

Ancymidol Drenches, Reversed Greenhouse Temperatures, Postgreenhouse Cold Storage, and Hormone Sprays Affect Postharvest Leaf Chlorosis in Easter Lily

Anil P. Ranwala^{1,2} and William B. Miller^{2,3}

Department of Horticulture, Clemson University, Clemson, SC 29634-0375

Terri I. Kirk⁴ and P. Allen Hammer³

Department of Horticulture, Purdue University, West Lafayette, IN 47907-1165

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ABSTRACT. The interactions of ancymidol drenches, postgreenhouse cold storage, and hormone sprays on postharvest leaf chlorosis and flower longevity of ‘Nellie White’ Easter lilies (*Lilium longiflorum* Thunb.) were investigated. Ancymidol drenches (0.5 mg/plant twice) during early growth resulted in leaf chlorosis in the greenhouse which intensified further during postharvest. Cold storage (4 °C) of puffy bud stage plants for 2 weeks also accelerated leaf chlorosis. The combination of ancymidol treatment with cold storage resulted in the most severe leaf chlorosis. Promalin (GA₄₊₇ and BA each at 100 mg·L⁻¹) sprays completely prevented postharvest leaf chlorosis, whereas ProGibb (GA₃ at 1000 mg·L⁻¹) was ineffective. Cold storage reduced flower longevity and increased bud abortion, however, the degree of bud abortion varied among experiments in different years. Both ProGibb and Promalin sprays increased flower longevity. Compared to positive DIF (difference between day and night temperature) grown plants, forcing under negative DIF (-8 °C) increased the severity of postharvest leaf chlorosis. Leaves were sampled from basal, middle, and upper sections of the stem after 4 and 12 days in a postharvest evaluation room, and analyzed for soluble carbohydrates and N. Total leaf soluble carbohydrates and N concentrations were less in basal and middle sections of negative DIF-grown plants than in positive DIF-grown plants. Leaf chlorosis was associated with depletion of soluble carbohydrates and N in the leaves. Chemical names used: α -cyclopropyl- α -(*p*-methoxyphenyl)-5-pyrimidinemethanol (ancymidol); gibberellic acid (GA₃); gibberellins A₄A₇ (GA₄₊₇); *N*-(phenylmethyl)-1*H*-purine 6-amine (benzyladenine).

Leaf chlorosis and senescence of Easter lilies (*Lilium longiflorum*) during the latter stages of forcing and postharvest can lead to significant economic loss. A “gradual” type of leaf yellowing, which occurs during greenhouse production, and an extremely rapid postharvest syndrome, termed “catastrophic” leaf yellowing have been described (Miller, 1991). Cultural factors such as the use of high levels of growth retardants, low phosphorus nutrition and root rot diseases can induce gradual leaf chlorosis in Easter lilies grown in greenhouses (Jiao et al., 1986, Tsujita et al., 1978, 1979). Postproduction leaf chlorosis can be induced by both preharvest factors such as high doses of growth retardants and early termination of fertilization (Prince and Cunningham, 1989), and postproduction factors such as cold storage before marketing, and shipping stress (Prince et al., 1987). However, the interactions of preharvest factors with

postproduction factors on postharvest leaf chlorosis in Easter lilies are not well understood.

Foliar sprays of gibberellins and cytokinins prevent leaf chlorosis and senescence in many plant species including Easter and hybrid lilies (Han, 1997; Hicklenton, 1991; Ranwala and Miller, 1998; van Doorn et al., 1992). Han (1997) reported that Promalin (GA₄₊₇ and BA) and Provide (GA₄₊₇) (Abbott Chemical Co, North Chicago, Ill.) sprays prevented postproduction leaf chlorosis in Easter lilies induced with or without cold storage. Our experiments with hybrid lilies (*Lilium* L. sp. ‘Stargazer’) also showed that sprays of GA₄₊₇ effectively prevent cold-storage-induced leaf chlorosis (Ranwala and Miller, 1998). Given the preventive effects of these hormone sprays on postproduction leaf chlorosis, it may be useful to test their effectiveness on leaf chlorosis induced by preharvest stresses, and by interactions of preharvest and postharvest stresses.

