis using the environmental factors studied in this experiment. It is thus determined that the predictor for the percent dry weight does not yield sufficiently reliable values and that a more detailed study may be necessary to develop a reliable predictor for the percent dry weight. Also useful is the fact that with increased irradiance there was an increase in the percentage of dry matter. Over all the treatments, from 7.0 to 18.4 percent of the fresh weight was dry matter.

Table 1. Mean influence of PPF, day and night temperature on the vegetative development of *Pelargonium hortorum* - Bailey 'Ringo Scarlet'.

Treatment number	Treatment Environment			Plant height^W	Leaf area^V	Fresh weight^U	Dry weight^S	Percentage dry weight^T
	PPF^Z	DT^Y	NT^X					
1	50	20	20	8.8	98.6	5.0	0.43	7.0
2	150	15	15	9.5	139.1	14.0	3.37	12.6
3	150	25	15	10.8	163.7	15.3	2.77	10.1
4	150	15	25	9.1	150.7	14.0	2.92	12.8
5	150	25	25	9.3	176.3	13.3	2.53	11.2
6	250	20	20	10.4	139.6	13.0	3.02	16.9
7	250	10	20	8.2	134.0	15.0	2.99	15.6
8	250	30	20	7.9	101.8	9.8	1.48	12.0
9	250	20	10	7.8	101.8	11.8	2.08	17.2
10	250	20	30	-	-	-	-	-
11	350	15	15	8.1	111.5	13.3	3.45	14.5
12	350	25	15	9.4	165.1	15.0	2.62	11.6
13	350	15	25	7.9	105.1	12.9	2.95	21.6
14	350	25	25	8.2	170.0	12.5	1.98	10.9
15	450	20	20	8.6	139.9	12.4	2.71	15.5

Z photosynthetic photon flux in the 400-700 nm range.
Y day temperature in ^{o}C.
X night temperature ^{o}C.
W plant height to the top of the leaf canopy measured in cm.
V plant leaf area measured in cm^2.
U plant shoot fresh weight measured in grams.
T plant shoot dry weight measured in grams.
S percentage of the shoot fresh weight that is dry weight.

Table 2. Average effects of PPF day and night temperature, and time on the vegetative development of <u>Pelargonium hortorum</u> - Bailey 'Ringo Scarlet' averaged over all treatment combinations.

Treatment environment	Plant height[Z]	Leaf area[Y]	Fresh weight[X]	Dry weight[W]	Percentage dry weight[V]
PPF[U]					
50	8.8	84.0	5.0	0.50	7.0
150	9.7	156.3	14.2	2.90	11.7
250	9.6	129.4	12.8	2.75	16.1
350	8.4	134.3	13.4	2.76	14.8
450	8.6	139.9	12.4	2.71	15.5
DT[T]					
10	8.2	134.0	15.2	2.99	15.6
15	8.7	126.3	13.6	3.15	15.4
20	9.7	129.9	11.9	2.63	15.7
25	9.4	167.9	14.0	2.48	10.9
30	7.9	101.8	9.7	1.48	12.0
NT[S]					
10	7.8	100.4	11.8	2.10	17.2
15	9.5	146.1	14.4	3.00	12.1
20	9.6	131.4	12.1	2.60	15.1
25	8.6	144.8	13.2	2.60	14.3
30	-	-	-	-	-
Days					
35[R]	3.8	32.6	1.9	0.22	11.5
49	5.7	69.7	3.9	0.71	11.5
56	6.5	98.2	5.5	0.60	11.3
63	8.0	-	7.4	0.77	10.9
70	7.7	95.7	8.8	1.16	12.4
77	9.7	126.5	11.3	1.35	12.0
84	10.6	170.2	13.6	1.62	15.8
91	11.1	199.6	16.9	2.11	12.6
anthesis[Q]	14.0	-	33.5	5.52	18.4

Z plant height to the top of the leaf canopy measured in cm.

