

## REGULATION OF CROP GROWTH AND DEVELOPMENT BASED ON ENVIRONMENTAL FACTORS

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### Abstract

Production of horticultural crops by growers is becoming increasingly difficult as markets write detailed specifications for products both in time of delivery and quality factors such as height and flower number. Such specifications require growers perform proper cultural procedures at the proper time. Environmental variation between and among seasons means proper cultural procedures will vary with every crop. All growers, especially those with little experience in a crop, benefit from information that assist in making proper cultural-procedure decisions. Decision-support tools based on environmental, chemical, or biological data can help provide such information. This presentation will describe examples of biological concepts associated with plant growth and developmental processes that especially lend themselves to decision-support. Types of decision-support tools developed from this information will be presented. For example, development of plants is highly temperature dependent. Relationships between temperature and development rate are often useful as they can be described by a linear relationship over a wide temperature range from the base temperature to near the optimum temperature. Degree-day decision-support tools can be developed from such information. Growth retardant chemicals are used widely in commercial production of flowering plants to meet height-control specifications. Simulation models incorporated into decision-support tools may be useful to maximize efficacy of applications as there is increasing pressure to minimize the use of growth retardants. Biological models relating plant morphological development to the environment, e.g., bud length and temperature to time to flower, can also be useful in creating decision-support tools for accurate crop timing.

## **1. Introduction**

Commercial production of high-quality horticultural plants requires a combination of appropriate genetics, cultural procedures, and environmental conditions. The challenge, of course, is to deliver these in the proper combinations and order. This paper will discuss some environmental principles and cultural procedures necessary for the production of high-quality plants, with specific reference to production in controlled environments. Methods for delivery in the proper order and combination also will be discussed.

Of the five environmental factors affecting a plant's survival and production, light, temperature, water, nutrients, and gases, the first two are different forms of energy: i.e., radiant and thermal. Quanta of visible light represent relatively large amounts of energy. For instance, blue light has about five to six times more energy per mole of photons ( $260 \text{ kJ mol}^{-1}$  at 460 nm) than the covalent chemical energy in ATP ( $40$  to  $50 \text{ kJ mol}^{-1}$ ). This high energy allows reactions that otherwise would be impossible if they depended on chemical energy. Radiant energy is converted to chemical energy through photosynthesis and stored in molecules that can be used later to power cellular processes and serve as the initial energy source for all forms of life.

Temperature is a description of average molecular motion or average kinetic energy. The rate of a biochemical reaction is related to temperature. As temperature increases, molecular motion increases following the Boltzmann energy distribution (Nobel, 1991). When the number of molecules with energy equal to or higher than the activation energy of a chemical reaction increases, the rate of a biochemical reaction increases. Consequently, cell maturation rate increases and plants mature faster as temperature increases.

Commercial horticulture is the process of manipulating energy to produce desirable plant products (flowers, fruits, vegetables, etc.) profitably. Growers adjust cultural practices throughout the year to maintain acceptable plant quality. For example, under normal ambient light conditions, chrysanthemum plants often are given at least one additional week of long days in the winter before the start of short days and flower induction. This additional time, which is required for adequate plant development prior to flower induction, occurs naturally at low greenhouse temperatures (less solar heating during the day) and allows the plant to harvest more radiant energy between planting and flowering. Alternatively, plants can be grown under supplemental light during long days, short days, or both without increasing crop production time. Here, radiant energy is increased while thermal energy remains constant.

Yield (quantity and quality) of horticultural plants is based on their growth, development, and correct morphology. Development refers to the maturation rate of leaf, stem, and flower cells or timing of critical events in the life cycle of a plant. Growth refers to the increase in weight, volume, length, or area of some or all of the plant (Ritchie and NeSmith, 1991). Generally, thermal energy drives plant development, while radiant energy drives photosynthesis and consequently dry weight accumulation. The other dimension of growth, expansion of the area or volume of plant parts, is not controlled by the net amount of carbon fixed, above some minimum daily light integral. Environmental factors and stresses that affect cell expansion are different from those that affect mass growth.