Although growing plants under higher night temperatures than day temperatures [negative difference between day and night temperature (DIF)] is commonly practiced for height reduction in many crops, negative DIF regimes can cause undesirable postharvest characteristics such as cyathia abscission in poinsettia (*Euphorbia pulcherrima* Willd.) (Moe et al., 1992). Miller et al. (1993) found that negative DIF regimes decreased carbohydrate levels in Easter lilies, but little work on negative DIF effects on postharvest characteristics in Easter lilies has been reported.

The physiology underlying postharvest leaf chlorosis in lilies is not clearly understood. The amounts of available carbohydrate and N are important factors that contribute to the vigor of an individual plant organ. Reduced soluble leaf carbohydrate levels have been reported in Easter lilies forced under negative DIF

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¹Research associate.

²Current address: Dept. of Floriculture and Ornamental Horticulture, Cornell University, Ithaca, NY 14853.

³Professor.

⁴Research technician.

(Miller et al., 1993), or treated with ancymidol (Bailey and Miller, 1989; Jiao et al., 1986). It may be hypothesized that depletion of carbohydrate and N reserves is related to the degree of postharvest leaf chlorosis in Easter lilies.

Here, we investigated the interactions of ancymidol drenches, cold storage, and hormone sprays on postharvest leaf chlorosis and flower longevity of 'Nellie White' Easter lilies. The differences in postharvest leaf chlorosis between Easter lilies grown under positive or negative DIF also were investigated. Leaf soluble carbohydrate and N concentrations of positive and negative-DIF plants were also determined during postharvest and correlated with leaf chlorosis.

Materials and Methods

Effects of ancymidol drenches, cold storage, and hormone sprays on postharvest leaf chlorosis and flower longevity

GENERAL CULTURAL PRACTICES. 'Nellie White' Easter lily plants were grown under natural photoperiod and irradiance in a greenhouse at Clemson University following standard cultural practices (Miller, 1992). Three separate experiments were conducted during Spring 1993, 1994, and 1998. In 1993 and 1994, bulbs (20 to 23 cm in diameter) precooled at 4 °C for 6 weeks were planted into 1.4-L plastic containers using a commercial potting mix (Fafard No. 4, Fafard, Inc., Anderson, S.C.). In 1998, plants were obtained from a commercial grower 31 d after planting (DAP). Plants were fertilized at each watering with a mixture containing 20N-4.4 P-16.6K with N at 200 mg·L⁻¹, and alternated with calcium nitrate plus potassium nitrate providing N and K at 200 mg·L⁻¹. A setpoint day/night temperature of 22/16 °C was used during the experiment.

GROWTH RETARDANT (ANCYMIDOL) TREATMENTS. In 1993 and 1994, A-Rest (a.i. ancymidol, SePro, Carmel, Ind.) was applied 32 DAP (when plants averaged 5 to 8 cm tall) as a 0.3 L medium drench containing 0.5 mg active ingredient. Controls were drenched with the same volume of water. A second drench was applied 11 d later. In 1998, ancymidol was drenched at this rate 33 DAP, and repeated 14 d later. Plants reached puffy bud stage 99, 102, and 90 DAP, respectively, in the 1993, 1994, and 1998 experiments.

HORMONE SPRAYS. At the puffy bud stage, half of the ancymidol-treated and control plants were sprayed with ProGibb (GA₃ at 1000 mg·L⁻¹, 1993 and 1994) or Promalin (GA₄₊₇ and BA each at 100 mg·L⁻¹, 1998), obtained from Abbott Laboratories (North Chicago, Ill.). Tween 20 (polyoxyethylene sorbitan monolaurate, 0.1%) was included as a surfactant. Entire plants were sprayed to runoff and allowed to dry for 2 h in the greenhouse before postharvest cold storage. The other plants were sprayed with water and the surfactant as the control.

COLD STORAGE TREATMENTS. Half of the plants in each treatment combination (ancymidol × hormone spray) were transferred directly to the postharvest evaluation room, the other half placed in dark, 4 ± 0.5 °C cold storage for 2 weeks before postharvest evaluation. Relative humidity (RH) during cold storage was 50% to 75%, based on hygrothermograph recordings.

