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Gibberellin$_{4+7}$, Benzyladenine, and Supplemental Light Improve Postharvest Leaf and Flower Quality of Cold-stored 'Stargazer' Hybrid Lilies

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Abstract. **Experiments were conducted to evaluate storage temperature, storage irradiance and prestorage foliar sprays of gibberellin, cytokinin or both on postharvest quality of Oriental hybrid lilies (*Lilium* sp. 'Stargazer'). Cold storage of puffy bud stage plants at 4, 7, or 10 °C in dark for 2 weeks induced leaf chlorosis within 4 days in a simulated consumer environment, and resulted in 60% leaf chlorosis and 40% leaf abscission by 20 days. Cold storage also reduced the duration to flower bud opening (days from the end of cold storage till the last flower bud opened), inflorescence and flower longevity, and increased flower bud abortion. Storage at 1 °C resulted in severe leaf injury and 100% bud abortion. Providing light up to 40 μmol·m^{-2}·s^{-1} during cold storage at 4 °C significantly delayed leaf chlorosis and abscission and increased the duration of flower bud opening, inflorescence and flower longevity, and reduced bud abortion. Application of hormone sprays before cold storage affected leaf and flower quality. ProVide (100 mg·L^{-1} GA$_{4+7}$) and Promalin (100 mg·L^{-1} each GA$_{4+7}$ and benzyladenine (BA)) effectively prevented leaf chlorosis and abscission at 4 °C while ProGibb (100 mg·L^{-1} GA$_3$) and ABG-3062 (100 mg·L^{-1} BA) did not. Accel (10 mg·L^{-1} GA$_{4+7}$ and 100 mg·L^{-1} BA) showed intermediate effects on leaf chlorosis. Flower longevity was increased and bud abortion was prevented by all hormone formulations except ProGibb. The combination of light (40 μmol·m^{-2}·s^{-1}) and Promalin (100 mg·L^{-1} each GA$_{4+7}$ and BA) completely prevented cold storage induced leaf chlorosis and abscission.**

Leaf chlorosis is a major postharvest problem in both Easter lily (*Lilium longiflorum* Thunb.) and hybrid lily (*Lilium* sp.) production. Rapid chlorosis and browning of leaves in the postharvest environment can severely reduce the quality and appearance of lilies. Studies conducted with Easter lilies suggest that preharvest factors such as growth retardants (Jiao et al., 1986) and postharvest factors such as cold storage of mature plants followed by high temperature shipping stress (Prince et al., 1987; Prince and Cunningham, 1989) contribute to these leaf disorders.

In Oriental hybrid lilies, most commercial cultivars including 'Stargazer' and 'Mona Lisa' are highly susceptible to cold storage induced leaf disorders. After cold storage, leaves rapidly turn yellow, then brown, and finally abscise. Leaf chlorosis begins from lower leaves and progresses towards upper leaves. In addition, some flower buds cease development and dry out (bud abortion), and longevity of open flowers is reduced. Our preliminary studies showed that providing 40 μmol·m^{-2}·s^{-1} light during cold storage was very effective in maintaining leaf and flower quality of 'Stargazer' hybrid lilies.

Gibberellin and cytokinins have been used successfully to prevent leaf senescence in some species (Dai and Paull, 1991; Hicklenton, 1991; van Doorn et al., 1992). In Easter lilies, foliar sprays of GA$_{4+7}$ and BA are effective in preventing leaf chlorosis during both production (Heins et al, 1996) and postproduction (Han, 1997). However, because gibberellins and cytokinins show diverse effects on leaf senescence depending on the species and cultivar (Thimman, 1980), further studies should be conducted to test their effects on hybrid lilies.

The objective of this study was to better define appropriate conditions for cold-storing 'Stargazer' hybrid lilies to preserve postproduction leaf and flower quality. We evaluated the effects of the cold storage temperature, hormone (GA$_3$, GA$_{4+7}$, and BA) sprays before cold storage, and supplemental light during cold storage on leaf and flower characteristics in the postharvest phase.