Y leaf area measured in cm^2.

X plant shoot fresh weight measured in grams.

W plant shoot dry weight measured in grams.

V percentage of the shoot fresh weight that is dry weight.

U photosynthetic photon flux in the 400-700 nm range.

T day temperature in °C.

S night temperature in °C.

R the sampling at 35 days is from treatment number 6 only.

Q samples were taken at anthesis and were not included in the analysis.

Table 3. Significance of the polynomial contrasts of PPF, day and night temperature and time on vegetative development in *Pelargaonium hortorum* - Bailey 'Ringo Scarlet'.

Environmental Factor	Plant height[Z]	Leaf area[Y]	Fresh weight[X]	Dry weight[W]	Percentage dry weight[V]
PPF[U]					
Between Levels	***[T]	***	***	**	***
Linear	***	n.s.	*	n.s.	**
Quadratic	**	n.s.	***	*	**
Cubic	**	***	***	*	n.s.
Deviations	n.s.	***	***	n.s.	n.s.
Day Temperature					
Between Levels	***	***	**	**	*
Linear	n.s.	*	n.s.	***	**
Quadratic	***	n.s.	n.s.	n.s.	n.s.
Cubic	*	***	*	n.s.	n.s.
Deviations	n.s.	***	**	n.s.	n.s.
Night Temperature					
Between Levels	***	***	*	n.s.	n.s.
Linear	n.s	*	n.s	n.s.	n.s.
Quadratic	***	n.s.	n.s.	n.s.	n.s.
Deviations	n.s.	***	**	*	*
Time					
Between Levels	***	***	***	***	n.s.
Linear	***	***	***	***	n.s.
Quadratic	n.s	***	***	n.s.	n.s.
Cubic	n.s.	n.s.	n.s.	n.s.	n.s.
Quartic	**	***	n.s.	n.s.	n.s.
Deviations	***	n.s.	n.s.	n.s.	n.s.

Z plant height to the top of the leaf canopy measured in cm.
Y leaf area measured in cm^2.
X plant shoot weight measured in grams.
W plant shoot dry weight measured in grams.
V percentage of shoot fresh weitht that is dry weight.
U photosynthetic photon flux in the 400-700 nm range.
T significance of the factor in describing the developmental response; * α = 0.05, ** α= 0.01, *** α= 0.001, n.s.= not significant.

Table 4. Prediction equations for plant height of Pelargonium hortorum - Bailey 'Ringo Scarlet' as a function of PPF, day and night temperatures, and time.

Environmental variables	Simple r[Z]	All terms forced[Y] coefficient	sign.[V]	Linear terms forced[X] coefficient	sign.	Step-wise addition[W] coefficient	sign.
Constant		344.376	n.s.	-105.067	*	-87.269	*
PPF	-.212	0.336	*	0.247	*	0.256	*
DT	.100	-6.812	n.s.	4.898	***	-	-
NT	-.039	34.161	***	12.119	***	7.821	***
T	.601	-24.721	**	-1.526	n.s.	-115.425E-3	*
PPF x DT	-.108	5.372E-3	*	6.045E-3	*	5.698E-3	*
PPF x NT	-.204	1.252E-3	n.s.	-	-	-	-
PPF x T	.005	-0.775E-3	n.s.	-	-	-	-
DT x NT	.049	-124.456E-3	*	-105.781E-3	*	-116.697E-3	*
DT x T	.384	-21.442E-3	n.s.	-	-	-	-
NT x T	.309	-17.252E-3	n.s.	-	-	-	-
$(PPF)^2$	-.191	-1.430E-3	**	-1.294E-3	**	-1.302	**
$(DT)^2$	.069	746.336E-3	*	-	-	275.340E-3	***
$(NT)^2$	-.064	-1.410	*	-0.249	***	-	-
$(T)^2$	.610	0.358	***	20.530E-3	**	-	-
$(PPF)^3$	-.169	1.263E-6	*	1.120E-3	*	1.130E-6	*
$(DT)^3$	.041	-15.445E-3	**	-2.894E-3	***	-7.462E-3	***
$(NT)^3$	-.081	20.835E-3	n.s.	-	-	-4.346E-3	***
$(T)^3$	.614	-1.542E-3	*	-	-	98.680E-6	**
R^2		.5704		.5517		.5520	
F-ratio		8.407		13.538		13.670	
Significance[U]		***		***		***	

Z imple correlation of the variable with the data.