POSTHARVEST EVALUATION. Air temperature in the postharvest evaluation room was 20 to 22 °C; RH was 50% to 70%. Plants received a photosynthetic photon flux of 15 to 20 μmol·m⁻²·s⁻¹ (measured with LI-185 quantum meter equipped with a quantum sensor; LI-COR Inc., Lincoln, Neb.) at the top of the plants for 12 h·d⁻¹ from cool-white fluorescent lamps, and were watered as required. The numbers of chlorotic or senesced leaves were recorded at 2-d intervals. A leaf was considered chlorotic if > 20% of the leaf area was yellow. Each flower was tagged as it opened, and the senescence date was recorded when petals began to wilt and discolor.

Flower longevity of a plant was calculated by averaging longevity of the first five flowers to open. The number of buds failing to open was recorded and expressed as the percentage of aborted buds.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS. Percentage leaf chlorosis, flower longevity, and bud abortion data were subjected to analysis of variance using a completely randomized design for a factorial arrangement of treatments (2 ancymidol × 2 cold storage × 2 hormone spray treatments). Each treatment combination had eight replicate plants. Percentage data were arcsin transformed before analysis of variance.

Effects of positive or negative DIF forcing on postharvest leaf chlorosis, leaf carbohydrate, and nitrogen levels

GENERAL CULTURAL PRACTICES AND POSTHARVEST EVALUATION. 'Nellie White' Easter lily plants were grown in glass greenhouses under negative (13.5/21.5 °C) or positive (24.0/15.5 °C) DIF at Purdue University under conditions as described by Miller et al. (1993). At the puffy bud stage, plants were sleeved, boxed, and shipped by truck to Clemson University. Plants arrived 2 d later and were unpacked immediately and placed in the postharvest evaluation room (described above). The number of chlorotic or

Fig. 1. Effects of ancymidol drenches, cold storage, and ProGibb (1000 mg·L⁻¹) sprays on leaf chlorosis of 'Nellie White' Easter lilies during postharvest evaluation phase (1993 experiment). (A) No ancymidol drenches, no cold storage; (B) no ancymidol drenches, cold stored at 4 °C for 2 weeks; (C) ancymidol drenched (0.5 mg per pot twice), no cold storage; and (D) ancymidol drenched (0.5 mg per pot twice), cold stored at 4 °C for 2 weeks. Data are means ± SE of eight replicate plants. Legend in A applies to all figures. Statistical analysis is presented in Table 1.

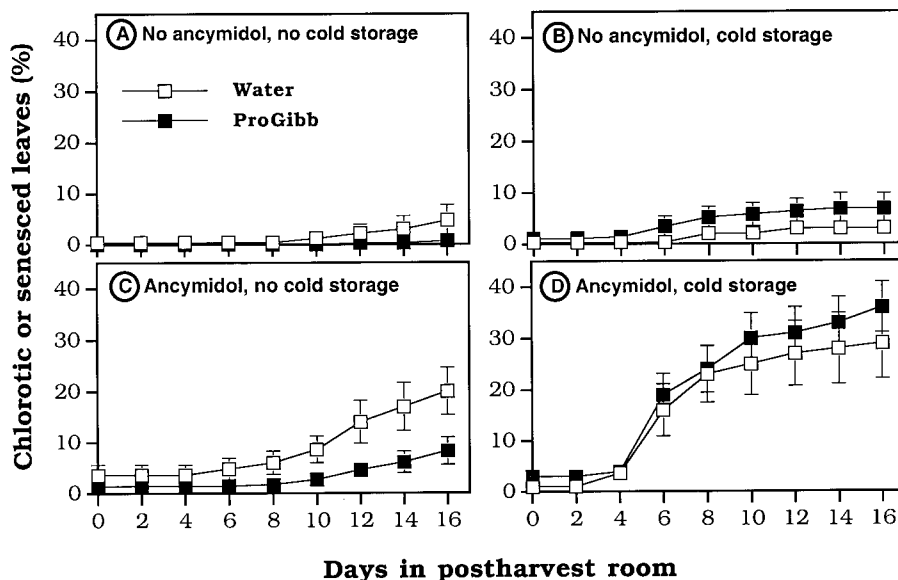


Table 1. Analysis of variance of percentage leaf chlorosis data of 'Nellie White' Easter lilies for the 1993 and 1998 experiments. Treatments were arranged in a three-way factorial structure with eight replicate plants per treatment combination.