## **2. Light and dry weight accumulation**

Dry weight accumulation requires absorption of photons of photosynthetically active radiation (PAR) and carbon fixation through photosynthesis. Thus, mass growth depends on the number of photons received from the sun and leaf surface available for its absorption. Monteith (1977) demonstrated that biomass production was related linearly to

cumulative seasonal light interception for field crops grown with adequate water and nutrients. Net photosynthesis rates (averaged every 15 minutes) of maize and cotton canopies had a reasonably linear relationship to light interception (Hesketh and Baker, 1967). Many other researchers showed similar results in horticultural crops such as tomato (Cockshull, 1988), cucumber (De Visser and Vesseur, 1982), and poinsettia (Liu and Heins, 1997). A 1% reduction in light would reduce cucumber yield by 1%, at least in the early part of the year (Cockshull *et al.*, 1992).

The slope of the linear relationship between cumulative biomass and light interception reflects the average radiation use efficiency (RUE). Charles-Edwards (1981) has summarized the canopy RUE ( $\text{g MJ}^{-1}$ ) based on dry weight gain for several crops: rice, 4.2; corn, 3.4; sweet potato, 3.1; sunflower, 3.1; and kale, 2.7. Based on fresh weight, the RUE values varied from 39.6 to 42.6  $\text{g MJ}^{-1}$  (Bailey and Hunter, 1988; Cockshull, 1988; De Koning, 1989) ( $1\text{MJ m}^{-2} \text{s}^{-1}$  for full waveband radiation is about  $2 \text{mol m}^{-2} \text{s}^{-1}$  PAR). The RUE may change with plant density, leaf area index (LAI), water and nutritional availability, and light level. According to Sinclair and Horie (1989), RUE is a function of the relative amounts of sunlit and shaded leaves. The RUE is reduced at a low LAI because of the high proportion of leaves that are light-saturated and therefore are less efficient photosynthetically than those that are shaded. When the proportion of shaded leaf area increases, RUE increases. For poinsettia plants, RUE is described as an exponential function of the ratio of LAI to interception of the daily light integral (IDLI) (Liu and Heins, 1998). It varied from  $0.22 \text{g mol}^{-1}$  at a low LAI (0.87) with high IDLI ( $13.64 \text{mol m}^{-2} \text{d}^{-1}$ ) to  $0.32 \text{g mol}^{-1}$  at a high LAI (2.23) with low IDLI ( $4.73 \text{mol m}^{-2} \text{d}^{-1}$ ) on plants growing at a medium ( $22 \times 22 \text{cm}$ ) plant density ( $20.7 \text{plants m}^{-2}$ ).

### 3. Temperature and development

The maturation rate of leaf, stem, and flower cells depends on the rate of biochemical reactions, which are controlled primarily by thermal energy (average daily temperature or, more appropriately, average plant temperature). All plant responses to temperature follow a similar pattern. Below some temperature (called the base temperature, or  $T_b$ ) there is no response. Above  $T_b$ , rates of reaction increase with increasing temperature until a maximum, which is the optimum temperature ( $T_o$ ). Once the temperature rises above that  $T_o$ , the response decreases, often rapidly. For many crops, leaf primordia initiation and leaf appearance rate increase nearly linearly with accumulated average temperature between the  $T_b$  and  $T_o$  (Vincent, 1989). Diurnal temperature fluctuations do not affect developmental rate of many crops within the linear temperature range (Yourstone and Wallace, 1990). A slower developmental rate occurs whenever temperatures fall outside of it (Erwin and Heins, 1990). The fastest developmental rate under any average daily temperature occurs at a constant day and night temperature (Coligado and Brown, 1975; Erwin and Heins, 1990).