Y all variables were forced into he prediction equation

X only simple linear variables were forced in with the remainder added step-wise if significant at $\alpha = 0.05$.

W all variables were added step-wise if significant at $\alpha = 0.05$.

V significance of the variables in the presence of the other variables in the equation; n.s. = not significant, * $\alpha = 0.05$, ** $\alpha = 0.01$, *** $\alpha = 0.001$.

U significance of the regression equation containing the listed coefficients.

Table 5. Prediction equations for leaf area of *Pelargonium hortorum* - Bailey 'Ringo Scarlet' as a function of PPF, day and night temperatures, and time.

Environmental variables	Simple r	All terms forced coefficient	All terms forced sign.	Linear terms forced coefficient	Linear terms forced sign.	Step-wise addition coefficient	Step-wise addition sign.
Constant		-1039.840	n.s.	-1063.876	***	-1120.359	***
PPF	-.051	2.533	***	1.290	**	1.807	***
DT	.026	40.720	***	48.807	***	48.801	***
NT	-.077	156.064	***	69.101	***	69.445	***
T	.512	-22.000	n.s.	0.991	n.s.	-	-
PPF x DT -.009	-.009	6.27E-3	n.s.	-	-	11.402E-3	*
PPF x NT	-.089	-10.444E-3	n.s.	-	-	-	-
PPF x T	.101	-7.004E-3	*	-	-	-4.781E-3	*
DT x NT	-.034	-1.280	***	-1.505	***	-1.534	***
DT x T	.233	-205.900E-3	**	-301.751E-3	***	-297.274E-3	***
NT x T	.166	-117.576E-3	n.s.	-204.442E-3	**	-196.449E-3	**
$(PPF)^2$	-.023	-7.882E-3	***	6.427E-3	***	-6.967E-3	***
$(DT)^2$	.004	0.000	n.s.	-	-	-	-
$(NT)^2$	-.113	-6.270	***	-711.954E-3	***	-725.933E-3	***
$(T)^2$	.541	316.245E-3	n.s.	-	-	27.656E-3	-
$(PPF)^3$	.010	9.581E-3	***	7.882E-6	***	8.542E-6	***
$(DT)^3$	-.019	-1.986E-3	n.s.	-	-	-	-
$(NT)^3$	-.135	103.091E-3	**	-	-	-	-
$(T)^3$	.564	-831.370E-6	n.s.	696.703E-1	***	571.280E-6	**
R^2		.5730		.5488		.5533	
F- ratio		8.446		10.846		8.957	
Significance		***		***		***	

Table 6. Prediction equations for fresh weight of *Pelargonium hortorum* - Bailey 'Ringo Scarlet' as a function of PPF, day and night temperatures, and time.