Treatment	Days in postharvest room									
	0	2	4	6	8	10	12	14	16	
	1993 Experiment									
Ancymidol (Anc) ^z	**	**	**	**	**	**	**	**	**	**
Cold storage (CS)	NS	NS	NS	**	**	**	**	**	**	**
ProGibb (PG)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Anc × CS	NS	NS	NS	**	**	**	**	**	**	**
Anc × PG	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CS × PG	*	*	NS	NS	NS	NS	NS	*	*	*
Anc × CS × PG	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	1998 Experiment									
Ancymidol (Anc)	**	**	**	**	**	**	**	**	**	**
Cold storage (CS)	NS	**	**	**	**	**	**	**	**	**
Promalin (Prom)	NS	**	**	**	**	**	**	**	**	**
Anc × CS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Anc × Prom	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CS × Prom	NS	**	**	**	**	**	**	**	**	**
Anc × CS × Prom	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

^zAncymidol was applied as two 0.5 mg a.i. drenches 32 and 43 d after planting (DAP) in 1993, and 33 and 47 DAP in 1998. Cold storage consisted of 2 weeks 4 °C dark storage at puffy bud stage. ProGibb (GA₃ at 1000 mg·L⁻¹, 1993) or Promalin (GA₄₊₇ and BA each at 100 mg·L⁻¹, 1998), were applied as whole-plant sprays 2 h before cold storage.

NS,*,** Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

senesced leaves, flower longevity, and bud abortion were recorded as above.

DETERMINATION OF LEAF CARBOHYDRATE AND N. Plants were destructively sampled for carbohydrate and N analysis after 4 or 12 d of postharvest evaluation. Five plants were sampled from each treatment, and each plant was dissected into three equal sections (basal, middle, and upper) based on its height. For carbohydrates, leaf samples were frozen immediately in liquid N, stored at -70 °C, freeze dried, ground, and stored desiccated at 22 °C. Soluble carbohydrates were extracted from 50 mg of leaf tissue with (by volume) 12 methanol : 5 chloroform : 3 water, and separated and quantified by high-performance liquid chromatography as described earlier (Miller and Langhans, 1989).

For N determination, 100 mg of freeze-dried tissue was digested for 1.5 h in the digestion mixture described by Parkinson and Allen (1975). Nitrogen was then determined by the colorimetric procedure described by Baethgen and Alley (1989).

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS. Percentage leaf chlorosis data were compared between positive and negative DIF treatments using Student's *t* test (unpaired). Postharvest carbohydrate and N data were subjected to analysis of variance according to split-plot design with DIF treatments as main plots and plant sections as subplots.

Results

Effects of ancymidol drenches, cold storage, and hormone sprays on postharvest leaf chlorosis and flower longevity

1993 EXPERIMENT. Ancymidol drenches reduced plant height. Mean height of ancymidol-treated plants and nontreated plants was 41.2 cm and 51.1 cm, respectively, at the puffy bud stage. At the beginning of the postharvest phase, ancymidol-treated plants averaged 3% chlorotic or senesced leaves, whereas control plants had none. Leaf chlorosis began to develop by day 4 of postharvest in basal foliage and progressed upward. Ancymidol-treated plants developed leaf chlorosis more rapidly than controls (Fig. 1). Cold

storage plus ancymidol increased leaf chlorosis. The combination of ancymidol treatment with cold storage produced the most severe leaf chlorosis. The main effects of both ancymidol and cold storage, and the ancymidol × cold storage interaction on leaf chlorosis were statistically significant from day 6 onwards in postharvest (Table 1). Although foliar sprays of ProGibb (GA₃ at 1000 mg·L⁻¹) delayed and decreased leaf chlorosis in ancymidol-treated plants that were not cold stored (Fig. 1C), ProGibb did not prevent leaf chlorosis when plants were given both ancymidol and cold storage (Fig. 1D).

Flower longevity was reduced by cold storage, but was not affected by ancymidol treatment (Table 2). GA₃ increased flower longevity in all ancymidol × cold storage treatment combinations (*P* ≤ 0.01). Bud abortion was induced by cold storage, but not affected by ancymidol or GA₃ sprays.