Materials and Methods

Cultural practices. Oriental hybrid lilies (*Lilium* sp. 'Stargazer') were grown in a greenhouse following standard cultural practices (Miller, 1992). On 2 Apr. 1997, bulbs (16 to 18 cm in diameter) precooled at 4 °C for 8 weeks, were planted into 15-cm-diameter plastic containers using a commercial potting mix (Metro Mix-360; Scotts-Sierra Horticultural Products Co., Marysville, Ohio). Two bulbs were planted in each pot. Plants were fertilized at each watering with a fertilizer mixture containing 20N–4.4P–16.6K at the concentration of 200 mg·L^{-1} N, and alternated with calcium nitrate plus potassium nitrate at the concentration of 200 mg·L^{-1} N. All plants received full natural sunlight in the greenhouse. A setpoint temperature of 22/16 °C (day/night) was used during the experiment. At the mature puffy bud stage (1 to 2 d before anthesis), uniform plants with healthy foliage were selected for cold storage treatments.

Experiment 1: effects of cold storage temperature. Plants at the puffy bud stage were stored in cold-rooms at 1, 4, 7, or 10 ± 0.5 °C in complete darkness. During cold storage, all plants were irrigated with water as required. After 2 weeks of cold storage, plants were transferred to a postharvest room for evaluation. There were six replicate pots per treatment. Control plants were transferred to the postharvest room without cold storage.

Experiment 2: effects of supplemental light during cold storage. Plants at the puffy bud stage were stored at 4 °C in

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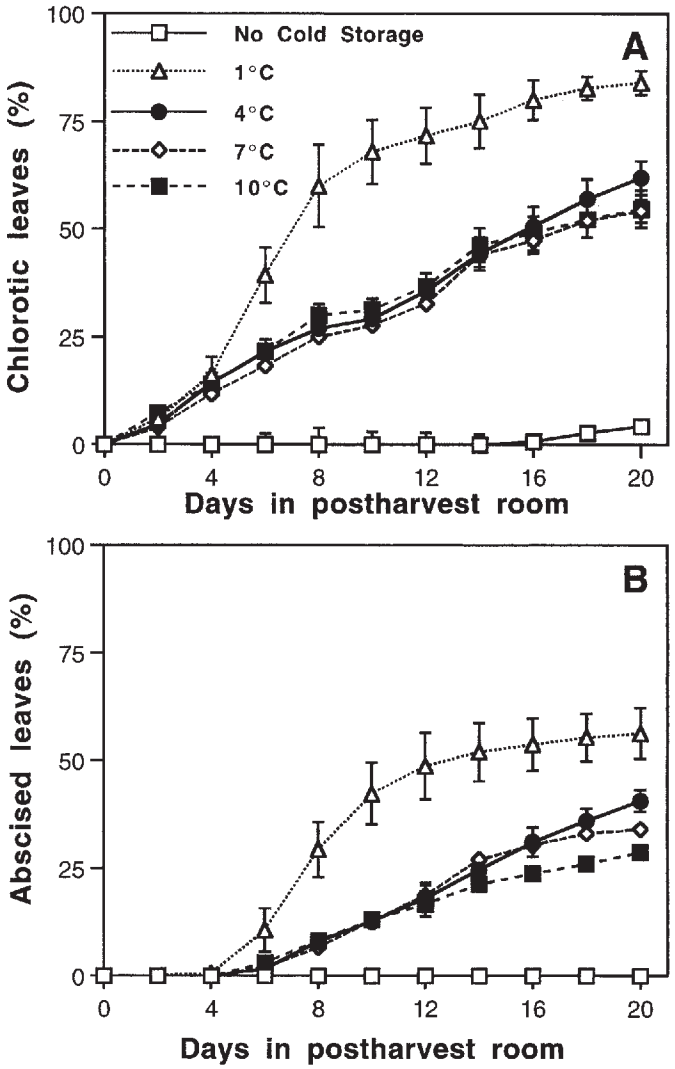

Fig. 1. Effects of cold storage of Oriental hybrid lily 'Stargazer' plants on leaf chlorosis (**A**) and abscission (**B**) during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were stored for 2 weeks at 1, 4, 7, or 10 °C in darkness, and then held at 22 °C for postharvest evaluation. A set of plants was transferred to postharvest room without cold storage as controls. Each point is a mean ± SE of six replications.

darkness or with constant irradiance of 10, 20, or 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light (measured at the top of the plants) from cool-white fluorescent lamps. Plants were spaced to yield ≈625 cm^2 per plant. After 2 weeks of cold storage, plants were transferred to a postharvest room for evaluation. There were six replicate pots per light treatment.

