

Controlling Height with Temperature

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SUMMARY. Temperature management has emerged as an important tool for plant height control in greenhouse production systems. This is particularly important in vegetable transplant production where chemical controls for plant height are limited or not legal. Plant height is a function of the number of nodes and the length of each internode, and both are strongly influenced by greenhouse temperatures. Node number, or formation rate, is primarily a function of the average greenhouse temperature, increasing as the average temperature increases. Internode length is strongly influenced by the relationship between the day and night temperature, commonly referred to as DIF (day temperature – night temperature). As DIF increases, so does internode length in most plant species studied. Although the nature and magnitude of temperature effects vary with species, cultivar, and environmental conditions, these two basic responses can be used to modify transplant growth. Although data are limited, controlling transplant height with temperature does not appear to adversely influence plant establishment or subsequent yield.

Controlled-environment production of transplants, including vegetables, bedding plants, ornamentals, and forest trees, is one of the major commercial uses of greenhouse facilities in the United States. Transplant production systems have become increasingly automated as new equipment has been developed in the latter half of the 21st century, but the successful application of this automation is largely dependent on growing high quality uniform transplants. Development and widespread use of computer-controlled environmental management systems has allowed the investigation and implementation of new control strategies where the environment is modified to regulate the rate of crop development and the morphology of the plant to improve transplant quality.

Temperature is the one of the most easily and frequently modified environmental factors influencing plant growth. One can find many early references documenting the profound effects of temperature on plant developmental rates, and morphology. Interactions between thermoperiod and photoperiod were well described as early as the 1940s and 1950s. (Went, 1944, 1957). This basic information remained a scientific curiosity, until the development of automated environmental control equipment made it possible to manage greenhouse temperature with a precision that was impractical before.

In the 1980s, a number of research groups in the United States and Europe began to reexamine the effects of temperature on the growth of plants in the greenhouse. The primary objective of these studies was to provide commercial producers with the information needed to take full advantage of the new control technologies (i.e., Karlsson et al., 1983). During one of these studies, while examining the effects of day and night temperatures between 14 and 30 °C on growth of Easter Lily (*Lilium longiflorum* Thunb.), it was observed that there was an interaction between day and night temperature that affected stem length (Erwin et al., 1989). This response was fit to a series of mathematical models. It was discovered that the interaction could be described with a single term made up of the day temperature minus the night temperature. This approach was then applied to a number of other crops including Went's (1944, 1957) tomato (*Lycopersicon esculentum* Mill.) data. It quickly became apparent that this relationship, coined DIF (Erwin et al., 1989), could be used to describe much of the stem elongation response to diurnal thermoperiod and photoperiod interactions (Erwin et al., 1989; Karlsson et al., 1989; Berghage and Heins, 1991). Subsequent research has shown near universality of the general response (Erwin and Heins, 1995), but it has also demonstrated that the magnitude, and nature of the thermomorphogenic effects varies between plant species, and among cultivars within a species, as well as with timing and duration of the temperature fluctuations (Erwin and Heins, 1995; Myster and Moe, 1995; Vogelezang et al., 1992).

The manipulation of thermomorphogenic stem elongation responses has been broadly applied in commercial horticulture to reduce, or in some cases eliminate the use of chemical growth regulators (Roberts, 1991). This has been particularly important in the production of transplants where concerns about chemical residues may make their use undesirable, or in many cases illegal.

Managing plant growth with temperature

Plant height or stem length is simply the sum of the lengths of each of the internodes. It follows then, that

to manage stem elongation, it is necessary to control or manage internode number, internode length, or both. Many environmental or genetic factors, and endogenous and exogenous chemicals can influence either node number or internode length. The purpose of this report is to review the effects of temperature on transplant height and quality. Other factors will be considered only as they relate to, or interact with temperature, responses.