1994 EXPERIMENT. Contrary to 1993 results, GA₃ sprays did not reduce leaf chlorosis in ancymidol-treated plants that were not cold stored (data not presented). The amount of leaf chlorosis in all treatment combinations was higher than in the 1993 experiment. For example, ancymidol and cold stored plants had 55% leaf chlorosis on day 16 postharvest, compared to 29% in 1993. Flower longevity and bud abortion showed the same treatment effects as in 1993.

1998 EXPERIMENT. Ancymidol drenches reduced plant height; mean height of ancymidol-treated plants and nontreated plants was 45.1 cm and 54.9 cm, respectively, at the puffy bud stage. At the beginning of the postharvest phase, ancymidol-treated plants had an average 13% chlorotic or senesced leaves whereas control plants showed no leaf chlorosis. Consistent with previous experiments, both ancymidol treatment and cold storage accelerated leaf chlorosis, and the combination of ancymidol and cold storage resulted in the most severe leaf chlorosis (Fig. 2). Promalin (GA₄₊₇ and BA each at 100 mg·L⁻¹) sprays before cold storage prevented postharvest leaf chlorosis in all treatment combinations.

Flower longevity was reduced by cold storage, but not affected

Table 2. Effects of ancymidol drenches, cold storage, and GA₃ (1993) or GA₄₊₇ plus BA (1998) sprays on postharvest flower longevity and bud abortion of 'Nellie White' Easter lilies. Values are means ± SE of eight replicate plants.

Ancymidol treatment	Cold storage	Hormone ^z spray	1993 Experiment		1998 Experiment	
			Flower longevity (d)	Bud abortion (%)	Flower longevity (d)	Bud abortion (%)
Ancymidol	Yes	Hormone	6.4 ± 0.1	51 ± 3	7.9 ± 0.1	0 ± 0
		Water	4.9 ± 0.2	58 ± 3	6.0 ± 0.1	9 ± 3
	No	Hormone	8.0 ± 0.2	0 ± 0	8.3 ± 0.1	0 ± 0
		Water	6.8 ± 0.2	4 ± 3	6.3 ± 0.1	0 ± 0
No Ancymidol	Yes	Hormone	6.6 ± 0.1	51 ± 5	7.9 ± 0.1	0 ± 0
		Water	5.7 ± 0.3	43 ± 8	6.2 ± 0.1	8 ± 4
	No	Hormone	8.1 ± 0.2	6 ± 6	8.1 ± 0.2	0 ± 0
		Water	7.3 ± 0.2	6 ± 4	6.7 ± 0.2	0 ± 0

F tests of main effects and interactions				
Ancymidol (Anc)	NS	NS	NS	NS
Cold storage (CS)	**	**	**	**
Hormone (Horm)	**	NS	**	NS
Anc × CS	NS	NS	NS	NS
Anc × Horm	*	NS	*	NS
CS × Horm	NS	**	NS	**
Anc × CS × Horm	NS	NS	NS	NS

^zHormone: ProGibb (GA₃ at 1000 mg·L⁻¹) used in 1993, Promalin (GA₄₊₇ and BA each at 100 mg·L⁻¹) used in 1998.

NS,*,** Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

by ancymidol treatment (Table 2). Promalin increased flower longevity in all ancymidol × cold storage treatment combinations (*P* ≤ 0.01). Bud abortion induced by cold storage was less in the 1998 experiment than the 1993 and 1994 experiments.

Effects of positive or negative DIF forcing on postharvest leaf chlorosis, leaf carbohydrate and nitrogen levels

Plants forced under both positive and negative DIF conditions at Purdue University had very little leaf chlorosis upon receipt at Clemson University for postharvest evaluation. Subsequently, however, plants grown under negative DIF developed very rapid leaf chlorosis (Fig. 3), the percentage chlorosis being greater in negative DIF than positive DIF plants throughout the postharvest phase.

