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GA_{4+7} plus benzyladenine reduce foliar chlorosis of *Lilium longiflorum*

Catherine M. Whitman, Royal D. Heins*, Roar Moe[1], Keith A. Funnell[2]

Department of Horticulture, A288 Plant and Soil Science Building, Michigan State University, East Lansing, MI 48824-1325, USA

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Abstract

The effectiveness of two commercial formulations of gibberellin (GA) and benzyladenine (BA) for reducing foliar chlorosis on Easter lily (*Lilium longiflorum* Thunb.) was compared. On a per liter basis, plants were sprayed with 0, 100, 200, or 400 mg (BA equivalent) of Accel (GA_{4+7}:BA of 1:10) or Promalin (GA_{4+7}:BA of 1:1) when the crop leaf area index (LAI) = 3. One group of plants was sprayed with 100 mg of Accel or Promalin (BA equivalent) per liter twice: once at LAI = 3 and again 3 weeks later. Plants were harvested when the largest flower bud on each plant measured 13 cm in length, stored for 0 or 3 weeks at 2.5°C in the dark, and then moved into a post-harvest evaluation room at 21°C, where foliar chlorosis was monitored for 3 weeks. Senescence of some lower leaves on plants in every treatment was evident at harvest, and incidence of senescence increased during the 21 days of post-harvest evaluation. Cold storage increased the number of leaves senescing during the subsequent evaluation period. Application of Promalin or Accel significantly reduced leaf senescence compared to that of untreated plants. At harvest, 21% of the leaves on untreated plants were senescent, while plants treated with Promalin or Accel averaged 3 or 9% senescent leaves, respectively. Following 7 days of post-harvest evaluation, Promalin was more effective in preventing chlorosis than Accel at the 400 mg l^{-1} (BA equivalent) level. Following 14 or 21 days of post-harvest evaluation, Promalin was more effective than Accel for the 100 mg l^{-1} 2× and 400 mg l^{-1} (BA equivalent) treatments.

Abbreviations: GA, gibberellic acid; BA, benzyladenine; LAI, leaf area index

* Corresponding author. Tel.: +1-517-353-6628; fax: +1-517-353-0890.
E-mail address: heins@msu.edu (R.D. Heins).

[1] Present address: Department of Horticulture and Crop Sciences, Agricultural University of Norway, P.O. Box 5022, N-1432 Aas, Norway.

[2] Present address: Institute of Natural Resources, Massey University, Plamerston North, New Zealand.

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Plants in all Promalin and Accel treatments were taller than untreated plants 1 week after sprays were applied. At harvest, plants sprayed with Promalin were between 6 and 14 cm taller than untreated plants, but those treated with Accel were the same height as untreated plants.

Neither Promalin nor Accel influenced the occurrence of malformed or aborted flowers in this study. However, cold storage significantly increased the number of plants with aborted buds and malformed flowers. Unstored plants averaged 0.16 aborted buds and 0.02 malformed flowers each, while those stored 3 weeks averaged 0.51 aborted buds and 0.18 malformed flowers each.

Keywords: Easter lily; Gibberellin; Senescence; Promalin; Accel

1. Introduction

Easter lily (*Lilium longiflorum* Thunb.) is an important flowering potted plant in the US, with nearly 12 million plants produced annually (United States Department of Agriculture, 1998). Foliar chlorosis is a major factor affecting quality at harvest and limiting post-harvest life of Easter lily plants (Staby and Erwin, 1977; Prince and Cunningham, 1989). Chlorosis can develop gradually during production, or suddenly during the post-harvest period. Basal leaves are affected first and chlorosis progresses upward. In severe cases, >80% of the foliage can be affected by the time the last flower opens (Prince et al., 1987).

