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Respiratory Changes Associated with Growth-regulator-delayed Leaf Yellowing in Easter Lily

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Abstract. Senescence of excised Easter lily leaves is typically marked by a rise in respiration without a concomitant production of ethylene. Treating excised leaves with 500 mg·L^{-1} of gibberellic acid (GA_3) or benzyladenine (BA) significantly delayed the onset of leaf yellowing, lowered the respiration rates by one-third to one-half, and markedly delayed the respiratory rise. Similar effects on respiration were detected in leaves treated with BA or GA_3 before a 4-week period of cold storage and in leaves treated after chlorosis had initiated. Results of this study indicate that excised Easter lily leaves respond to the growth regulators with a significant decrease in respiration rate.

Foliar chlorosis is one of the factors causing the loss of postproduction longevity of potted Easter lilies (Staby and Erwin, 1977). Leaf yellowing symptoms are worse when plants have been treated with growth retardants (Jiao et al., 1986) or have been cold stored before marketing (Prince et al., 1987, Staby and Erwin, 1977). Treatments that delay the onset of chlorosis would significantly enhance the value of the plants.

Delayed leaf senescence with exogenous application of cytokinins or gibberellins has been reported in various plant species. Plant species in which GA_3 delays senescence include nasturtium (*Tropaeolum majus* L.) (Beevers, 1966) and lettuce (*Lactuca sativa* L.) (Aharoni and Richmond, 1978). Those that respond to BA include broccoli (*Brassica oleracea* L.) (Rushing, 1990), cocklebur (*Xanthium pennsylvanicum* L.) (Leshem, 1986), oat (*Avena sativa* L.) (Tetley and Thimann, 1974), and potted rose (*Rosa ×hybrida* L.) (Clark et al., 1991). Others such as Easter lilies (*Lilium longiflorum* Thunb.) respond to BA and GA_3 (Han, 1995).

Low levels of carbohydrates have been related to leaf senescence of Easter lilies (Jiao et al., 1986). Paclobutrazol and ancymidol, used to reduce plant height, decrease the concentration of total soluble sugars in all leaves and increase the rate of senescence of the lower leaves. Low carbohydrate levels have also been associated with the yellowing of leaves on plants grown under negative DIF (difference between day and night temperatures) (Miller et al., 1993). Changes in respiration rate and pattern have been reported in leaves treated with BA. Respiratory rise of oat leaves was repressed (Tetley and Thimann, 1974) and the respiration rates of broccoli were reduced to 50% of the untreated controls (Rushing, 1990) when treated with BA.

The objectives of this work were to determine the changes in foliar chlorosis, respiration rates, and ethylene production during leaf senescence of excised Easter lily leaves treated or not treated with BA or GA_3. In addition, leaves that had been cold stored and leaves with visible signs of yellowing were treated with BA or GA_3 to determine the effectiveness of these growth regulators in delaying leaf yellowing.

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Materials and Methods

General procedures. Precooled 'Nellie White' Easter lily bulbs were planted in 1.4-L (15-cm-diameter) pots containing a peat-based mix (Pro-Mix BX; Premier Brands Inc., Stamford, Conn.). The lilies were grown in a glasshouse at the Univ. of Massachusetts, Amherst (lat. 42°22.5'N), at 21/19 °C (day/night) under natural daylength using standard cultural practices. Air temperatures were recorded by a datalogger (LI-1000; LI-COR, Lincoln, Neb.) equipped with a thermistor (LI-1000-16).

To minimize variation associated with location of leaves on the stem, leaves were excised from the center section of the plant at the puffy bud stage. Leaves were then dipped in growth regulator solutions or in deionized water for the control. All treatments contained 0.1% surfactant Tween 20, [polyoxyethylene (20) sorbiton monolaurate]. BA and GA_3 were purchased from Sigma Chemical Co. (St. Louis) and solubilized in alkaline solutions before dilution with deionized water to the predetermined concentrations. Following the treatments, leaves were allowed to dry in a darkened room and then placed individually in 20-mL vials containing 5 mL of water. Water levels were refilled every other day and the vials were replaced every week to deter decay. Unless otherwise stated, leaves were maintained in a 20 °C, dark growth chamber (model 818; Precision Scientific, Chicago) for the extent of each experiment, as described previously (Han, 1995). There were five leaves per treatment.