Environmental variables	Simple r	All terms forced coefficient	All terms forced sign.	Linear terms forced coefficient	Linear terms forced sign.	Step-wise addition coefficient	Step-wise addition sign.
Constant		-94.927	*	-38.721	**	-6.694	*
PPF	.074	0.165	***	0.145	***	0.160	***
DT	-.012	-3.099	**	0.266	n.s.	-	-
NT	-.095	13.014	***	1.938	***	-	-
T	.602	0.945	n.s.	0.242	n.s.	-	-
PPF x DT	.066	1.064E-3	*	1.181E-3	*	-	-
PPF x NT	.012	-0.526E-3	n.s.	-	-	-	-
PPF x T	.289	26.724E-3	n.s.	-	-	87.953E-6	*
DT x NT	-.076	-24.652E-3	*	-26.602E-3	*	-	-
DT x T	.282	6.130E-3	n.s.	-	-	-	-
NT x T	.250	-8.33E-3	n.s.	-17.256E-3	**	-	-
$(PPF)^2$	.069	-0.662E-3	***	-635.610E-6	***	-629.696E-6	***
$(DT)^2$	-.007	203.679E-3	***	-	-	-	-
$(NT)^2$	-.095	-674.038E-3	***	-	-	-	-
$(T)^2$	.608	-11.299E-3	n.s.	-	-	-1.650E-3	*
$(PPF)^3$	.0715	.749E-6	***	0.749E-6	***	0.724E-6	***
$(DT)^3$	-.004	-3.410E-3	***	-	-	-	-
$(NT)^3$	-.088	12.395E-3	***	-	-	-	-
$(T)^3$	.611	77.852E-6	n.s	23.847E-6	***	31.777E-6	*
R^2		.5491		.4915		.4668	
F-ratio		7.712		11.792		18.762	
Significance		***		***		***	

Table 7. Prediction equation for dry weight of *Pelargonium hortorum* - Bailey

Table 7. Prediction equation for dry weight of *Pelargonium hortorum* - Bailey 'Ringo Scarlet as a function of PPF , day and night temperatures, and time.

Environmental variables	Simple r	All terms forced		Linear terms forced		Step-wise addition	
		coefficient	sign.	coefficient	sign.	coefficient	sign.
Constant		-5.589E-3	n.s.	-3.165	*	-1.886	***
PPF	.201	20.641E-3	**	27.749E-3	***	21.138E-3	***
DT	-.243	53.702	n.s.	84.240E-3	n.s.	86.540E-3	*
NT	-.071	537.157E-3	n.s.	12.032E-3	n.s.	-	-
T	.497	384.312E-3	n.s.	7.596E-3	n.s.	-	-
PPF x DT	.007	10.495E-6	n.s.	-	-	-	-
PPP x NT	.127	54.702E-6	n.s.	-	-	-	-
PPF x T	.380	605.002E-6	n.s.	-	-	-	-
DT x NT	-.242	-2.275E-3	n.s.	-	-	-	-
DT x T	.0179	-1.788E-3	*	-1.581E-3	*	-1.621E-3	*
NT x T	.221	609.601E-6	n.s.	-	-	-	-
$(PPF)^2$	.1764	-90.855E-6	***	-94.209E-6	***	-87.995E-6	***
$(DT)^2$	-.238	4.802E-3	n.s.	-	-	-	-
$(NT)^2$	-.071	-310.007E-3	n.s.	-	-	-	-
$(T)^2$	.502	-5.589E-3	n.s	-	-	-	-
$(PPF)^3$	.159	98.107E-9	***	10.165E-6	***	96.174E-6	***
$(DT)^3$	-.225	-81.766E-6	n.s.	-	-	-	-
$(NT)^3$	-.066	565.751E-6	n.s.	-	-	-	-
$(T)^3$	.504	29.747E-6	n.s.	4.201E-6	**	3.727E-6	***
R^2		.4503		.4388		.4402	
F-ratio		5.189		12.120		14.040	
Significance		**		***		***	

Figure 1. Plant height of Pelargonium hortorum - Bailey 'Ringo Scarlet' as a function of time, PPF, day and night temperature.

(a) 90 days old.
(b) 70 days old.
(c) 50 days old.