Foliar chlorosis on Easter lily plants is associated with many production and postproduction factors. Chlorosis is increased by the use of paclobutrazol or ancymidol (Jiao et al., 1986; Prince and Cunningham, 1989; Ranwala et al., 2000), or ancymidol in combination with low phosphorus nutrition (Tsujita et al., 1978). Forcing under negative DIF (night temperature greater than day temperature) reduces leaf carbohydrates (Miller et al., 1993) and increases chlorosis (Erwin et al., 1989). Chlorosis has been related to poor root function and environmental stresses including close plant spacing during production (Miller and Ranwala, 1998). Chlorosis is more severe if plants have been cold stored before marketing (Staby and Erwin, 1977; Prince et al., 1987; Ranwala et al., 2000) or exposed to warm temperatures during shipping (Miller and Ranwala, 1998).

The physiological basis for this disorder is not clearly understood. Gibberellins may be involved, since treatments associated with chlorosis, such as paclobutrazol, ancymidol, or negative DIF, reduce elongation through a reduction in endogenous gibberellins (Davis et al., 1988; Grindal et al., 1998; Shive and Sisler, 1976). Senescence in Easter lily leaves has been correlated with reduced leaf carbohydrates (Jiao et al., 1986; Ranwala et al., 2000) and a rise in respiration (Franco and Han, 1997). Close spacing of plants during greenhouse production results in reduced leaf carbohydrates as well as a higher incidence of leaf yellowing (Han, 1995; Miller and Ranwala, 1998). Plant density also

influences the onset of senescence in agronomic crops including maize (Tollenaar, 1991) and rice, where senescence of leaves was affected by leaf area index (LAI; Dingkuhn et al., 1990).

Exogenous application of gibberellins (GA) and cytokinins has delayed leaf senescence in Easter lilies (Han, 1995, 1996, 1997; Heins et al., 1996; Ranwala and Miller, 1999; Ranwala et al., 2000) and other *Lilium* spp. (Funnell and Heins, 1998; Ranwala and Miller, 1998). Postproduction sprays of benzyladenine (BA), GA_3, or a combination of GA_{4+7} + BA as Promalin (GA_{4+7}:BA of 1:1; Valent BioSciences, Chicago) alleviated leaf senescence on Easter lily plants, with Promalin reportedly most effective (Han, 1996). Treatment with commercial formulations of GA_{4+7} (Provide) or Promalin prevented the development of postproduction foliar chlorosis on Easter lily, with concentrations of GA_{4+7} as low as 25 mg l^{-1} effective (Han, 1997). Promalin also reduced leaf yellowing during production (Heins et al., 1996; Ranwala and Miller, 1999). On cold-stored hybrid 'Stargazer' lilies, products containing GA_{4+7} effectively prevented leaf chlorosis (Ranwala and Miller, 1998).

Several workers report that BA delays the onset of leaf chlorosis in Easter lily and has a synergistic effect when combined with GA (Han, 1995; Franco and Han, 1997). When Promalin was compared with another commercial formulation of GA_{4+7} + BA, Accel (GA_{4+7}:BA of 1:10), both reduced leaf senescence on hybrid Asiflorum (Funnell and Heins, 1998) and 'Stargazer' (Ranwala and Miller, 1998) lilies, but Promalin was more effective in both cases. When comparing responses to Promalin versus Accel, it is important to note that treatments in these experiments were based on BA concentrations, which resulted in a 10-fold greater concentration of GA_{4+7} in the Promalin treatments than in the Accel treatments.

GA treatments promote stem elongation, which can result in an undesirable increase in height of Easter lily (Heins et al., 1996; Miller and Ranwala, 1998; Ranwala and Miller, 1999). Whole-plant Promalin sprays applied early in the crop (30 days after emergence) caused significant stem elongation and deformed flowers (Heins et al., 1996). When only the lower parts of plants were sprayed, Promalin prevented chlorosis without affecting final height or flower bud quality (Heins et al., 1996). Since Promalin was not mobilized in Easter lily plants, and only treated leaves were affected (Han, 1997), restricting the application to lower parts of the plant has been suggested (Miller and Ranwala, 1998; Ranwala and Miller, 1999).