Senescence of untreated leaves (expt. 1). Change in leaf color and respiration, ethylene production, and longevity of each leaf was monitored on untreated leaves. Leaf color, by measuring L*,a*,b* values with a tristimulus colorimeter (model XL–23; Gardner, Bethesda, Md.), was determined every other day until 50% of the leaf area was yellow. Following each measurement, the three replicate leaves were discarded. This method was chosen because a preliminary study, using the same set of leaves for the duration of the experiment, revealed that exposing leaves to the brief flash of light from the colorimeter markedly delayed foliar chlorosis. The hue value –(a/b) of each leaf was calculated.

Respiration rates of 10 replicate leaves were measured by placing each leaf into a 470-mL foil-covered jar in a 20 °C growth chamber for 2 h. Two 1-mL gas samples were removed from each jar and injected into a gas chromatograph equipped with a methanizer and a flame ionization detector (GC–9A; Shimadzu, Kyoto, Japan). Data were expressed on a fresh weight basis as CO_2 evolved (in mg·kg^{-1}·h^{-1}).

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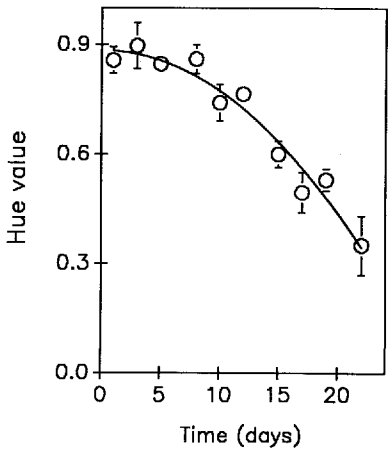

Fig. 1. Changes in hue value of excised Easter lily leaves. Leaves were kept in deionized water in a 20 °C dark growth chamber. The means ± standard errors of three replicate leaves are reported.

Ethylene production was monitored from the commencement of the experiment until necrosis. Ten leaves were placed individually in 470-mL foil-covered jars in a 20 °C dark growth chamber for 4 h. Two 1-mL gas samples were then removed from each jar and injected into a gas chromatograph fitted with a flame ionization detector. Data were expressed on a fresh weight basis as C_2H_4 produced (in $nL \cdot g^{-1} \cdot h^{-1}$).

Possible ethylene involvement in senescence was further determined by pulsing leaves with silver thiosulfate (STS), an inhibitor of ethylene action, or with aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis. The treatments included 0.5, 1, or 2 mM of STS, or 100 $mg \cdot L^{-1}$ of AVG for 4, 8, or 16 h and a water control. There were five replicate leaves per treatment. The development of foliar chlorosis was monitored every other day until the leaf area was ≥50% yellow. Leaf longevity was defined as the period over which yellowing of 50% of the leaf area occurred.

Growth regulators (expt. 2). Excised leaves were treated with deionized water, 500 $mg \cdot L^{-1}$ of BA, 500 $mg \cdot L^{-1}$ of GA_3, or 500 $mg \cdot L^{-1}$ each of BA and GA_3 (BA+GA_3). Leaf color, leaf longevity, and respiration rate were determined using the methods previously described in Expt. 1.

Cold storage (expt. 3). Excised leaves were treated with 500 $mg \cdot L^{-1}$ of BA or 500 $mg \cdot L^{-1}$ of GA_3 before storage in a 2 ± 0.7 °C cold room for 4 weeks. Control leaves were treated with deionized water. Leaf longevity and respiration rates were determined using the methods described in Expt. 1.