Experiment 3: effects of hormone sprays before cold storage. Hormone formulations—ProGibb (4% GA_3), ProVide (2% GA_{4+7}), ABG-3062 (2% BA), Promalin (1.8% GA_{4+7} and 1.8% BA), and Accel (1.8% BA and 0.18% GA_{4+7})—were obtained from Abbott Laboratories, North Chicago, Ill. Hormone solutions were diluted with deionized water to give final concentrations as follows: ProGibb (100 $mg \cdot L^{-1}$ GA_3), ProVide (100 $mg \cdot L^{-1}$ GA_{4+7}), ABG-3062 (100 $mg \cdot L^{-1}$ BA), Promalin (100 $mg \cdot L^{-1}$ each GA_{4+7} and BA), and Accel (100 $mg \cdot L^{-1}$ BA and 10 $mg \cdot L^{-1}$ GA_{4+7}). All hormone solutions contained 0.1% Tween 20 (polyoxyethylene sorbitan monolaurate) as a surfactant. The entire plant was sprayed with hormone solution to runoff and left for 2 h in the greenhouse to allow foliage to dry before cold storage. A set of plants was sprayed with water containing surfactant as the control.

Hormone sprayed plants were stored at 4 °C in complete darkness. After 2 weeks of cold storage, plants were transferred to a postharvest room for evaluation. There were six replicate pots per treatment.

Experiment 4: effects of light and promalin sprays. This experiment was conducted to evaluate the combination of supplemental light and hormone sprays. Plants were sprayed with Promalin (100 $mg \cdot L^{-1}$ each GA_{4+7} and BA) or water as described in Expt. 3. Plants were then stored at 4 °C in either dark or with constant irradiance (40 $\mu mol \cdot m^{-2} \cdot s^{-1}$). After 2 weeks of cold storage, plants were transferred to a postharvest room for evaluation. There were six replicate pots per treatment.

Postharvest evaluation. Cold-stored lilies were transferred to a room with simulated indoor environment for postharvest evaluation. Air temperature of the room was 22 ± 1 °C and relative humidity ranged from 50% to 70%. Plants received 15 to 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (12 $h \cdot d^{-1}$) light at the top of the plant from cool white fluorescent lamps. All plants were watered as required. The number of chlorotic leaves and abscised leaves were recorded at 2-d intervals. A leaf was considered chlorotic if >50% of leaf area was yellow or brown. Each flower was tagged as it opened, and the date of senescence was recorded when the petals began wilting and discolored. Flower longevity of a plant was calculated by averaging longevity of all opened flowers. The number of buds failed to open was recorded and expressed as percentage of aborted buds.

Statistical analysis. In Expts. 1, 2, and 3, percentage chlorotic leaves and percentage abscised leaves, and flower characteristics (days to open last flower, inflorescence and flower longevity, and percentage buds aborted) were subjected to analysis of variance according to completely randomized design with six replications. Mean separation was done according to Duncan's multiple range test. Percentage data were arcsin transformed before analysis. In Expt. 4, all variables were subjected to analysis of variance according to a split-plot design with light treatments assigned to main plots and hormone sprays assigned to subplots.

Table 1. Effects[z] of cold storage of Oriental hybrid lily 'Stargazer' plants on flower opening and longevity during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were stored for 2 weeks at various temperatures in darkness, and then held at 22 °C for postharvest evaluation.

Cold storage temp	Days to last open flower bud	Flower longevity (days)	Total inflorescence longevity (days)	Buds aborted (%)
No cold storage	12.2 a[y]	7.7 a	19.2 a	0 c
1 °C	---[x]	---[x]	---[x]	100 a
4 °C	6.5 b	6.2 b	12.7 b	33 b
7 °C	5.2 c	6.4 b	12.0 b	26 b
10 °C	5.7 bc	6.7 b	12.4 b	28 b

[z]Each value is a mean of six replications.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
[x]No data because all flower buds were aborted.