Lily growers prefer to apply growth regulator sprays for chlorosis control early in production because developing buds interfere with the spraying process, and plants often are knocked over by the spray equipment. However, the effects of Promalin sprays on Easter lily stem elongation are greatly influenced by timing of the application. Early Promalin treatments (36 or 55 days after planting) stimulated stem elongation (Ranwala and Miller, 1999). Our experience has shown that Promalin applied before visible bud can induce significant stem elongation and may

not control chlorosis throughout plant development, harvest, storage, and use by the consumer. Our objective in this study was to identify a product and rate that could be used early in production and would control leaf chlorosis on Easter lily throughout all stages of crop production and use, without inducing excessive stem elongation.

2. Materials and methods

2.1. Plant material

Easter lily plants (*L. longiflorum* Thunb.) 'Nellie White' in 17.5 cm diameter (1.7 l volume) round containers were delivered to Michigan State University (MSU) by a commercial greenhouse producer on 9 January 1998. Average date of emergence was 20 December 1997.

2.2. Plant culture

Plants were placed on two greenhouse benches at a density of 32 m^{-2}, a spacing which previous experience has shown promotes chlorosis of lower leaves, and is a density greater than the standard commercial density (11–24 m^{-2}; Dole and Wilkins, 1999). A single row of guard plants surrounded the experimental plants.

Overall average daily air temperature during the experiment was 20.6°C. Average day temperature was 21.0°C and night temperature was 20.3°C, resulting in a positive DIF of 0.7°C.

Plants were fertilized at every irrigation by using well water (EC of 0.65 ms cm^{-1} and 105, 35, and 23 mg Ca, Mg, and S per liter, respectively) acidified (two parts H_3PO_4 plus one part H_2SO_4, which provided P at 80 mg l^{-1}) to a titratable alkalinity of 130 mg $CaCO_3$ l^{-1} and containing 200N–0P–155K (mg l^{-1}; 36% ammoniacal N) from KNO_3 and NH_4NO_3. Micronutrients as part of a commercially available blended chelated material (Compound 111, Scotts, Marysville, OH) were added at a constant 50 mg l^{-1}. Nutrient solutions were applied by top-watering with minimal leaching.

High-pressure sodium lamps provided a supplemental photosynthetic photon flux (PPF) of ≈50 μmol m^{-2} s^{-1} at plant level, initiated when ambient PPF was below 200 μmol m^{-2} s^{-1} and terminated when PPF exceeded 400 μmol m^{-2} s^{-1} from 08.00 to 17.00 h.

2.3. Height control

Height of plants was controlled to produce a 30–35 cm plant, a size corresponding to commercial standards. Twice per week, height from the rim of the pot was

measured on 10 untreated plants. Graphical tracking (Carlson and Heins, 1990) was used to compare actual height with target height, and spray applications of uniconizole at 200 ml m^{-2} were made six times during the experiment: 3 mg l^{-1} on 14 and 19 January, 9 and 16 February; 5 mg l^{-1} on 23 and 27 January.

2.4. Treatments

Leaf area index (LAI) was determined by measuring the leaf area of five plants weekly with a LI-COR portable leaf area meter, model LI-3000 (LI-COR, Lincoln, NE), and when LAI reached three, treatments were applied. On 3 February 1998 (45 days after emergence), each plant was treated with 15 ml of 0, 100, 200, or 400 mg (BA equivalent) of either Promalin or Accel (Valent BioSciences, Chicago, IL) per liter, combined with 0.1 mg l^{-1} wetting agent (Olympic; Olympic Horticultural Products Co., Mainland, PA). Treatment solutions were mixed according to the BA concentrations in Promalin and Accel, which resulted in a 10-fold greater concentration of GA_{4+7} in the Promalin treatments than in the Accel treatments. One group of plants received an initial 100 mg l^{-1} (BA equivalent) on 3 February and 100 mg l^{-1} (BA equivalent) again on 25 February 1998. All treatments were applied as a spray to the lower 12 cm of the leaf canopy. To ensure even coverage, each plant was removed from the bench, placed on a revolving platform, and rotated during treatment. Plants reached the visible bud stage ≈11 days after the 3 February treatment.