Node number

The rate of node development is, like most other development rates (i.e., Karlsson et al., 1989a), driven primarily by short and long term average temperature. Leaf unfolding rate (a measure of node, and internode formation) shows a curvilinear response to temperature, increasing as temperature increases to an optimum, then decreasing if temperature becomes too high. For many plants optimum temperatures for leaf unfolding fall between 22 and 30 °C. For example, with sweet pepper (*Capsicum annuum* L.) seedlings, Yaping and Heins (1996) reported maximum leaf count at an average temperature of ≈ 26 °C. Other greenhouse crops with optima in this range include poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch). (Berghage, 1989), dahlia (*Dahlia pinnata* Cav.) (Brondum and Heins, 1993), and Boston fern (*Nephrolepis exaltata* (L.) Schott) (Erwin et al., 1993). Some species have optima above or below this range. For example, optimum temperature for leaf unfolding exceeds 30 °C in Easter lily (Karlsson et al., 1988), and 30 to 35 °C in vinca [*Catharanthus roseus* (L.)] (Pietsch et al., 1995). In each of the studies cited above, average daily temperature was highly correlated with leaf unfolding while the relationship between day and night temperature (DIF) was not. While the rate of leaf unfolding may not be influenced by DIF, the total node number often is. This is frequently reported in determinant species where flower initiation is influenced by night temperature (poinsettia, Berghage, 1989), or temperature fluctuations, [chrysanthemum (*Den-dranthema grandiflora* Tzvelev) Jensen, 1993].

The rate of temperature-driven leaf unfolding in many plants is influenced by light. Leaf unfolding rate increases as irradiance increases,

(Pietsch et al., 1995) or photoperiod lengthens (Kozai et al., 1995), although much of this response is often attributed to increased leaf temperature. Other factors may also influence the rate of node formation. For example, McCall and Atherton (1995) report a lower leaf number for tomato plants grown with high salinity compared with low salinity in a positive DIF environment.

Internode length

RESPONSE TO DIF. Internode length in many plants is greatly influenced by diurnal temperature fluctuations. Day-night temperature fluctuations (DIF) have been used to describe some, or in a few cases, nearly all of the temperature-driven internode, or stem elongation responses in plants. For example, Easter Lily internode elongation (length) increases as DIF increases between -16 and 16 °C (Erwin et al., 1989). The response in lily is curvilinear with the magnitude of the response increasing as DIF increases. In practice this means commercial growers can often achieve adequate height control by simply reducing a large positive DIF to a smaller positive or zero DIF. The effect of DIF on internode length is due to increased cell elongation rather than an increase in cell number in Easter lily (Erwin et al., 1994). Stem and internode length responses to DIF have been reported for many other ornamental and vegetable crops including: *Dendranthema grandiflora* (Karlsson et al., 1989b), *Euphorbia pulcherrima* (Berghage and Heins, 1991), *Xanthium pensylvanicum* L. (Erwin, 1991), *Nephrolepis exaltata* (Erwin et al., 1993), *Streptocarpus nobilis* C.B. Clark (Erwin, 1991), *Campanula isophylla* Moretti (Moe et al., 1991), *Kalanchoe blossfeldiana* Poelln. (Mortensen, 1994), *Begonia × hiemalis* Fotsch (Grindal and Moe, 1994), *Begonia × cheimanthia* T.H. Everett ex C.Web. (Bakken and Moe, 1995), *Catharanthus roseus* (Pietsch et al., 1995), *Brassica* (*B. napus* L. *rapifera* Metzg., *B. oleracea* L. *capitata* L., and *B. oleracea* L. *gemmifera* Zenk.) (Bakken and Flones, 1995), *Solanum tuberosum* L. (Kozai et al., 1995), *Cucumis sativus* L. (Grimstad and Frimanslund, 1993), *Lycopersicon esculentum* (Grimstad, 1993), and *Capsicum annuum* (Yaping and Heins, 1996). For a more complete list see Myster and Moe (1995).

Plants respond rapidly to a change in DIF; altered growth rates can often be observed in as few as 24 h (Erwin and Heins, 1995). The response does not appear to have much of a residual effect; that is, plants respond to the current environmental regime with little lag or long term carry over (Berghage, 1989). Although a response to DIF has been described for nearly all plants examined, exceptions include spring bulbs or ephemerals (Erwin and Heins, 1995), the magnitude and nature of the response is affected by other environmental conditions, timing of the temperature fluctuations during the photo-skotoperiods, genetics, and plant maturity, or growth stage.

ENVIRONMENTAL FACTORS THAT CONFOUND OR MODIFY THE DIF RESPONSE.