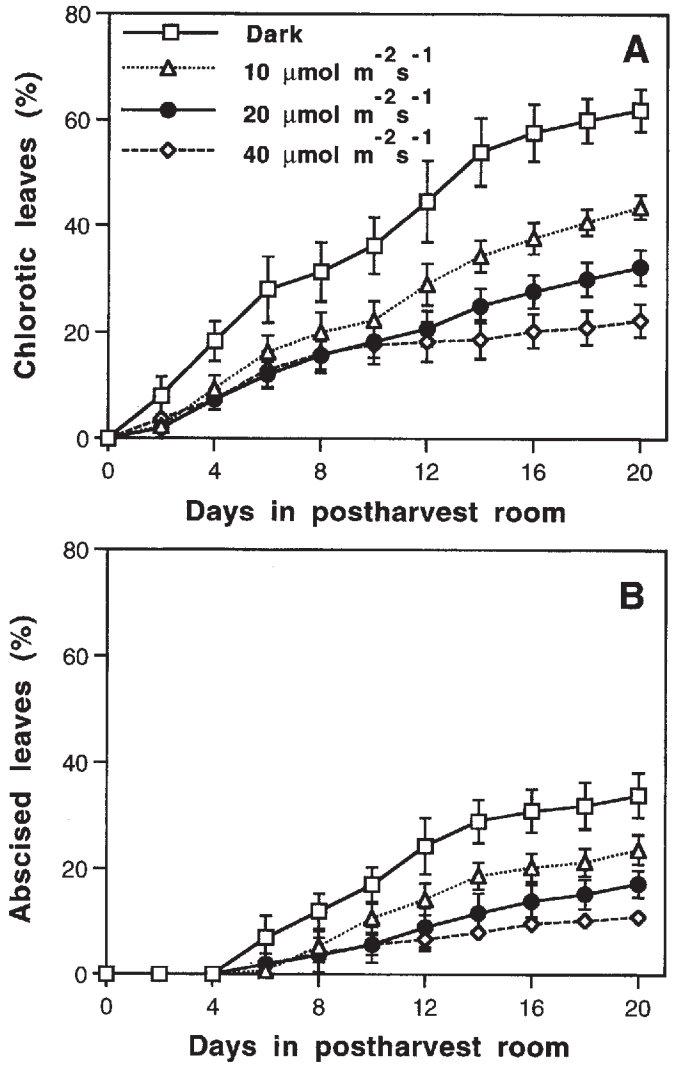

Fig. 2. Effects of supplemental light during cold storage of Oriental hybrid lily 'Stargazer' plants on leaf chlorosis (**A**) and abscission (**B**) during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were stored for 2 weeks at 4 °C in dark , with an irradiance of 10, 20, or 40 μmol·m^{-2}·s^{-1} provided by cool-white fluorescent lamps. Plants were then held at 22 °C for postharvest evaluation. Each point is a mean ± SE of six replications.

Results

Effects of cold storage temperature. Cold storage at 1 or 4 °C halted flower development and opening, whereas on average, more than one and three flower buds opened per plant during the 2-week cold storage at 7 and 10 °C, respectively. Plants did not show any leaf chlorosis when they were removed from the coolers. Within 2 to 4 d poststorage, lower leaves became chlorotic and then turned necrotic in all treatments (Fig. 1). Chlorosis initiated in the lower leaves and progressed upwards. Brown leaves started to abscise after 6 d in postharvest room and continued gradually. Storage at 1 °C had severe adverse effects on leaf quality. After 8 d poststorage, >60% of the leaves were chlorotic in plants stored at 1 °C, compared to ≈25% in plants stored at other temperatures. Leaf chlorosis and abscission in plants stored at 4, 7, or 10 °C were not significantly different except reduced leaf abscission occurred during later stages of postharvest in plants stored at 10 °C.

Cold storage had adverse effects on flower characteristics (Table 1). Cold storage reduced the duration of flower bud opening (days in postharvest room until the last flower bud opened) and inflorescence and flower longevity, and increased flower bud abortion. Plants stored at 1 °C aborted all flower buds while plants stored at higher temperatures aborted ≈30% of flower buds.