2.5. Post-harvest treatments

Plants were harvested when the largest bud on each measured 13 cm in length, equivalent to that of a bud that would become an open flower in 2 days at 20°C. Half were moved directly into the post-harvest room from the greenhouse and remained there for 3 weeks. Average daily temperature in the post-harvest room was 21°C. Plants were illuminated by cool-white fluorescent lamps, providing ≈10 μmol m^{-2} s^{-1} at bench level. Remaining plants were placed in cardboard boxes, which were taped closed, and placed in a cooler set at 2.5°C for 3 weeks. Plants were removed from the boxes and placed in the post-harvest room for an additional 3 weeks.

2.6. Data collection and analysis

When spray applications were made, total plant height was measured and senesced leaves were removed. A leaf was considered senesced if >50% of the leaf area was chlorotic or necrotic. Heights were measured again 1 week after spray. At harvest, total number of leaves, yellow leaves, leaf scars indicating

removed leaves, height, and total number of buds were recorded. After plants were placed in the post-harvest room, the number of yellowed leaves was counted every 7 days for 3 weeks. The number of malformed or aborted flowers was recorded at final evaluation.

There were 10 single-plant replications within each rate × chemical × cold treatment combination. Plants were divided between two blocks established on the basis of bench position in the greenhouse. Data were analyzed using the SAS (SAS Institute, 1994) analysis of variance (ANOVA), general linear models (GLM), and MIXED procedures. Percentage data were arc sine transformed before analysis. Data for both blocks were pooled because analysis of variance revealed no significant differences between the blocks.

3. Results

At harvest, senescence of lower leaves on plants was evident to some degree in every treatment, and increased during the 21 days of post-harvest evaluation (Fig. 1). Leaves did not senesce during cold storage, but storage increased the number of leaves that senesced during the subsequent evaluation period ($P \leq 0.001$). Following 7 and 14 days of post-harvest evaluation of untreated plants, significantly ($P \leq 0.05$) more leaves had become senescent on those that had been stored 21 days at 2.5°C than on those not stored. This period encompasses the time when the plants were most attractive, as their flowers were opening. By 21 days of post-harvest evaluation on the untreated plants, stored and unstored plants had similar numbers of senescent leaves and all flowers had senesced.

Application of Promalin or Accel reduced the incidence of leaf senescence at harvest compared to that of untreated plants, and Promalin was more effective than Accel at the concentrations used in this work (Fig. 1). At harvest, 21% of the leaves on untreated plants were senescent, while plants treated with Promalin averaged 3% senescent leaves; significantly ($P \leq 0.001$) fewer than those treated with Accel, which had 9% senescent leaves.

Plants treated with Promalin or Accel had significantly fewer senescent leaves than untreated plants after 7, 14, or 21 days of post-harvest evaluation. Promalin at the 400 mg l^{-1} (BA equivalent) level was more effective than Accel on both stored and unstored plants after 7, 14, or 21 days of post-harvest evaluation. Promalin was also more effective than Accel in the 100 mg l^{-1} 2× (BA equivalent) treatment after 14 or 21 days post-harvest evaluation, regardless of cold storage.

Accel treatments tested in this experiment had a similar effect on leaf senescence irrespective of treatment concentration (Fig. 1). In contrast, treatment with higher concentrations of Promalin resulted in less chlorosis. For unstored