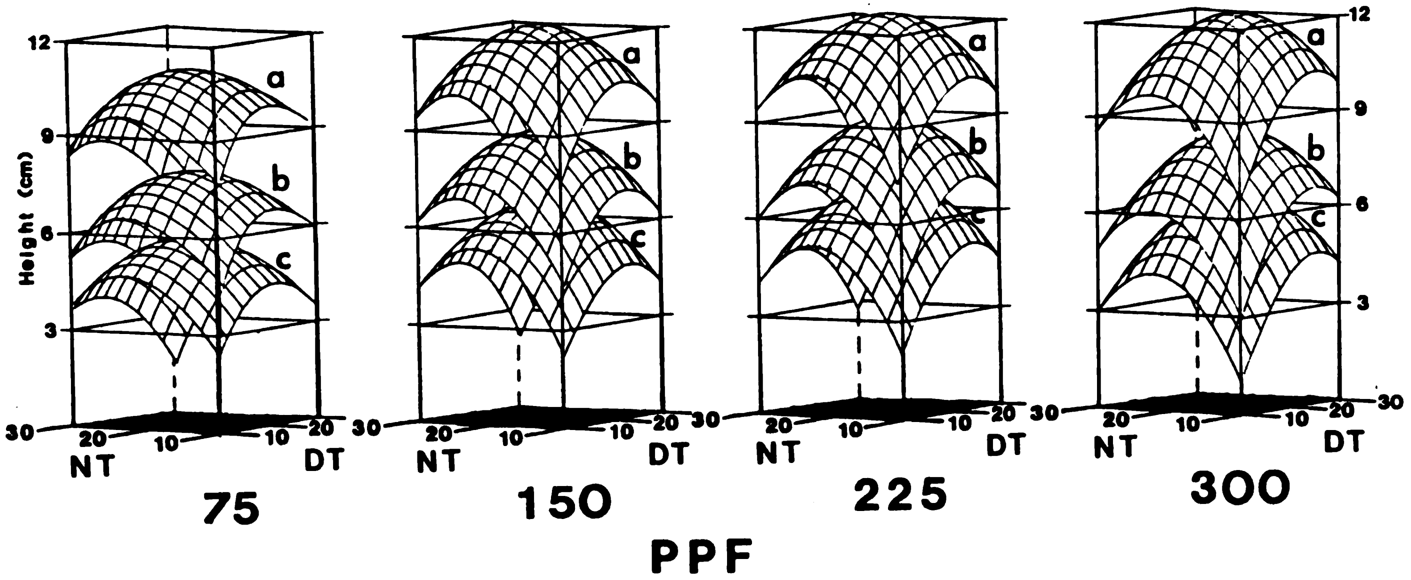

Height (cm)
12
9
6
3
30
20
10
NT
DT
a
b
c
75
150
225
300
PPF

Figure 2. Leaf area of _Pelargonium_ _hortorum_ - bailey 'Ringo Scarlet' as a function of time, PPF, day and night temperature.

(a) 90 days old.
(b) 70 days old.
(c) 50 days old.