Since a plant's developmental rate increases the same amount per degree increase in temperature in the linear temperature range, it can be tracked using average daily temperature as long as the temperature does not fall below or exceed the temperature range. The rate cannot be measured directly, but it can be calculated by taking the reciprocal of the time taken to reach an end point. The units for inverse of the slope of the linear response line are degree-days per event. This number represents how many degree-days must accumulate for the event to occur. The concept of degree-days generally is defined for temperatures below  $T_o$  and above  $T_b$ :

$$\theta = \sum_{i=1}^{i=n} (ADT - T_b); \quad ADT < T_b, \quad ADT - T_b = 0 \quad (1)$$

where ADT is the average daily temperature and  $n$  is the number of days of temperature observations. Degree-days can be accumulated to indicate crop development over time as long as the temperature stays within the linear range. Several techniques have been developed to deal with temperature outside the linear range. Pearson *et al.* (1993) assumes that the developmental rate response to temperature is similar, but opposite, above and below  $T_0$ , and an effective temperature ( $T_e$ ) is defined as

$$T_e = T_0 - |T_0 - T_a| \text{ and } T_b < T_a < T_c \quad (2)$$

where  $T_a$  is the actual temperature and  $T_c$  is the ceiling temperature at which the rate of progress is zero. Supraoptimal temperatures can be converted into effective temperatures ( $T_e$ ), which represent the suboptimal temperature equivalents of supraoptimal temperatures in relation to developmental rate.

When temperature falls outside the linear range during part of the day, one tracking technique is to accumulate development over time by multiplying a rate function by the average temperature on an hourly basis (Karlsson *et al.*, 1988).

#### 4. Integrating radiant and thermal energy

As mentioned previously, radiant energy drives plant photosynthesis and, consequently, plant biomass production. The developmental rate of a crop is determined primarily by thermal energy. A concept of the ratio of radiant to thermal energy (RRT) has been developed to deal with the interactive effect of light and temperature on plant growth, development and quality (Liu and Heins 1997, 1998). Maturation of many crops requires a fixed amount of thermal time. Assuming that radiant energy is similar between years, crop yield has the potential to be higher in "cool" growing seasons than "warm" growing seasons because low temperatures slow plant developmental rate and extend the maturation duration, thus allowing plants to harvest more photons prior to maturation and senescence. This response has been observed in field crops such as corn (Muchow *et al.*, 1990), spring wheat (Amir and Sinclair, 1991), and soybean (Spaeth *et al.*, 1987).

In horticultural crops, similar results have been reported on the combined effect of light and temperature on plant quality. When light levels remain constant, increasing temperature (i.e., decreasing RRT) resulted in lower quality of petunia because of increased plant height and reduced lateral branching (Kaczperski *et al.*, 1991; Merritt and Kohl, 1982; Piringer and Cathey, 1960). The dry weight of unshaded carnation flowers (1.43 g) under low temperature (high RRT) was much higher than that of shaded ones (0.29 g) under high temperatures (low RRT) (Harris and Scott, 1969). Poinsettia plant-quality parameters of dry weight, stem diameter, and stem strength also were related closely to RRT; they increased linearly as RRT increased (Liu and Heins, 1998).

Horticulturists normally try to balance temperature and light to maintain adequate plant quality (dry weight) while minimizing production time. The RRT concept can be considered a predictor of plant quality. To correct a low RRT value, light must be increased or temperature must be lowered. While lower temperatures under low light may be desirable, significantly lowering temperature to adjust RRT is not realistic in many situations because most plants are shipped to market on a fixed date and lowering temperature delays flowering. The choice is thus limited to increasing intercepted light. Obviously, reducing overhead shading via cleaner glazing or fewer overhead objects (e.g., hanging baskets) is one way to increase light transmission and therefore interception in a greenhouse. Lighting conditions also can be improved through proper plant spacing. During poinsettia vegetative development (from pinch to six unfolded leaves on the second lateral shoot), light interception by individual plants increased about 30% when plant spacing increased from 15 x 15 to 22 x 22 cm and 20% from 22 x 22 to 30 x 30 cm (Liu and Heins, unpublished data). Another method of increasing light interception is by using higher temperatures during early developmental stages to accelerate leaf development and area, thereby increasing interception of photons that otherwise would

have been wasted by striking the ground.