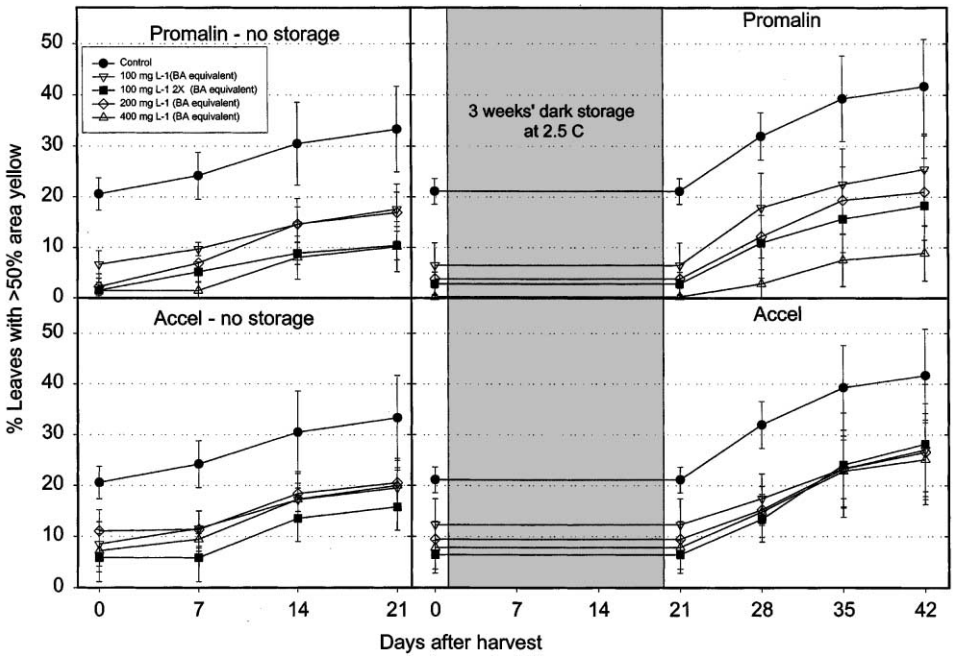

Fig. 1. Effect of Accel (GA_{4+7}:BA of 1:10) or Promalin (GA_{4+7}:BA of 1:1) sprays made 45 days after emergence on development of post-harvest foliar chlorosis in Easter lily. Plants were sprayed with 0, 100, 200, or 400 mg l^{-1} (BA equivalent), and one group of plants was treated twice with 100 mg l^{-1} (BA equivalent). Plants were harvested when the largest flower bud on each measured 13 cm in length, and stored for 0 or 3 weeks at 2.5°C in the dark. They were then moved to a post-harvest evaluation room at 21°C, where foliar chlorosis was monitored for 3 weeks. Vertical bars indicate the standard error of the means.

plants following 21 days post-harvest evaluation, Promalin at 100 2× or 400 mg l^{-1} (BA equivalent) were similarly effective, and more effective than the other Promalin treatments. For stored plants following 21 days post-harvest evaluation, the 400 mg l^{-1} (BA equivalent) Promalin treatment was more effective than all the other Promalin treatments.

To compare the effects of Promalin versus Accel on rates of leaf senescence during the post-harvest evaluation period, rates at which leaves became chlorotic (chlorotic leaves/day) were determined using linear regression. While the absolute number of chlorotic leaves differed, rates of senescence were similar in Promalin and Accel treatments at each BA concentration, except in the 200 and 400 mg l^{-1} (BA equivalent) treatments on unstored plants (data not presented). Since the rates of leaf senescence following harvest were similar for Promalin and Accel, the number of chlorotic leaves present at the end of the post-harvest evaluation was primarily determined by the number of chlorotic leaves at the end

Table 1
Effect of Promalin and Accel sprays made 45 days after emergence on height of Easter lily[a]

Treatment[b]	Total height at harvest (cm)	Increase in total height			
		Spray to 1 week after spray (cm)	Spray to harvest (cm)	Spray to 1 week after spray (% of control)	1 Week after spray to harvest (% of control)
Control	48.7 ± 3.8	2.3	30.6	100	100
Promalin (mg l^{-1})					
100	54.9 ± 2.3	5.2	36.5	223	111
100 2×[c]	57.0 ± 3.6	5.4	39.5	229	121
200	57.1 ± 3.4	6.4	39.8	271	118
400	62.3 ± 3.9	6.8	44.6	291	133
Accel (mg l^{-1})					
100	48.6 ± 3.4	3.3	30.4	141	96
100 2×[c]	50.4 ± 2.8	4.0	31.7	171	98
200	50.9 ± 3.8	3.7	32.5	159	102
400	50.8 ± 3.4	5.2	33.6	221	100
Significance					
Chemical (Ch)	***	***	***		
Concentration (Co)	***	***	***		
Ch × Co	**	NS[d]	*		

[a] Plants were harvested when the largest bud on each measured 13 cm. Data are mean ± S.E. of 10 plants per replicate.