Effects of light during cold storage. Providing light during cold storage significantly delayed leaf chlorosis and abscission (Fig. 2). Increasing irradiance from 10 to 40 μmol·m^{-2}·s^{-1} reduced the rate of leaf chlorosis and abscission. After 20 d poststorage, plants stored in the dark had 60% chlorotic leaves compared to <20% chlorotic leaves in plants provided with 40 μmol·m^{-2}·s^{-1} light. Duration of flower bud opening as well as inflorescence and flower longevity were increased and bud abortion was reduced by increasing irradiance in cold storage (Table 2).

Effects of hormone sprays before cold storage. ProVide (100 mg·L^{-1} GA_{4+7}) and Promalin (100 mg·L^{-1} each GA_{4+7} and BA) effectively prevented cold storage induced leaf chlorosis and abscission while ProGibb (100 mg·L^{-1} GA_3) and ABG-3062 (100 mg·L^{-1} BA) were not effective (Fig. 3). Accel (10 mg·L^{-1} GA_{4+7} and 100 mg·L^{-1} BA) showed intermediate effects. Although leaf chlorosis and browning was almost completely prevented by ProVide and Promalin, leaves began to abscise 10 d poststorage, but at a lower rate compared to control or plants treated with ProGibb or ABG-3062.

Promalin, ABG-3062, ProVide, and Accel significantly increased the duration of flower bud opening and inflorescence longevity (Table 3). Although ProGibb increased the duration of flower bud opening, the effect was not statistically significant. Flower longevity was increased and bud abortion was significantly reduced by all hormone formulations except ProGibb.

Plant height measurements at the end of the postharvest phase revealed no significant height change due to any hormone treatment (data not shown).

Effects of hormone sprays and light in cold storage. The combination of light (40 μmol·m^{-2}·s^{-1}) and Promalin sprays (100 mg·L^{-1} each GA_{4+7} and BA) was more effective in preventing leaf chlorosis and abscission than individual treatments. Leaf abscis-

Table 2. Effects[z] of supplemental light during cold storage of Oriental hybrid lily 'Stargazer' plants on flower opening and longevity during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were stored for 2 weeks at 4 °C with supplemental light at the indicated irradiance provided by cool-white fluorescent lamps. Plants were then held at 22 °C for postharvest evaluation.

Irradiance (μmol·m^{-2}·s^{-1})	Days to last open flower bud	Flower longevity (days)	Total inflorescence longevity (days)	Buds aborted (%)
0 (dark)	6.8 b[y]	5.8 c	12.2 b	27 a
10	7.3 b	6.4 b	13.2 b	21 a
20	12.2 a	6.5 b	18.8 a	11 b
40	13.5 a	7.2 a	20.2 a	6 b

[z]Each value is a mean of six replications.
[y]Mean separation within columns by Duncan's multiple range test (P = 0.05).