## **5. Control of morphological development**

Many different environmental parameters and cultural practices affect plant morphology. In addition, application of chemicals and, more recently, genetic engineering are used to produce plants with desirable growth characteristics. Plant height and branching are the most commonly manipulated components of plant architecture, particularly in the floriculture industry, but other characteristics (e.g., flower number and size) also are regulated. Promotion of stem extension is useful for production of cut flowers, but more often, plant height is suppressed for a variety of bedding and potted plants, containerized ornamentals, and vegetables. Controlling plant height specifically is important, since buyers demand strict plant morphological specifications, namely narrow windows of acceptable plant heights. Production of a crop that fails to meet preset guidelines often translates to lower crop quality and thus reduced crop value or, at worst, a crop rejected by the buyer.

One of the most common and often most effective methods of retarding stem extension is application of plant growth regulators (e.g., ancymidol, chlormequat, daminozide, paclobutrazol, and uniconazole), which inhibit various steps in the gibberellin (GA) biosynthetic pathway. Chemical concentration and application frequency can be adjusted readily given the desired reduction of stem elongation. However, there are several limitations to height control by use of chemicals. First, efficacy varies by chemical and species; for example, some species of herbaceous perennials responded to five different growth retardants, while others showed no response to any of the five (Hamaker *et al.*, 1996). Second, some people perceive these chemicals as environmentally unfriendly, and in certain countries, some growth retardants are no longer available. When growth retardants are not available, alternative methods must be used. Many of these methods are discussed below.

Control of plant height can be achieved by a variety of cultural techniques. Pinching plants is used to promote lateral branching, but a secondary effect is reduced plant height. The timing of a pinch prior to flower induction affects shoot length by affecting internode number. Height at flowering is generally shorter for plants (e.g., poinsettia and chrysanthemums [*Chrysanthemum grandiflorum*]) exposed to inductive conditions shortly after pinching compared to those grown under noninductive conditions for longer periods prior to flower induction.

Container size and shape can affect stem length and canopy width by restricting root growth; restricted root growth often reduces shoot growth. Plant height and width of wax-apple (*Syzygium samarangense* Merr. & Perry) decreased as container volume decreased (Hsu *et al.*, 1996). Similarly, in muskmelon (*Cucumis melo* L.) subsequent vine elongation decreased linearly as the transplant container cell volume decreased (Maynard *et al.*, 1996). Container shape affected shoot growth of tomato seedlings (*Solanum lycopersicon* L.): plant height decreased as the cell shape changed from a square to a narrow cell with the same volume (Liptay and Edwards, 1994).

Fertilization regimens can influence plant height, primarily by the use of very low or high fertility rates, although the effect varies by species. In one study, tomato plants were fertilized three times per week, and as the nitrogen concentration decreased from 225 to 25 mg L<sup>-1</sup> plant height decreased  $\geq 30\%$  (Melton and Dufault, 1991). Coffee (*Coffea arabica* L.) plants provided with low nitrogen rates were shorter than those given a high nitrogen concentration (Fahl *et al.*, 1994). In contrast, plant height of potato (*Solanum tuberosum*) and poinsettia decreased as applied nitrogen concentration increased (Blom and Piott, 1994; Evans, 1993). Use of low nitrogen concentrations when producing bedding plants, such as petunia and impatiens, is common to control plant height during the seedling stage.

Limited water availability can be used to control plant height. The rate of shoot elongation of maize seedlings decreased as water availability decreased (Sharp, 1990). However, excessive watering also can cause reduced shoot growth: frequently watered Scotch pine (*Pinus sylvestris* L.) were shorter than plants watered less frequently (Heiskanen, 1995). Water stress is also a practice common among plug and bedding plant growers (Liptay *et al.*, 1997).

Mechanical stimulation (thigmomorphogenesis) reduces plant height for many bedding and vegetable species during the plug stage (Latimer, 1997). Brushing plants daily with polystyrene reduced stem elongation of tomato and pansy (*Viola tricolor*) by 20% (Garner *et al.*, 1997). Responses were more dramatic in another study; seven of eight tomato genotypes brushed with a steel bar were 30% to 33% shorter than those untreated (Johjima *et al.*, 1992).