Daily average temperature influences internode length and thus the response to DIF in many plants. Sweet pepper seedling internode length was correlated with average temperature as well as with DIF (Yaping and Heins, 1996). Poinsettia has an optimum average temperature for internode elongation of $\approx 24^{\circ}\text{C}$, as well as a correlation with DIF (Berghage, 1989). Similarly, Grimstad and Frimanslund (1993) report independent effects of average temperature, and DIF on cucumber internode length. Internode length increased with increasing average temperature and increasing DIF, except at low day temperature (15°C) where there was little response to DIF.

Internode elongation response to DIF is affected by light and photoperiod. Light quality has been shown to influence the response to DIF, presumably through effects related to phytochrome photoequilibria (Moe and Heins, 1990; Myster and Moe, 1995; Erwin and Heins, 1995). Incandescent lighting used for day length extension can eliminate a plant's response to negative DIF while fluorescent lighting can enhance the response (Moe et al., 1991). Increasing irradiance decreases DIF response (Myster and Moe, 1995). For example, increasing irradiance from 100 to 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in a growth chamber decreased the stem elongation of petunia (*Petunia \times hybrida* Hort.) in response to a positive DIF compared with a negative DIF (Kaczperski et al., 1991). Kozai et al. (1995) report that with *Solanum tuberosum*, the shortest internodes were produced with plants grown with higher irradiance (140

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) longer photoperiods (16 h), and a negative DIF, while the longest internodes were produced with low irradiance (70 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and positive DIF. In general, the response to DIF has been found to decrease as photoperiod increases (Erwin and Heins, 1995; Myster and Moe, 1995).

Nutrient solution salinity effects the magnitude of the response to DIF in tomato seedling stem elongation (McCall and Atherton, 1995). Reduced internode length in response to a negative DIF was greater with lower nutrient solution salinity (EC 3) than high salinity (EC 15). Plants had reduced y_p when grown under a positive DIF environment, however, since there were no significant interactions between water relations and DIF, the authors conclude that the mechanisms for inhibitory effects may be different.

GENETICS. The magnitude and nature of the DIF response is influenced by plant species and cultivar. Easter lily response is fairly large and straightforward (Erwin et al., 1989). In contrast, plant height and internode length in *Kalanchoe blossfeldiana* increases with either positive or negative DIF (Mortensen, 1994; Jensen, 1994). In a trial of 20 seed geranium (*Pelargonium \times hortorum* Bailey) cultivars, Strefeler (1995) found that, although the potential for elongation varied among cultivars, the response to DIF was the same. *Euphorbia pulcherrima* cultivars however, vary in their response to DIF (Moe et al., 1992a, 1992b). Tomato, corn, (*Zea mays* L.) and cucumber have strong responses to DIF, while squash, (*Cucurbita melopepo* var. *pepo* C. watermelon, (*Citrullus lanatus* Thunb. pea (*Pisum sativum* L.), and bean (*Phaseolus vulgaris* L.) are less responsive (Erwin and Heins, 1995).

TIMING OF TEMPERATURE CHANGES.

The timing and length of temperature changes influences the response to photo-skotoperiod temperature responses. Although there are a number of conflicting reports in the literature (Erwin and Heins, 1995), there is a general consensus that many plants are sensitive to a temperature drop, or low temperature pulse, during the first 2 to 4 h of the photoperiod (Myster and Moe, 1995). For example, a low temperature pulse given during the first 2 h of the day reduced internode length of cucumber and tomato seedlings (Grimstad, 1993). Plant height was

reduced in direct response to the magnitude of the low temperature pulse (between -2 and -10°C). In contrast to the relatively consistent response to temperature pulse immediately after dawn, pulses at other times of the day or night have provided inconsistent results. A temperature pulse before dawn was not effective in salvia (*Salvia splendens* F.) or petunia (Erwin, 1991) but has been effective with *Begonia \times hiemalis* (Grindal and Moe, 1994). A temperature pulse provided during the middle of the dark period has generally proved to be least effective in reducing stem elongation (Jensen, 1994; Grindal and Moe, 1994; Erwin and Heins, 1995).

Daily stem elongation in a number of greenhouse crops follows a pattern similar to the response to a low temperature pulse. Stem elongation is greatest during the end of the night and beginning of the day, decreasing during the day and increasing again during the night (Erwin and Heins, 1995; Lecharny et al., 1985). However, this pattern does not appear to be consistent for all plants and the relationship does not seem correlated with response to temperature DIF or pulses. For example, Bertram and Karlsen (1994) report that there was no clear pattern in elongation in the DIF-sensitive plants poinsettia or pelargonium, and that in petunia, also a DIF-sensitive species, elongation occurred mostly during the day.