[b] Concentrations given are those of BA. In Promalin treatments, this provides an equal concentration of GA_{4+7}. In Accel treatments, resulting GA_{4+7} concentration is 0.1 times the given BA concentration.

[c] Plants were sprayed twice: 45 and 67 days after emergence. Height increase 1 week after spray was measured after the first spray.

[d] NS: nonsignificant.

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

*** Significant at $P \leq 0.001$.

of production. In other words, controlling leaf chlorosis during production was essential to limiting chlorosis after harvest.

One week after sprays were applied, plants in all Promalin and Accel treatments were taller than untreated plants. At harvest, plants sprayed with Promalin were between 6 and 14 cm taller than untreated plants, but those treated with Accel were the same height as untreated plants (Table 1).

Promalin and Accel treatments reduced the number of senescent leaves while inducing stem elongation. We calculated the magnitude of these two responses in each treatment by subtracting the differences between treated and untreated plants. The relationship between reduction in foliar senescence and increase in plant height was linear in the Promalin treatments but not in Accel treatments (Fig. 2). Because of Promalin application, plant height increased ≈0.77 cm for every leaf that did not become chlorotic.

Neither Promalin nor Accel influenced the occurrence of aborted or malformed flowers in this study. Cold storage significantly increased the number of plants with aborted buds ($P < 0.001$) and malformed flowers ($P < 0.01$). Unstored plants averaged 0.16 aborted buds and 0.02 malformed flowers each, while those stored 3 weeks averaged 0.51 aborted buds and 0.18 malformed flowers each.

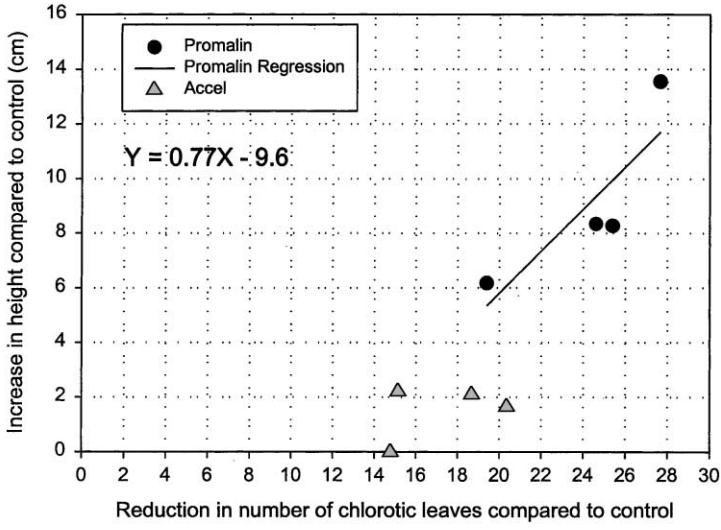

Fig. 2. The relationship between the reduced number of chlorotic leaves and the increase in height in Easter lily plants in response to sprays of Accel (GA_{4+7}:BA of 1:10) or Promalin (GA_{4+7}:BA of 1:1). The relationship between reduction in foliar senescence and increase in plant height was linear in the Promalin treatments but not in Accel treatments. Because of Promalin application, plant height increased ≈0.77 cm for every leaf that did not become chlorotic.

4. Discussion

Development of foliar chlorosis late in production and after harvest of Easter lily reduces post-harvest life significantly (Staby and Erwin, 1977; Prince and Cunningham, 1989). Foliar chlorosis is associated with many factors during production, including close plant spacing (Miller and Ranwala, 1998). We have observed that foliar chlorosis increases linearly as plant density increases above $\approx 20\ m^{-2}$ (unpublished data). This experiment was intentionally conducted at a plant spacing expected to generate leaf yellowing ($32\ m^{-2}$), and this was accomplished. Chlorosis is more severe if plants are cold stored after harvest (Staby and Erwin, 1977; Prince et al., 1987; Ranwala et al., 2000). Easter lilies are marketable for a very brief season in US, and natural variability in bloom time frequently compels growers to store the plants in coolers before sale. Results of our study verify that cold storage increases post-harvest chlorosis.