Light quality has a pronounced effect on plant morphology of sun-loving plants: a low red (R) to far-red (FR) ratio promotes stem elongation and a high R : FR suppresses it. Thus, the lamp type used to provide photoperiodic lighting can affect stem extension, since lamps emit different light spectra and establish different phytochrome photoequilibria. For example, long-day plants (LDP) such as *Campanula carpatica* and *Coreopsis grandiflora* under day-extension lighting were taller under incandescent lamps (which have a low R : FR) than other lamp types (which had a higher R : FR) (Whitman *et al.*, 1998). Plant height also can be reduced by excluding FR light. Copper sulfate filters, which selectively absorb FR light, reduced plant height of chrysanthemum by one-third compared to that of those grown under natural light (Rajapakse and Kelly, 1992). If stem extension is desired, such as for production of cut flowers or stem cuttings, blue or red light can be filtered to produce longer internodes (Khattak and Pearson, 1997). In addition, close plant spacing promotes stem elongation more than wider plant spacing. Filtering of specific bands of light offers great potential for future control of plant growth.

In some LDP, lighting regimens can affect height of flowering plants. For example, *Echinacea purpurea* 'Bravado' under 30 min of night interruption (NI) lighting or under a cyclic lighting regimen of 6 min on/54 min off for 4 h were shorter than plants under 1 h of continuous NI lighting (Runkle *et al.*, 1998). In many instances, limiting the number of inductive cycles (known as limited induction photoperiod) of LDP can suppress plant height. For example, height of *Rudbeckia hirta* increased from 8 to 85 cm as the number of inductive LD increased from 8 to 66 (Harkess and Lyons, 1994). In addition, plants grown under high daily light levels are often shorter than those grown under low light levels. *Petunia ×hybrida* was shorter when grown under a high daily light integral compared with one 50% lower (Kaczperski *et al.*, 1991).

Temperature affects plant morphology, including internode elongation, in a wide variety of plants. Across all photoperiod response types, many species show a quantitative suppression or enhancement in stem elongation when the day temperature (DT) is lower or higher than the night temperature (NT), respectively (Erwin *et al.*, 1989a; Erwin and Heins, 1995; Myster and Moe, 1995). Erwin *et al.* (1989b) quantified this phenomenon in relation to the sign and magnitude of the difference between DT and NT (DIF). Stem elongation also can be suppressed by a transient (i.e., 2- to 4-h) drop in temperature (DROP) in some species and is often most effective when timed with the onset of the photoperiod (Cockshull *et al.*, 1995; Erwin *et al.*, 1989a; Langton *et al.*, 1992; Moe *et al.*, 1992). In general, the amplitude of DIF and DROP responses increases with increases in the magnitude of temperature fluctuations.

There is a variety of genetic mutants and engineering approaches in which plants have suppressed stem growth. Many of these mutants and transgenic plants have an altered sensitivity to or higher levels of endogenous GA, although other plant hormone and proteins also are involved. For example, endogenous application of GA or auxin, an especially both, elicited an increase in stem growth in GA1 mutants of pea (*Pisum sativum* L.) (Yang *et al.*, 1996). The complexity of endogenous plant height regulation can be illustrated by two studies in which oat phytochrome A was overexpressed in transgenic tobacco (*Nicotiana tabacum*) (Jordan *et al.*, 1995) and hybrid aspen (*Populus*)

(Olsen *et al.*, 1997), which led to reduced levels of active gibberellins and produced dwarfed phenotypes. The technology to create shorter or taller plants through genetic engineering by under- or overexpressing native genes or by inserting novel genes continues to advance rapidly.

Temperature and light quantity influence plant morphology by affecting flower number and size. In general, plants grown at cool temperatures develop more, larger, and more intensely colored flowers than those grown at warm temperatures. In *C. carpatica* 'Blue Clips', for example, flower number and size increased by >40% and 30%, respectively, as the temperature at which plants were grown decreased from 27 to 16°C (Whitman *et al.*, 1997). Flower size of pansy (*Viola ×wittrockiana*) increased linearly as temperature decreased from 31 or 9 °C (Pearson *et al.*, 1995). High light levels also can improve flowering characteristics. Carnation (*Dianthus* sp.) flower dry weight was higher for unshaded plants than those grown at 60% shade (Harris and Scott, 1969).