Delayed applications (Expt. 4). Excised leaves in vials containing water were placed in a 20 °C dark growth chamber. On the seventh or tenth day, leaves were treated with 500 $mg \cdot L^{-1}$ of BA or GA_3, allowed to air dry, and were then moved back to the growth chamber. The two dates were chosen because, on the seventh day, the respiration rate was low and leaf chlorosis was first apparent and, on the tenth day, the respiration rate had begun to increase and foliar chlorosis had increased to about 5% of the leaf area. Control leaves were treated with deionized water upon removal from the plant. Leaf longevity and respiration rate were determined.

Statistical analysis. A completely randomized design was used in all experiments. Data were analyzed with SAS's General Linear Model procedure (SAS Institute, Cary, N.C.). Differences among treatments were further analyzed with either Dunnett's *t* test, Duncan's multiple range test, or paired comparisons.

Results and Discussion

Experiment 1. An inverse relationship between the increase of yellowing and the decrease in the hue value was established during senescence of Easter lily leaves (Fig. 1). The calculated hue value of the dark green leaves was 0.9. As the leaves became increasingly yellow, the hue value continued to decrease until, at day 19, the leaves were 50% yellow and the corresponding hue value was about 0.45. A correlative relationship between hue value and pigment content was reported in *Beta vulgaris* (Swiss chard) leaves (Ihl et al., 1994).

The respiration rate of a typical, untreated, excised leaf, measured as CO_2 evolved, was 140 $mg \cdot kg^{-1} \cdot h^{-1}$ 24 h after the leaves were removed from the plant (Fig. 2). The respiration rate decreased thereafter. After 10 d, the respiration rate increased into a typical rise. The leaf area was 50% yellow at the peak of the rise 20 d after removal from the plant. The respiration rate then decreased as the leaf became necrotic. A similar pattern of respiration was associated with senescence of oat leaves in the dark (Tetley and Thimann, 1974).

A rise in respiration is often associated with ethylene production (Saks and van Staden, 1992). Ethylene was not detected at any time from the day following excision until the end of the experiment at 23 d (Fig. 2). The possibility that ethylene was produced, but in undetectable levels, was further tested by treating leaves with STS or AVG. Longevity of leaves treated with different concentrations of STS for varying lengths of time was not greater than those of the nontreated leaves (Table 1). Longevity of leaves pulsed with 100 $mg \cdot L^{-1}$ AVG for varying lengths of time was also comparable to those not treated. However, increasing exposure time of 2 mM STS from 4 to 8 h appeared to have a phytotoxic effect, resulting in decreased leaf longevity. Data from studies on ethylene production and inhibitors of ethylene suggested that ethylene was not associated with the yellowing of excised Easter lily leaves and concurred with the results of whole-plant studies reported by Prince et al. (1987).

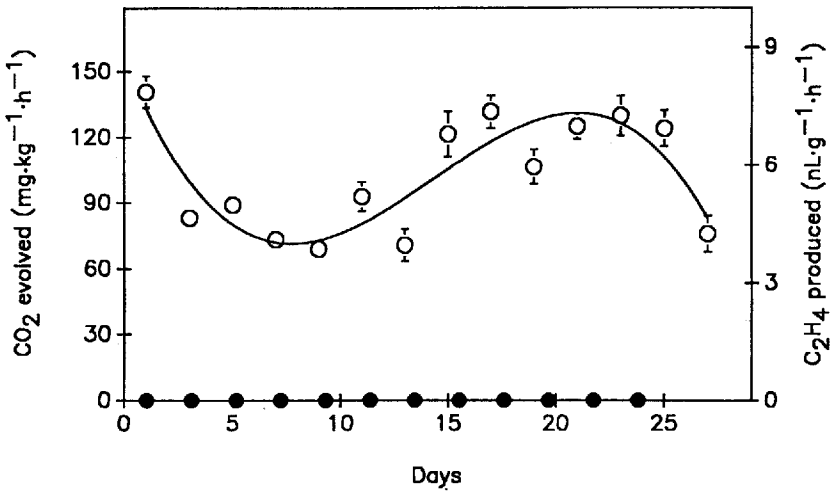

Fig. 2. Respiration rate (○) and ethylene evolution (●) of excised Easter lily leaves kept in deionized water in a 20 °C dark growth chamber. The experiment was terminated when the leaves were fully chlorotic and/or necrotic. The means ± standard errors of 10 replicate leaves are reported.