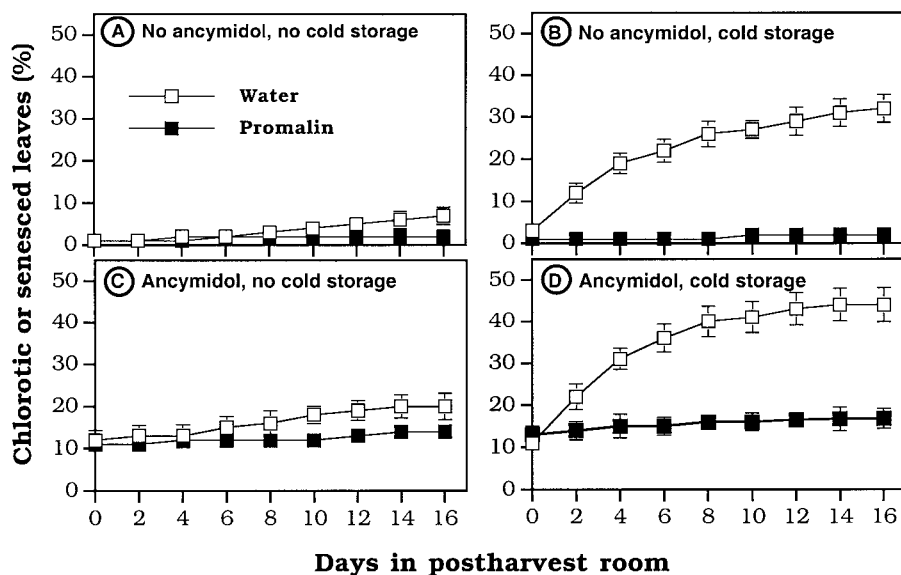
Longevity of individual flowers and flower bud abortion was affected by DIF regime. Plants grown under negative DIF showed 8% bud abortion versus 2% for plants grown under positive DIF (*P* ≤ 0.05). Individual flower longevity of negative DIF-grown plants was 5.0 d versus 5.6 d for positive DIF plants (*P* ≤ 0.05).

Leaves were sampled from basal, middle, and upper sections of the stem on days 4 and 12 of postharvest, and analyzed for soluble carbohydrates and N. For all stem sections on both sampling days, total leaf soluble sugar concentrations were significantly lower in negative DIF plants than in positive DIF plants (*P* ≤ 0.05) (Fig. 4). From days 4 to 12 of postharvest, total soluble sugar concentrations decreased in basal and middle leaves of both negative and positive DIF plants. Low initial carbohydrate concentrations presumably caused negative DIF plants to exhaust carbohydrates in basal and middle

leaves earlier than in positive DIF plants. The DIF × section interaction was significant only on day 12 (*P* ≤ 0.05).

Soluble sugars in leaves were sucrose, glucose, fructose, and a low-concentration unknown sugar eluting between sucrose and glucose during HPLC. Some characteristics of this unknown sugar have been described by Miller and Langhans (1989). Overall, in basal and middle sections, glucose and fructose

Fig. 2. Effects of ancymidol drenches, cold storage, and Promalin (100 mg·L⁻¹) sprays on leaf chlorosis of 'Nellie White' Easter lilies during postharvest evaluation phase (1998 experiment). (A) No ancymidol drenches, no cold storage; (B) no ancymidol drenches, cold stored at 4 °C for 2 weeks; (C) ancymidol drenched (0.5 mg per pot twice), no cold storage; and (D) ancymidol drenched (0.5 mg per pot twice), cold stored at 4 °C for 2 weeks. Data are means ± SE of eight replicate plants. Legend in A applies to all figures. Statistical analysis is presented in Table 1.



concentrations were higher than sucrose, and all three sugars were present in upper sections in similar concentrations. DIF regime had no effect on leaf sugar composition in any section of plant.

Leaf N concentration varied by leaf position, with upper leaves > middle leaves > basal leaves (Fig. 5). On day 4 of postharvest, most of the basal leaves were chlorotic in negative DIF plants, whereas basal leaves were just beginning to become chlorotic in positive DIF plants. On day 12 of postharvest, most of the basal and middle leaves were chlorotic in negative DIF plants, whereas only basal leaves were chlorotic in positive DIF plants. Lowest N concentration was observed in basal sections of the negative DIF plants on day 4 of postharvest (<15 mg·g⁻¹ dry weight) where leaves were already chlorotic. From days 4 to 12, leaf N concentrations decreased significantly (below 20 mg·g⁻¹ dry weight) in middle leaves of negative DIF plants and basal leaves of positive DIF plants. All the upper leaves remained green in both negative and positive DIF plants during the sampling period, and N levels remained fairly constant.