## **6. Decision support**

Production of horticultural crops has become increasingly difficult as markets write more detailed product specifications for delivery time and quality factors such as height and flower number. Such specifications require that growers perform appropriate cultural procedures at the right time. Environmental variation between and within seasons means appropriate cultural procedures will vary with every crop. All growers, especially those with little experience growing a crop, benefit from information that helps them make proper cultural-procedure decisions. Decision-support tools based on environmental, chemical, or biological data can help provide such information.

Decision support can take many forms but in controlled environments such as glasshouses, it typically is directed at providing information to assist with proper development (timing) and morphology (e.g., height). Developmental processes, as described previously, are driven primarily by temperature. Decision-support tools can be based on degree-day models or monitoring of plant developmental stages. Degree-day tools, although often used in outdoor production, never have gained widespread use in controlled environments, probably because temperature is under better control. However, such control is imperfect and air temperatures can vary from the setting. Additionally, plant temperature is correlated with air temperature but seldom equals it (Faust and Heins, 1997). Therefore, for precise control of maturation, decision support depends on repeated appraisal of plant developmental stage over time and recommendations for the appropriate developmental rate change.

*Lilium longiflorum* Thunb. (Easter lily) exemplifies the control needed because flowering must be timed each year to coincide with the changing date of Easter. An important and easily identified developmental stage for this plant is the first appearance of visible flower buds. Timing of the crop can be controlled easily by achieving visible bud on a certain date based on a fixed number of days from visible bud until flower. Quantitative relationships exist between leaf unfolding rate (Karlsson *et al.*, 1988) and temperature and flower bud size and temperature (Fisher *et al.*, 1996). Both relationships have been developed into decision-support tools. One is graphical: growers compare the actual number of unfolded leaves with that expected over time (Fisher and Heins, 1996); the other is a "bud meter": the quantitative relationship among bud length, temperature, and time to open bloom have been reduced to a simple tool (Fisher *et al.*, 1996). In this case, both tools are used for control of temperature; for plants growing outdoors, such tools can be used for prediction of maturation but not temperature control.

Another useful application of decision support is for control of plant morphology such as height. Markets often require plants with specific heights or stem lengths. Both internode number and length control final stem length. On determinate flowering plants, timing of flower initiation controls internode number. Final height then is determined by the manipulation of the factors that affect stem elongation. Deciding which methods to use and when to use them is the problem the grower faces. One decision-support tool that

has proven useful is graphical tracking (Heins and Carlson, 1990), which requires that a reasonable *a priori* relationship between plant height and time exists for a given crop. Crop height then is measured over time and compared to expected height on that particular date. This comparison tells the grower both the relative height (too short, too tall, or acceptable) and, when repeated measurements are made, the relative growth rate for the date (too fast, too slow, or acceptable). Graphical tracking relationships have been developed for crops such as poinsettia (Heins and Fisher, 1997, Fisher *et al.*, 1997a), Easter lily (Fisher and Heins, 1997, Fisher *et al.*, 1997b), Oriental lily (Fisher *et al.*, 1997c), geranium (Fisher *et al.*, 1998), and chrysanthemum (Karlsson and Heins, 1994).

## 7. Conclusions

Horticulture has been called the art and science of growing plants. Much of the art historically was knowing what to do and when. Today, although the art component is still important, science is increasing our understanding of how plants grow and develop, and this information increases our ability to grow plants to market demands by using decision-support tools. These tools facilitate informed grower decisions and, when combined with an understanding of alternative strategies, the most appropriate and environmentally desirable choices can be made.