Experiment 2. Changes in the hue values, longevity, and respiration rates were studied on leaves treated with growth regulators. The hue values of the leaves were highest at day 1 when the leaves were removed from the plants (Fig. 3, top). By day 10, the hue value of the nontreated, yellowing leaves was significantly lower than those of the treated leaves, which remained green (Fig. 3, middle). At day 19, when about 50% of the area of nontreated leaves was yellow, the hue value was again significantly lower than those of the treated leaves (Fig. 3,

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Table 1. Longevities of excised Easter lily leaves treated with silver thiosulfate (STS) or aminoethoxyvinylglycine (AVG) were determined as the time until the leaf area was 50% yellow. Leaves were pulsed with the treatments and then kept in deionized water in a 20 °C, dark growth chamber. The means ± standard errors of five replicate leaves are reported.

Treatment	Length of treatment (h)	Concn	Longevity[z] (d)
Control			16.0 ± 0
STS	4	0.5 mM	15.0 ± 0.9
		1.0 mM	15.0 ± 0.9
		2.0 mM	15.0 ± 0.9
	8	0.5 mM	15.0 ± 0.9
		1.0 mM	14.0 ± 1.1
		2.0 mM	12.0 ± 0.9*
	16	0.5 mM	15.0 ± 0.9
		1.0 mM	13.0 ± 1.1
		2.0 mM	11.0 ± 0*
AVG	4	100 mg·mL^{-1}	16.0 ± 0
	8	100 mg·mL^{-1}	15.0 ± 0.9
	16	100 mg·mL^{-1}	15.0 ± 0.9

[z]Differences in longevity between the untreated and the treated leaves were determined with Dunnett's t test, $P = 0.05$.

bottom). Furthermore, leaves treated with GA_3 were beginning to develop chlorosis and demonstrated a lower hue value than those treated with BA or BA+GA_3. Tristimulus measurements of alstroemeria leaves treated with BA and/or GA_3 have also shown that these treatments reduce rate of chlorophyll loss (Hicklenton, 1991). The longevity of the leaves treated with BA, GA_3, or BA+GA_3 was significantly longer than those not treated (data not shown), as previously reported by Han (1995).

The respiration rate of leaves was highest at the day of excision and began to decrease 2 d later (Fig. 4). The respiration rate of the nontreated leaves leveled at day 5, while those of the treated leaves continued to decrease until day 12 before leveling off. In addition, the rise of the nontreated leaves began at day 7 and reached its peak when the leaves were 50% yellow at day 16, whereas those of the BA- or GA_3-treated leaves remained low for >30 d and exhibited a peak at about 37 d. The peak of the BA+GA_3-treated leaves was further delayed until about day 49.

Experiment 3. Cold storage of Easter lilies often results in rapid development of postproduction foliar chlorosis (Han, 1995; Prince et al., 1987). The respiration rates of the treated and untreated leaves remained at comparable levels while in the cold room (Fig. 5). Upon removal from cold storage, however, leaves treated with growth regulators had significantly lower respiration rates than the untreated leaves and exhibited a delayed rise. The respiration rates of leaves were not significantly different among those treated with growth regulators. Similarly, when broccoli was stored at 16 °C for 6 d, chlorosis was delayed and respiration was reduced after treatment with BA (Rushing, 1990).

Experiment 4. In a subsequent experiment, leaves were treated, following visual detection of leaf yellowing, to determine if BA or GA_3 could prevent further development of yellowing. Treatment of leaves on the seventh day (when yellowing was first apparent on some of the leaves and the respiration rate was still low) and on the tenth day (when leaf yellowing was more advanced and the respiratory rise had commenced) significantly extended longevity and lowered the respiration rate (Figs. 6 and 7). Leaf longevity increased from 16 d for the nontreated leaves to about 35 d with treatment (Fig. 6).