EFFECTS OF DIF ON OTHER QUALITY FACTORS FOR TRANSPLANTS. Leaf expansion and orientation can be affected by DIF (Erwin and Heins, 1995). Leaf area of *Solanum tuberosum* plantlets (Kozii et al., 1995), and *Brassica* transplants (Bakken and Flones, 1995) was reduced when grown with a negative DIF. Likewise, Yaping and Heins (1996) report that leaf area of sweet pepper seedlings was highly correlated with DIF, but in this case, only when average daily temperature was considered. In contrast, leaf area of Easter lily was correlated with night temperature and not DIF (Erwin et al., 1989). Leaves on plants grown with a negative DIF tend to point downward, while those grown with a positive DIF point upward (Erwin et al., 1989).

Leaf chlorophyll content is reduced in plants grown with a negative DIF (Berghage et al., 1991). Total leaf chlorophyll increases as DIF increases in *Fuchsia* (*Fuchsia \times hybrida* Hort. ex Vilm.) and *Dendranthema* (Erwin and

Heins, 1995). Reduced leaf chlorophyll results in visibly chlorotic plants in negative DIF environments. For example, sweet pepper leaf reflectance at 550 nm decreased as DIF increased (Yaping and Heins, 1996). DIF-induced leaf chlorosis is often reversible, with plants greening rapidly after removal from the negative DIF environment (Erwin and Heins, 1995).

Lower day temperatures and reduced leaf chlorophyll have been considered responsible for the frequently reported reduction in dry weight of plants grown in negative DIF environments. Grimstad (1993) reported reduced plant dry weight in both cucumber and tomato in response to a low temperature pulse. Likewise, dry matter production in chrysanthemum is reduced in negative DIF grown plants (Jensen, 1993). Negative DIF has been shown to reduce total soluble carbohydrate content of *Lilium* (Miller et al., 1993), and affects carbohydrate partitioning in many plants (Erwin and Heins, 1995). In contrast, there are a number of reports where DIF did not influence plant dry weight (Kozii et al., 1995; Bakken and Flonas, 1995), or where plants grown with a negative DIF had greater dry weight than those grown with a positive DIF (Bakken and Flonas, 1995).

EFFECTS OF DIF ON TRANSPLANT ESTABLISHMENT AND YIELD. Although little research has been reported on the effects of DIF on transplant establishment and yield, work to date suggests that using a negative DIF to control transplant height does not adversely affect establishment or crop yields, and may in some cases improve yield or crop quality. Bakken and Flonas (1995) report that swede (*Brassica napus* L. *rapifera* Metzg.) dry weight at harvest was not affected by transplant production temperature regime, but that harvested root quality was better from transplants grown with a negative DIF. They also reported that yield of cabbage (*Brassica oleracea* L. *capitata* L.) and Brussels sprouts *Brassica oleracea* L. *gemmifera* Zenk.) was increased using negative DIF-grown transplants. Similarly, early yield and fruit quality of greenhouse cucumber was unaffected by a low temperature pulse (Grimstad, 1993). Early fruiting in greenhouse tomato was delayed by a low temperature pulse, but only when given for long time periods (4 or 5 weeks) and large temperature differ-

ences (9 and 6 °C) (Grimstad, 1993). Adequate height reduction could be obtained with a shorter treatment period or smaller pulse (Grimstad, 1993).

Conclusion

Managing plant height in the greenhouse is an important quality consideration for transplant producers. Alternatives to the use of chemical growth regulators are needed because of environmental, or health concerns, and the unavailability of chemical controls for many plants. Height control through temperature management is achieved by two basic mechanisms, reduced node and internode number, primarily a function of average temperature, and reduced internode elongation, primarily through increased night and or decreased day temperatures, or low temperature pulses at or near the beginning of the day (negative or zero DIF). Although negative DIF has been shown to reduce leaf chlorophyll, and plant dry weights in some cases, this has not translated into adverse effects on transplant establishment or yield. The most effective management strategies will take both number and internode length into account to produce compact transplants using greenhouse temperature as one of a number of height management tools.

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