## References

- Amir, J., Sinclari, T.R.. *Field Crops Res.*, 28: 47-58
- Bailey, B.J., Hunter, A. 1988. *Acta Horticulturae*, 229: 165-171.
- Blom, T.J., Piott, B.D. 1994. Response of Eckespoin Lilo poinsettia to nitrite, substrate pH and etridiazole in a subirrigation system. *Can. J. Plant Sci.*, 74: 151-154
- Charles-Edwards, D.A. 1981. *Physiological determinants of crop growth*, New York, Academic Press
- Cockshull, K.E. 1988. The integration of plant physiology with physical changes in the greenhouse climate. *Acta Horticulturae*, 229: 113-132
- Cockshull, K.E., Graves, C.J., Cave, R.J. 1992. The influence of shading on yield of glasshouse tomatoes. *Journal of Horticultural Science*, 67: 11-24
- Cockshull, K.E., Langton, F.A., Cave, C.R.J. 1995. Differential effects of different DIF treatments on chrysanthemum and poinsettia. *Acta Horticulturae*, 378: 15-25
- Coligado, M.C., Brown, D.M. 1975. A bio-photo-thermal model to predict tassel initiation time in corn (*Zea mays* L.). *Agr. Meteorol.*, 15: 11-13
- De Koning, A.N.M. 1989. Development and growth of a commercially grown tomato crop. *Acta Horticulturae*, 248: 329-336
- De Visser, A., Vesseur, W.P. 1982. Daylight, one of the production influencing factors. *Tuinderij*, 62: 38-39
- Erwin, J.E., Heins, R.D., Berghage, R., Kovanda, B.J., Carlson, W.H., Biernbaum, J. 1989a. Cool mornings can control plant height. *GrowerTalks*, 52: 73-74
- Erwin, J.E., Heins, R.D., Karlsson, M.G. 1989b. Thermomorphogenesis in *Lilium longiflorum* Thunb. *Amer. J. Bot.*, 76: 47-52
- Erwin, J.E., Heins, R.D. 1990. Temperature effects on lily development rate and morphology from the visible bud stage until anthesis. *J. Amer. Soc. Hort. Sci.* : *Journal of the American Society for Horticultural Science*, 115(4): 644-646
- Erwin, J.E., Heins, R.D. 1995. Thermomorphogenic responses in stem and leaf development. *HortScience*, 30: 940-949
- Evans, N.E. 1993. A preliminary study on the effects of nitrogen supply on the growth in vitro of nine potato genotypes (*Solanum* spp). *J. Expt. Bot.*, 44: 837-841
- Fahl, J.I., Carelli, M.L.C., Vega, J., Magalhães, A.C. 1994. Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants (*Coffea arabica* L.). *J. Hort. Sci.*, 69: 161-169