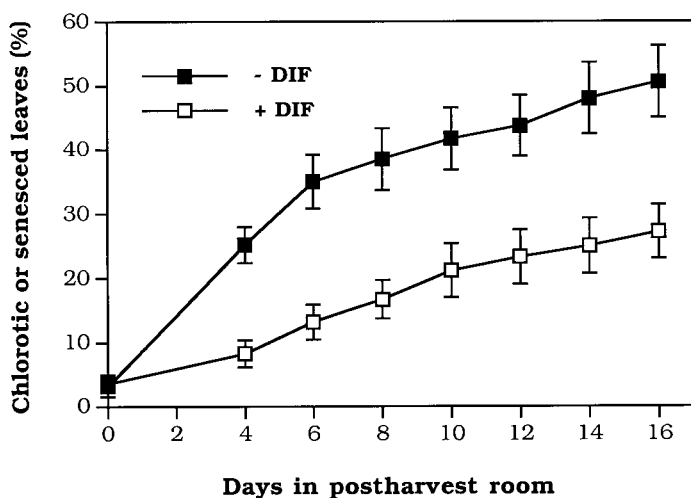


Fig. 3. Occurrence of leaf chlorosis during postharvest evaluation phase of 'Nellie White' Easter lilies grown under positive or negative DIF conditions. Data are means \pm SE of 10 replicate plants.

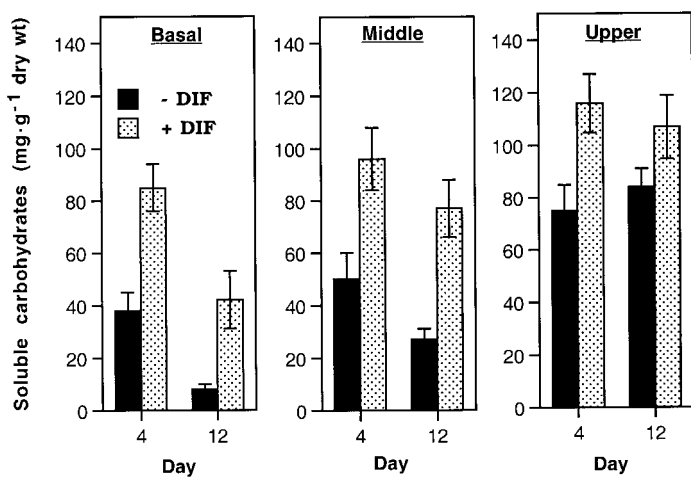


Fig. 4. Total soluble carbohydrate concentration in leaves after 4 and 12 d of postharvest storage of 'Nellie White' Easter lilies grown under positive or negative DIF conditions. Leaves were sampled from basal, middle or upper sections of plant. Data are means \pm SE of five replicate plants.

Discussion

This study shows that many preharvest and postharvest factors can contribute to postharvest leaf chlorosis in Easter lily. The differences in the rate of leaf chlorosis in experiments conducted in different years under similar conditions indicate that factors other than the ones investigated may also have been involved in this leaf senescence disorder. A long-standing observation is that the growth regulator ancymidol promotes leaf chlorosis (Jiao et al., 1986; Prince and Cunningham, 1989; Tsujita et al., 1978, 1979). In this study, we investigated how growth retardants interact with postharvest cold-storage-treated plants. Jiao et al. (1986) showed that ancymidol treatment resulted in low carbohydrate levels in leaves indicating reduced vigor. Reduced plant vigor from chemical growth regulator treatment may increase plant vulnerability to leaf chlorosis induced by cold storage. We have also observed gradually declining levels of soluble carbohydrates in leaves when Easter lilies were placed in dark storage at 4 °C (A.P. Ranwala and W.B. Miller, unpublished data).

ProGibb (GA₃) sprays as high as 1000 mg·L⁻¹ did not prevent leaf chlorosis induced by ancymidol treatment and cold storage. However, Promalin (GA₄₊₇ and BA) at 100 mg·L⁻¹ concentration completely prevented leaf chlorosis development under the same conditions (Fig. 2). The effectiveness of Promalin versus ProGibb in preventing leaf chlorosis has been observed in previous experiments with Easter lilies (Han, 1997) and hybrid lilies (Ranwala and Miller, 1998). The present study shows that Promalin sprays at harvest can prevent further development of leaf chlorosis already induced by high levels of growth retardants applied in the greenhouse. Additional studies are warranted to study the use of Promalin in preventing leaf chlorosis induced in the greenhouse by growth retardants and other stress factors.