Several strategies have been attempted to control chlorosis on Easter lily, including terminating fertilizer application, lining storage boxes with polyethylene, applying spermidine (Prince and Cunningham, 1989), and spraying silver thiosulfate (Prince et al., 1987), with little success. Applications of GA and BA offer a very effective treatment to reduce chlorosis, whether the chemicals are sprayed at harvest (Han, 1996; Han, 1997) or during production (Heins et al., 1996). Our results confirm that treatment with GA and BA can successfully reduce chlorosis.

At harvest, all treated plants averaged between 0 and 12% chlorotic foliage. Further differences between treatments became evident during post-harvest evaluation. Promalin at 400 mg l^{-1} (BA equivalent) effectively delayed chlorosis throughout the entire crop cycle. Less than 10% of the foliage became chlorotic on plants treated with Promalin at 400 mg l^{-1} (BA equivalent), even 42 days after harvest (Fig. 1). Plants treated with Accel developed unacceptable levels of chlorosis. The concentration of GA_{4+7} is 10-fold higher in Promalin than in Accel, and since the role of GA_{4+7} in controlling leaf yellowing is more important than that of BA (Han, 1997; Ranwala and Miller, 1998), the higher concentrations of GA_{4+7} in the Promalin treatments probably explain their effectiveness.

Despite multiple applications of uniconizole for height control, at harvest all plants were too tall by commercial standards. Plants not treated with Promalin or Accel were ≈14 cm taller than our target height. The tallest plants were ≈27 cm taller than the target height, despite restriction of the Promalin and Accel sprays to the lower portion of the plants. This elongation was due to internode elongation, not an increase in leaf number, because the treatments were applied after plants became reproductive and leaf production had ceased. There was some advantage to making two sprays of Promalin at 100 mg l^{-1} instead of one spray at 400 mg l^{-1} (BA equivalent), since the two sprays provided good control of

chlorosis and the plants were ≈5 cm shorter than those treated with 400 mg l^{-1} (BA equivalent).

The relationship between the reduction in foliar senescence and increase in plant height was linear in the Promalin treatments, but not in the Accel treatments (Fig. 2). The rates of Accel used in this experiment delayed chlorosis similarly, so it may be valuable to test higher rates of Accel. Since BA reportedly reduces chlorosis (Han, 1995; Franco and Han, 1997), its presence in Accel offers the potential for chlorosis control with less elongation.

None of these treatments completely eliminated leaf senescence, but one application of Promalin at 400 mg l^{-1} (BA equivalent) or two applications at 100 mg l^{-1} (BA equivalent) markedly reduced chlorosis throughout the entire crop cycle. An alternative strategy, not tested, would be to apply Accel before visible bud when plants are susceptible to induction of stem elongation, and apply Promalin after visible bud, when most elongation is complete. The Accel treatment may provide protection from chlorosis until the more-effective Promalin could be applied. The risk of excessive elongation would be reduced, and prevention of chlorosis more likely.

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References

Carlson, W.H., Heins, R.D., 1990. Get the plant height you want with graphical tracking. Grower Talks 53, 62–68.

Davis, T.D., Steffens, G.L., Sankhla, N., 1988. Triazole plant growth regulators. Hort. Rev. 10, 63–103.

Dingkuhn, M., Schnier, H.F., De Datta, S.K., Dorffling, K., Javellana, C., Pamplona, R., 1990. Nitrogen fertilization of direct-seeded flooded vs. transplanted rice: II. Interactions among canopy properties. Crop Sci. 30, 1284–1292.

Dole, J.M., Wilkins, H.F. (Eds.), 1999. Floriculture Principles and Species. Prentice Hall, Upper Saddle River, NJ.

Erwin, J.E., Heins, R.D., Karlsson, M., 1989. Thermomorphogenesis in *Lilium longiflorum*. Am. J. Bot. 76, 47–52.

Franco, R.E., Han, S.S., 1997. Respiratory changes associated with growth-regulator-delayed leaf yellowing in Easter lily. J. Am. Soc. Hort. Sci. 122 (1), 117–121.

Funnell, K.A., Heins, R.H., 1998. Plant growth regulators reduce postproduction leaf yellowing of potted Asiflorum lilies. HortScience 33 (6), 1036–1037.