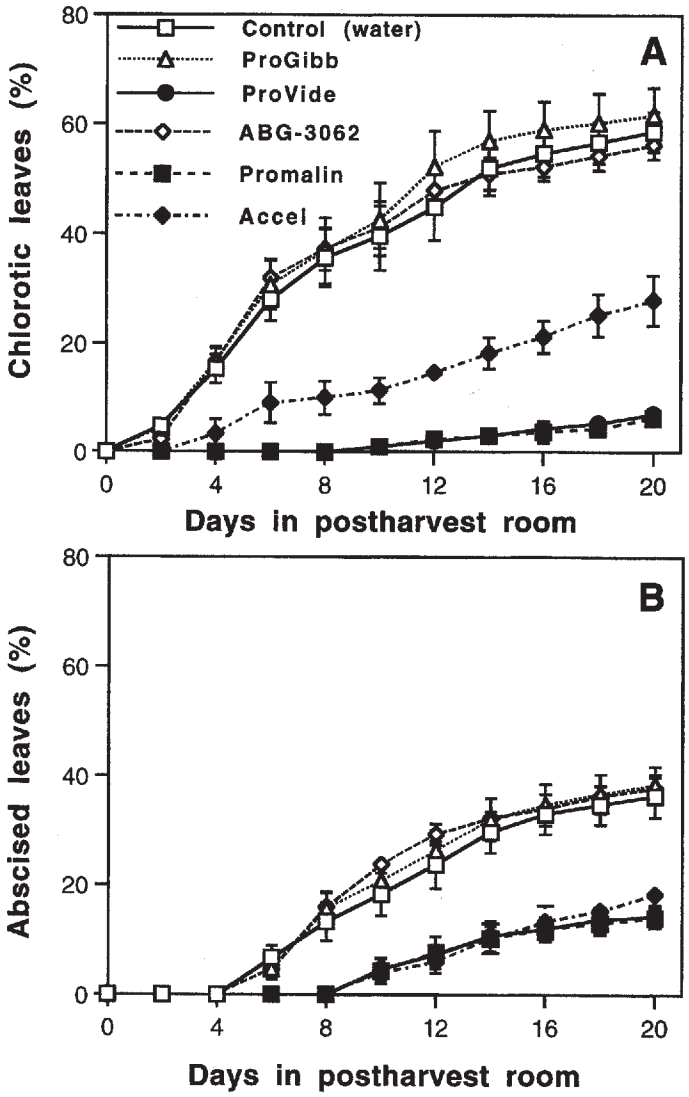

Fig. 3. Effects of hormone sprays before cold storage of Oriental hybrid lily 'Stargazer' plants on leaf chlorosis (**A**) and abscission (**B**) during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were sprayed with hormone solutions at 100 mg·L^{-1} of the major active ingredient, and stored for 2 weeks at 4 °C. Plants were then held at 22 °C for postharvest evaluation. Each point is a mean ± SE of six replications.

sion seen after 10 d poststorage in Promalin-treated plants was completely eliminated by the combination of light and Promalin sprays (Fig. 4). Conversely, while flower bud opening and flower longevity were increased and bud abortion was prevented by treatments of light and Promalin sprays individually, the combination of light and Promalin had no significant additional effects (Table 4). Apparently, light or Promalin alone are able to effect the maximum flower and inflorescence longevity possible under these storage conditions.

Discussion

Although storage of mature 'Stargazer' hybrid lilies at low temperature is an effective way of halting further development and opening of flower buds, it induces severe leaf chlorosis and flower opening disorders during the subsequent postharvest (poststorage) phase. Storage temperature is a critical factor affecting postharvest leaf and flower quality. Storage of hybrid lilies at 1 °C results in severe damage to leaves and flowers (Fig. 1 and Table 1). Higher storage temperatures reduce the severity of poststorage leaf chlorosis and abscission, and flower bud abortion caused by storage at 1 °C . However, because storage at higher temperatures does not completely halt flower development and opening processes, total inflorescence longevity and duration of flower bud opening are reduced. Since storage at 4 °C showed minimum flower development without detrimental effects on leaves observed in 1 °C, we used 4 °C as the storage temperature to evaluate preventive effects of irradiance and prestorage hormone sprays on cold storage induced leaf and flower disorders. However, it is possible that the effects of light and hormones may vary at higher storage temperatures.

The effects of light during cold storage in preventing leaf chlorosis and abscission may be due to the increased levels of soluble carbohydrates in leaves. The amount of soluble carbohydrates has been implicated as a factor affecting postharvest leaf quality in many species. For example, in *Protea neriifolia* R.Br., addition of sucrose to vase solutions of floral stems during a 7-d dark postharvest period significantly reduced leaf blackening (McConchie and Lang, 1993). Experiments we have conducted with Easter lilies showed the provision of 50 µmol·m^{-2}·s^{-1} of light during 3-week 4 °C storage of mature plants resulted in large increases in leaf soluble carbohydrate levels compared to gradually declining carbohydrate levels under dark conditions (unpublished data).