Consistent with previous observations (Prince et al., 1987; Prince and Cunningham, 1989), cold storage reduced flower longevity and increased bud abortion. Both ProGibb and Promalin were equally effective in increasing flower longevity. In Easter lilies, GA₃ increases flower longevity (Kelly and Schlamp, 1964). In hybrid lilies, however, while Promalin (GA₄₊₇ and BA) increases flower longevity, ProGibb (GA₃) has no effect (Ranwala and Miller, 1998). The effectiveness of GA₄₊₇ in Promalin may be enhanced by the BA present in the hormone formulation. We have

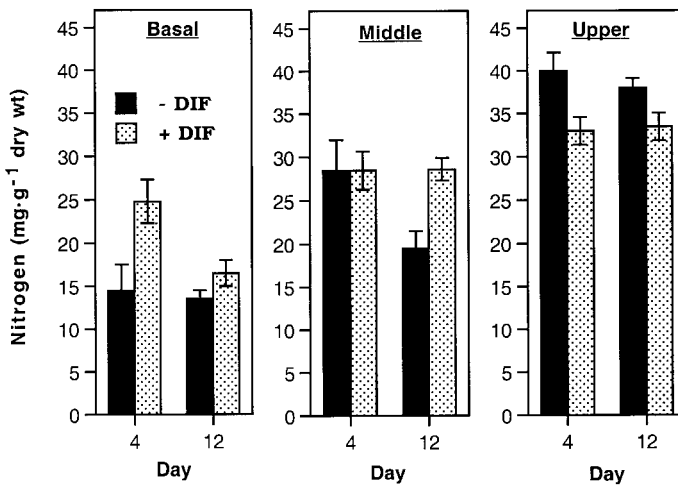


Fig. 5. Total N concentration in leaves after 4 and 12 d of postharvest storage of 'Nellie White' Easter lilies grown under positive or negative DIF conditions. Leaves were sampled from basal, middle or upper sections of plant. Data are means \pm SE of five replicate plants.

not seen any abnormalities in flower opening or development with hormone sprays. No stem or flower pedicel elongation was evident with Promalin or ProGibb treatments in the present study.

Negative DIF-grown Easter lilies developed more rapid and more severe leaf chlorosis in the postharvest phase compared to positive DIF-grown lilies. Our study indicates that depletion of soluble carbohydrates and N in leaves correlated with the occurrence of chlorosis. It is known that negative DIF-grown plants reach anthesis with lower levels of leaf soluble carbohydrates than positive DIF plants, possibly due to higher dark respiration (Miller et al., 1993). The present study shows that the leaves of negative DIF-grown plants become exhausted of soluble carbohydrates and N earlier than positive DIF plants (especially in basal and middle sections of the plant where chlorosis occurred).

Results of the present study suggest that reduced levels of endogenous GA concentrations in leaves may initiate leaf chlorosis in lilies. It is known that growing plants under negative DIF regimes reduces endogenous gibberellin concentrations in tissues. For example, stems and leaves of negative DIF-grown peas (*Pisum sativum* L.) contained lower concentrations of GA₁ and precursors to GA₁ compared to positive DIF or constant-temperature-grown plants (Grindal et al., 1998). Acceleration of leaf chlorosis by ancymidol treatment and delaying of chlorosis by exogenous foliar application of GA provide further evidence for involvement of GA in leaf chlorosis in lilies. The beneficial effects of GA in preventing leaf chlorosis have also been observed in other species such as in cut flowering stems of *Alstroemeria pelegrina* L. (Jordi et al., 1995).

The practical applications of our findings for improving postharvest leaf and flower quality of Easter lilies are several-fold. Stresses that reduce the vigor of plants in greenhouse such as extreme doses of growth regulators or large negative DIFs should be avoided. Postproduction cold storage should be minimized to prevent rapid postharvest leaf chlorosis. Foliar sprays of Promalin are a very effective method of preventing further leaf chlorosis even if it already has been induced by those stresses. Our recent research indicates that Promalin sprays can delay leaf chlorosis in Easter lilies during postharvest as well as greenhouse production (Ranwala and Miller, 1999).

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