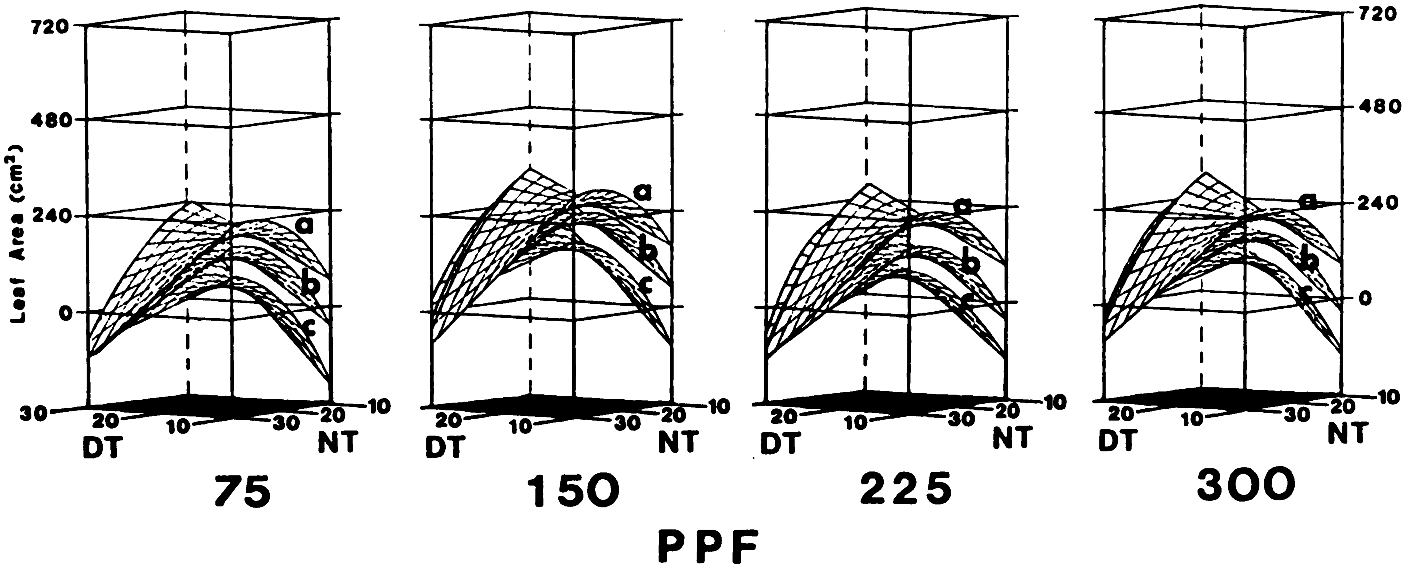

Leaf Area (cm^2)
720
480
240
0
30
20
10
30
20
10
DT
NT
a
b
c
75
150
225
300
PPF

Figure 3. Fresh weight of Pelargaonium hortorum - Bailey 'Ringo Scarlet' as a function of time, PPF, day and night temperature.

(a) 90 days old.
(b) 70 days old.
(c) 50 days old.