- Faust, J.E., Heins, R.D. 1998. Modeling shoot-tip temperature in the greenhouse environment. *J. Amer. Soc. Hort. Sci.*, 123(2): 208-214
- Fisher, P.R., Heins, R.D. 1996. A graphical control chart for monitoring leaf count of Easter lily to support crop timing decisions. *HortTechnology*, 6(1): 68-70
- Fisher, P.R., Heins, R.D. 1997. Tracking Easter lilies. *Greenhouse Grower*, 15(13): 65-66
- Fisher, P.R., Heins, R.D., Lieth, J.H. 1997a. Hitting the right curve. *Greenhouse Grower*, 15(9): 103-104
- Fisher, P.R., Heins, R.D., Liu, B., Bilodeau, L. 1997c. Tracking Oriental and Hybrid Lilies. *Greenhouse Grower*, 16(1): 39-40
- Fisher, P.R., Lieth, J.H., Heins, R.D. 1996. Modeling flower bud elongation in Easter lily (*Lilium longiflorum* Thunb.) in response to temperature. *HortScience*, 31(3): 349-352
- Fisher, P.R., Lieth, J.H., Heins, R.D. 1997b. Timing Easter Lilies. *Greenhouse Grower*, 15(14): 25-26
- Garner, L., Langton, F.A., Björkman, T. 1997. Commercial adaptations of mechanical stimulation for the control of transplant growth. *Acta Horticulturae*, 435: 219-230
- Hamaker, C.K., Engle, B.E., Heins, R.D., Carlson, W.H., Cameron, A.C. 1996. Using growth regulators to control height of herbaceous perennials. *GrowerTalks*, 60(6): 46-53
- Harkess, R.L., Lyons, R.E. 1994. Floral initiation in *Rudbeckia hirta* (Asteraceae) under limited inductive photoperiodic treatments. *Amer. J. Bot.*, 81: 1021-1026
- Harris, G.P., Scott, M.A. 1969. Studies on the glasshouse carnation: Effects of light and temperature on the growth and development of the flower. *Ann. Bot.*, 33: 143-152
- Heins, R.D., Carlson, W.H. 1990. Understanding and applying graphical tracking. *Greenhouse Grower*, 8(5): 73-80
- Heins, R.D., Fisher, P.R. 1997. Graphical Tracking 101. *Greenhouse Grower*, 15(6): 81-82
- Heiskanen, J. 1995. Irrigation regime affects water and aeration conditions in peat growth medium and the growth of containerized Scots pine seedlings. *New Forests*, 9: 181-195
- Hesketh, J., Baker, D. 1967. Light and carbon assimilation by plant communities. *Crop Sci.*, 7: 285-293
- Hsu, Y.M., Tseng, M.J., Lin, C.H. 1996. Container volume affects growth and development of Wax-apple. *HortScience*, 31: 1139-1142
- Johjima, T., Latimer, J.G., Wakita, H. 1992. Brushing influences transplant growth and subsequent yield of four cultivars of tomato and their hybrid lines. *J. Amer. Soc. Hort. Sci.*, 117: 384-388
- Jordan, E.T., Hatfield, P.M., Hondred, D., Talon, M., Zeevaart, J.A.D., Vierstra, R.D. 1995. Phytochrome A overexpression in transgenic tobacco. *Plant Physiol.*, 107: 797-805
- Kaczperski, M.P., Carlson, W.H., Karlsson, M.G. 1991. Growth and development of *Petunia xhybrida* as a function of temperature and irradiance. *J. Amer. Soc. Hort. Sci.*, 116: 232-237
- Karlsson, M.G., Heins, R.D., Erwin, J.E. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. *J. Amer. Soc. Hort. Sci.*, 113(1): 70-74
- Karlsson, M.G., Heins, R.D. 1994. A model of chrysanthemum stem elongation. *J. Amer. Soc. Hort. Sci.*, 119(3): 403-407
- Khattak, A.M., Pearson, S. 1997. The effects of light quality and temperature on the growth and development of chrysanthemum cvs. Bright Golden Anne and Snowdon. *Acta Horticulturae*, 435: 113-121
- Langton, F.A., Cockshull, K.E., Cave, C.R.J., Hemming, E.J. 1992. Temperature regimens to control plant stature: Current R&D. *Acta Horticulturae*, 327: 49-59
- Latimer, J.G. 1997. Transplant production and performance: Mechanical conditioning for height control. *Transplant Proceedings*. Vavrina, C.: 43-46, Columbus, Ohio State Univ

- Liptay, A., Edwards, D. 1994. Tomato seedling growth in response to variation in root container shape. *HortScience*, 29: 633-635
- Liptay, A., Sikkema, P., Fonteno, W. 1997. Transplant production and performance: Transplant growth control through water stress. *Transplant Proceedings*. Vavrina, C. (Ed.): 51-53, Columbus, Ohio State Univ
- Liu, B., Heins, R.D. 1997. Is plant quality related to the ratio of radiant energy to thermal energy?. *Acta Horticulturae*, 435: 171-182
- Liu, B., Heins, R.D. 1998. Modeling poinsettia vegetative growth and development: The response to the ratio of radiant to thermal energy. *Acta Horticulturae*, 465: 133-142
- Maynard, E.T., Vavrina, C.S., Scott, W.D. 1996. Containerized muskmelon transplants: Cell volume effects on pretransplant development and subsequent yield. *HortScience*, 31: 58-61
- Melton, R.R., Dufault, R.J. 1991. Nitrogen, phosphorus, and potassium fertility regimes affect tomato transplant growth. *HortScience*, 26: 141-142
- Merritt, R.H., Kohl, Jr., J.C. 1982. Effect of root temperature and photoperiod on growth and crop productivity efficiency of petunia