The effects of gibberellins and cytokinins on leaf senescence vary depending on the species and whether leaves are intact or excised or in cut branches. In *Alstroemeria hybrida* L., both GA_3 and BA added to the vase solutions delayed leaf chlorosis in cut stems (Dai and Paull, 1991; Hicklenton, 1991). Although GA_3 prevents chlorosis of excised Easter lily leaves (Han, 1995), it has no effect on intact leaves (Han, 1997). In our study, among hormones tested at 100 mg·L^{-1} concentration, hormone formulations containing GA_{4+7} were most effective in preventing leaf

Table 3. Effects[z] of hormone sprays before cold storage of Oriental hybrid lily 'Stargazer' plants on flower opening and longevity during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were sprayed with hormone solutions, and stored for 2 weeks at 4 °C in darkness. Plants were then held at 22 °C for postharvest evaluation.

Hormone treatment	Days to last open flower bud	Flower longevity (days)	Total inflorescence longevity (days)	Buds aborted (%)
Control (water)	7.7 d[y]	6.4 c	13.8 c	27 a
ProGibb (100 mg·L^{-1} GA_3)	8.7 cd	6.7 c	14.6 c	20 a
ProVide (100 mg·L^{-1} GA_{4+7})	10.7 bc	7.3 ab	17.7 b	2 b
ABG-3062 (100 mg·L^{-1} BA)	11.7 b	7.1 b	19.8 b	8 b
Promalin (100 mg·L^{-1} GA_{4+7} and 100 mg·L^{-1} BA)	15.7 a	7.6 a	22.3 a	4 b
Accel (10 mg·L^{-1} GA_{4+7} and 100 mg·L^{-1} BA)	11.8 b	7.2 ab	19.2 b	2 b

[z]Each value is a mean of six replications.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).

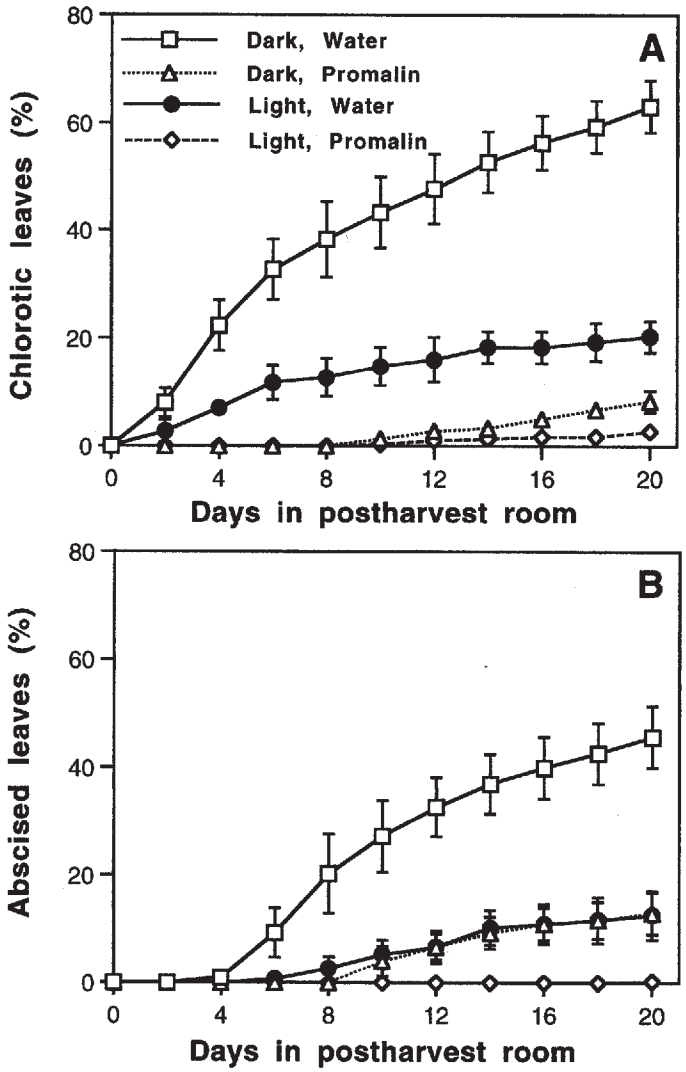

Fig. 4. Effects of Promalin (GA_{4+7} and BA) sprays and supplemental light during cold storage of Oriental hybrid lily 'Stargazer' plants on leaf chlorosis (**A**) and abscission (**B**) during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were sprayed with Promalin (100 mg·L^{-1} each GA_{4+7} and BA) or water, and stored for 2 weeks at 4 °C in dark or in light (40 μmol·m^{-2}·s^{-1}). Plants were then held at 22 °C for postharvest evaluation. Each point is a mean ± SE of six replications.