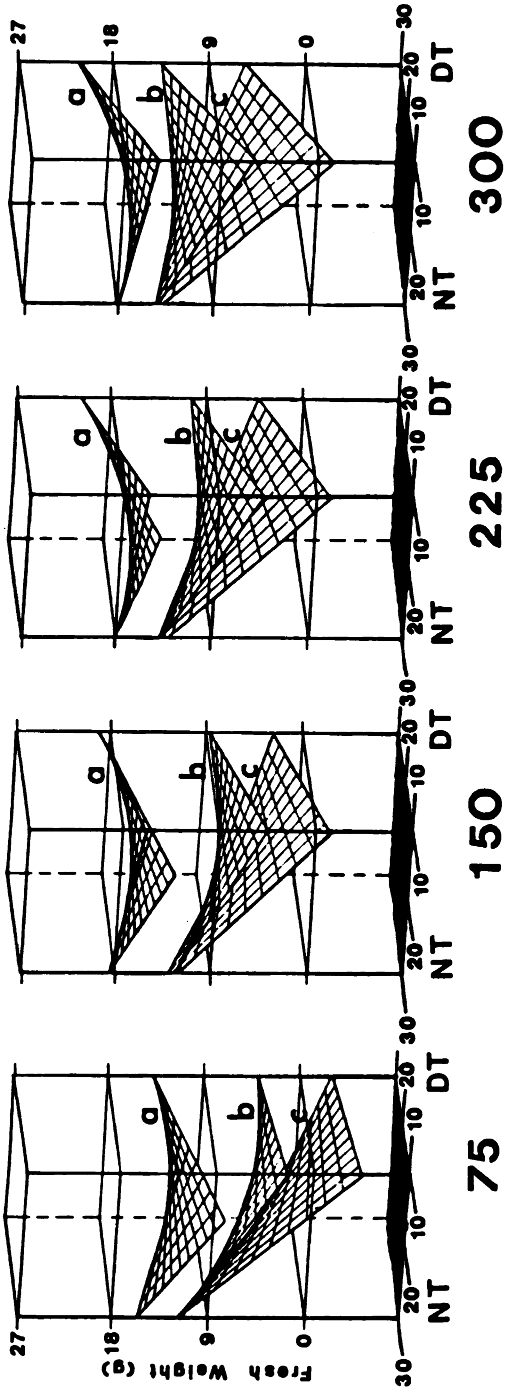
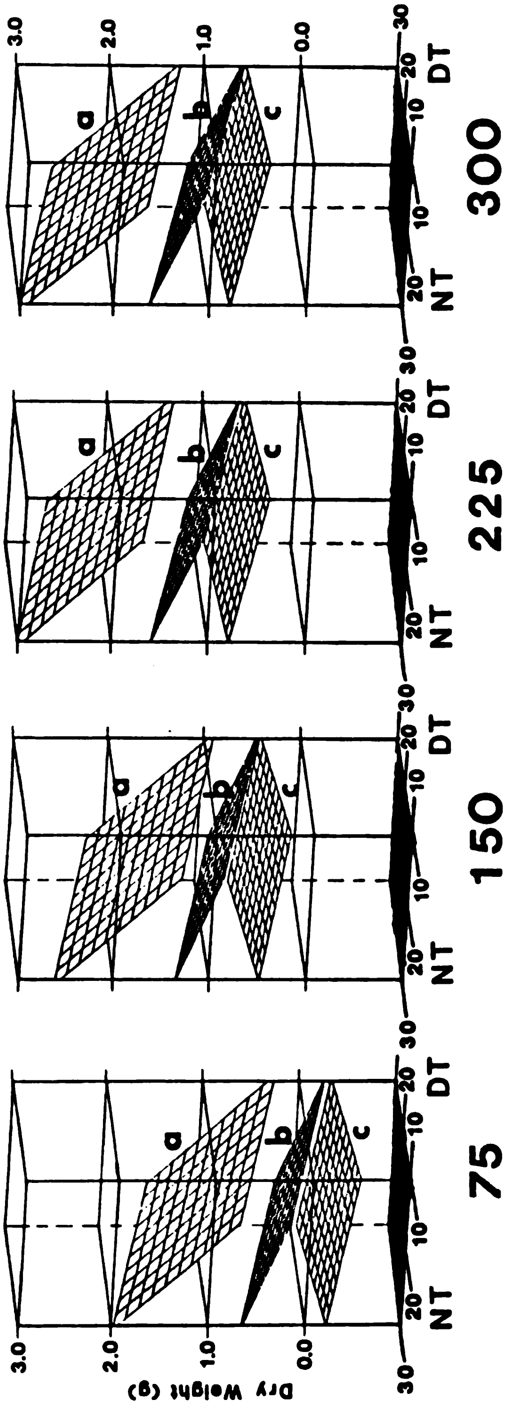

Fresh Weight (g)
27
18
9
0
30
20
10
NT
DT
a
b
c
75
150
225
300
PPF

Figure 4. Dry weight of *Pelargonium hortorum* - Bailey 'Ringo Scarlet' as a function of time, PPF, day and night temperature.

(a) 90 days old.
(b) 70 days old.
(c) 50 days old.


Dry Weight (g)
3.0
2.0
1.0
0.0
30
20
10
NT
DT
a
b
c
75
150
225
300
PPF

SUMMARY AND CONCLUSION

The application of response surface methods and the central composite design to the study of whole plant physiological responses in hybrid geraniums has resulted in expansion of our knowledge on how geraniums respond to the environment. Three dimensional response surface presentations of complex functional relationships graphically represent the responses.