Grindal, G., Ernstsen, A., Reid, J., Junttila, O., Lindågrd, B., Moe, R., 1998. Endogenous gibberellin A_1 levels control thermoperiodic stem elongation in *Pisum sativum*. Physiol. Plant. 102, 523–531.

Han, S.S., 1995. Growth regulators delay foliar chlorosis of Easter lily leaves. J. Am. Soc. Hort. Sci. 120 (2), 254–258.

Han, S.S., 1996. Enhancement of postproduction quality of Easter lily by growth regulators. HortScience 31 (6), 912 (Abstract).

Han, S.S., 1997. Preventing postproduction leaf yellowing in Easter lily. J. Am. Soc. Hort. Sci. 122 (6), 869–872.

Heins, R.D., Wallace, T.F., Han, S.S., 1996. GA_{4+7} plus benzyladenine reduce leaf yellowing of greenhouse Easter lilies. HortScience 31 (4), 597 (Abstract).

Jiao, J., Tsujita, M.J., Murr, D.P., 1986. Effects of paclobutrazol and A-rest on growth, flowering, leaf carbohydrate and leaf senescence in 'Nellie White' Easter lily (*Lilium longiflorum* Thunb.). Sci. Hort. 30, 135–141.

Miller, W.B., Hammer, P.A., Kirk, T.I., 1993. Reversed greenhouse temperatures alter carbohydrate status in *Lilium longiflorum* Thunb. 'Nellie White'. J. Am. Soc. Hort. Sci. 118 (6), 736–740.

Miller, W.B., Ranwala, A.P., 1998. New findings for preventing leaf yellowing in Easter and hybrid lilies. Greenhouse Product News, August 1998, pp. 42–44.

Prince, T.A., Cunningham, M.S., Peary, J.S., 1987. Floral and foliar quality of potted Easter lilies after STS or phenidone application, refrigerated storage, and simulated shipment. J. Am. Soc. Hort. Sci. 112 (3), 469–473.

Prince, T.A., Cunningham, M.S., 1989. Production and storage factors influencing quality of potted Easter lilies. HortScience 24 (6), 992–994.

Ranwala, A.P., Miller, W.B., 1998. Gibberellin$_{4+7}$, benzyladenine, and supplemental light improve post-harvest leaf and flower quality of cold-stored 'Stargazer' hybrid lilies. J. Am. Soc. Hort. Sci. 123 (4), 563–568.

Ranwala, A.P., Miller, W.B., 1999. Timing of gibberellin$_{4+7}$ + benzyladenine sprays influences efficacy against foliar chlorosis and plant height in Easter lily. HortScience 34 (5), 902–903.

Ranwala, A.P., Miller, W.B., Kirk, T.I., Hammer, P.A., 2000. Ancymidol drenches, reversed greenhouse temperatures, postgreenhouse cold storage, and hormone spays affect post-harvest leaf chlorosis in Easter lily. J. Am. Soc. Hort. Sci. 125 (2), 248–253.

SAS Institute, 1994. SAS User's Guide, Version 6, 4th Edition. SAS Institute, Cary, NC.

Shive Jr., J.B., Sisler, H.D., 1976. Effects of ancymidol (a growth retardant) and triarimol (a fungicide) on the growth, sterols, and gibberellins of *Phaseolus vulgaris* (L.). Plant Physiol. 57, 640–644.

Staby, G.L., Erwin, T.D., 1977. The storage of Easter lilies. Florists' Rev. 161, 38.

Tollenaar, M., 1991. Physiological basis of genetic improvement of maize hybrids in Ontario from 1959 to 1988. Crop Sci. 31, 119–124.

Tsujita, M.J., Murr, D.P., Johnson, A.G., 1978. Influence of phosphorus nutrition and ancymidol on leaf senescence and growth of Easter lily. Can. J. Plant. Sci. 58, 287–290.

United States Department of Agriculture, Economics and Statistics System. National Agricultural Statistics Service. Floriculture Crops 1998 Summary. ⟨http://usda.mannlib.cornell.edu⟩.