chlorosis. Similar effects have been reported in Easter lilies where hormone sprays containing GA_{4+7} were most effective in controlling cold storage induced leaf chlorosis (Han, 1997). In those experiments, concentrations as low as 25 mg·L^{-1} GA_{4+7} were effective in preventing leaf chlorosis. ProVide and Promalin were most effective at preventing leaf chlorosis in our study. The intermediate effect of Accel may be due to the lower rate of GA_{4+7} present at 10 mg·L^{-1}. However, a range of concentrations should be tested with these materials to find optimum rates.

As leaf senescence is a complex process with chlorophyll breakdown associated with carbohydrate and protein turnover, and activation of several enzyme systems (Thimann, 1980; Thomas and Stoddard, 1980), light and exogenous hormones may affect leaf chlorosis through similar or different pathways. It is also possible that effects of light and hormones on leaf chlorosis may be different from leaf abscission. This was evident when the low rate of abscission of green leaves seen in Promalin treated plants at late stages of postharvest phase was prevented by combining Promalin sprays with light during cold storage (compare Figs. 3 and 4).

Although BA (at 100 mg·L^{-1}) was not effective in preventing leaf chlorosis it had positive effects on flower characteristics such as duration of flower bud opening, inflorescence and flower longevity and reduction of bud abortion. The effects of GA_{4+7} seem to be enhanced by BA as Promalin had the longest flower opening duration. The improvement of flower longevity in Easter lilies by a different cytokinin, 6-(benzylamino)-9-(2-tetrahydropyranyl)-9*H*-purine (PBA) has been reported in a recent study (Pemberton et al., 1997). Although GA_3 is known to improve flower longevity in Easter lilies (Kelly and Schlamp, 1964), it showed no effect in 'Stargazer' hybrid lilies in this study.

This study demonstrated that supplemental light and sprays of GA_{4+7} and BA counteract most of the adverse effects of short-term cold storage of 'Stargazer' hybrid lilies. Combining light and prestorage sprays of GA_{4+7} and BA (each 100 mg·L^{-1}) virtually eliminated leaf chlorosis and abscission problems. We are continuing further experiments to investigate appropriate concentrations and timing of hormone sprays. Additional research is underway in our laboratory to investigate the physiological basis of the preventive effects of light and GA_{4+7} on leaf chlorosis in 'Stargazer' hybrid lilies.

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Table 4. Effects[z] of Promalin (GA_{4+7} and BA) sprays and supplemental light during cold storage of Oriental hybrid lily 'Stargazer' plants on flower opening and longevity during the subsequent poststorage evaluation phase. Hybrid lilies at puffy bud stage were sprayed with Promalin (100 mg·L^{-1}) or water, and stored for 2 weeks at 4 °C in dark or with supplemental light (40 μmol·m^{-2}·s^{-1}). Plants were then held at 22 °C for postharvest evaluation.

Light treatment	Promalin spray	Days to last open flower bud	Flower longevity (days)	Total inflorescence longevity (days)	Buds aborted (%)
Dark	Water	9.0 ± 0.5	6.0 ± 0.3	14.3 ± 0.7	20 ± 2
	Promalin	14.5 ± 1.3	7.7 ± 0.2	22.2 ± 1.2	2 ± 2
Light	Water	12.0 ± 1.0	7.1 ± 0.2	18.7 ± 0.9	3 ± 3
	Promalin	14.0 ± 1.0	8.1 ± 0.2	21.5 ± 0.6	0 ± 0
F tests					
Light (L)		NS	**	NS	**
Promalin (P)		**	***	**	**
L × P		NS	*	*	*

[z]Mean ± SE of six replications.
NS,*,**,***Nonsignificant or significant at $P = 0.05$, 0.01, or 0.001, respectively.

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