The functional relationships employing environmental inputs of irradiance, and day and night temperatures over time can describe a large portion of the variance observed in vegetative development. Over a wide range of environmental conditions, up to 57% of the variance in plant height and leaf area, 34% of the variance in shoot fresh weight, and 45% of the variance in shoot dry weight, and only 10.6% of the variance in the fresh weight to dry weight ratio could be described.

Total plant height is greatly influenced by irradiance and day and night temperatures. Day and night temperatures of 18-24 ^{o}C and irradiance of 150 μmols^{-1} m^{-2} yielded the tallest plants. The shortest plants were produced at high irradiance and low or high day and night temperatures. The model may be most effective in predicting when the application of growth regulators is necessary to achieve the desired height.

Leaf area responses are very complex. Increases in leaf area occur with increased irradiance to about 150 μmols^{-1} m^{-2} after which a steady decrease occurs. Day and night temperatures interact in a reciprocal manner. High day temperatures yield low leaf areas when NT is high but when NT is low the leaf area is high. At low day temperatures and high NT leaf area is high, and low at low NT. Over time, leaf area increases slow down at the time of flower bud development. The lowest leaf area is produced at high day and night temperatures. The highest leaf areas occur when either day or night temperature is high and the irradiance is in the lower regions (below 150 µmols $^{-1}$ m $^{-2}$). The complexity of the leaf area responses indicates that partitioning of photosynthate is highly regulated to optimize the light harvesting efficiency of the plant.

Fresh weight was most influenced by NT and irradiance in addition to time. Differences in DT showed interactions with differences in NT over time. Irradiances below 150 µmols $^{-1}$ m $^{-2}$ yielded smaller plants. The highest fresh weights were observed at irradiances of 150 µmols $^{-1}$ m $^{-2}$. A general leveling off of fresh weight occurred above 150 µmols $^{-1}$ m $^{-2}$. High NT increased fresh weight rapidly in the early stages of development. However, in the later stages of development, plants grown at low NT showed a continued gain in fresh weight to levels at or above those grown at a high NT.

Dry weight is most highly influenced by PPF and DT aside from time. DT is negatively correlated to dry weight and NT has little effect on dry weight. Over time, the accumulation of dry weight is greater at low DT and high PPF.

The fresh weight to dry weight ratio was not consistent enough for the development of a reliable predictor. However, the data did indicate that, as irradiances increased, the percent dry weight increased and, as the DT increased, the percent of dry weight decreased.

In summary, irradiance and day and night temperatures can serve as effective predictive variables for plant height, leaf area and fresh and dry weight during vegetative development of hybrid geraniums. Functional relationships have been developed which provide useful definitions of vegetative responses. These predictors can be used to anticipate responses to any growth regime and thus assist in the decisions necessary to grow the desired product.

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SUMMARY AND CONCLUDING STATEMENTS

Much greater definition of the responses of hybrid geraniums to light and temperature are available as a result of this work. Vegetative and reproductive development in response to: time, irradiance, day and night temperature, and supplemental light was studied. Flower development in response to supplemental light was found to be influenced by irradiance level, temperature and duration of irradiance, and age of the plants. Days to anthesis was more closely correlated with mean daily irradiance than with total cumulative irradiance. A threshold irradiance level of at least 10 mol day^{-1} was necessary for simultaneous reductions in days to flower and number of nodes in 'Ringo Scarlet'. A hypothesis attempting to explain the flower induction response was presented.

Prediction equations were developed for days to initiation, visible bud, and anthesis. Irradiance and day temperature were shown to have the greatest influence on flower initiation and development to visible bud, while temperature alone was most contributory from visible bud to anthesis. Three-dimensional response surface plots were developed to represent the functions graphically. Prediction equations were also developed for total plant height, leaf area, and fresh and dry weights as functions of time, irradiance, and day and night temperatures.

Much of the existing contradictory data and unexplainable responses are explainable in the light of this work. However, more questions can now be raised and the need for more extensive work with hybrid seed-propogated geraniums is evident.

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