Respiration rates of all leaves were highest following their removal from the plants and then dropped over the first week before beginning to rise again (Fig. 7). The respiration rates of the nontreated leaves began to increase at day 7 and continued to increase until 50% of the leaf area was yellow. In comparison, the rise in respiration rate was delayed significantly in those treated with BA or GA_3 on the seventh or tenth day and the respiration rates

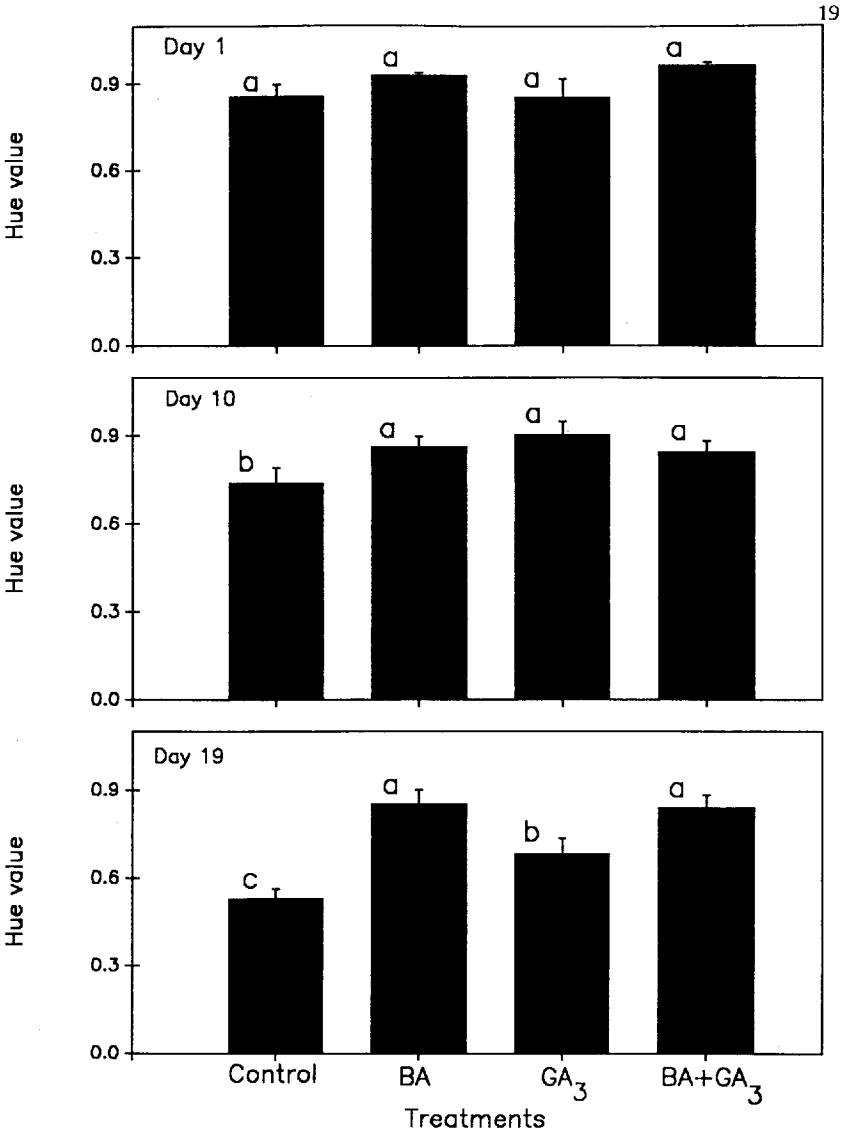

Fig. 3. Hue values of excised Easter lily leaves treated with deionized water, 500 mg·L^{-1} BA, 500 mg·L^{-1} GA_3, or 500 mg·L^{-1} each of BA and GA_3 were measured at three time intervals on day 1 (**top**), day 10 (**center**), and day 19 (**bottom**). Excised leaves were kept in deionized water in a 20 °C dark growth chamber. The means ± standard errors of three replicate leaves are reported. Letters indicate significance among treatments determined with Duncan's multiple range test at $P = 0.05$.

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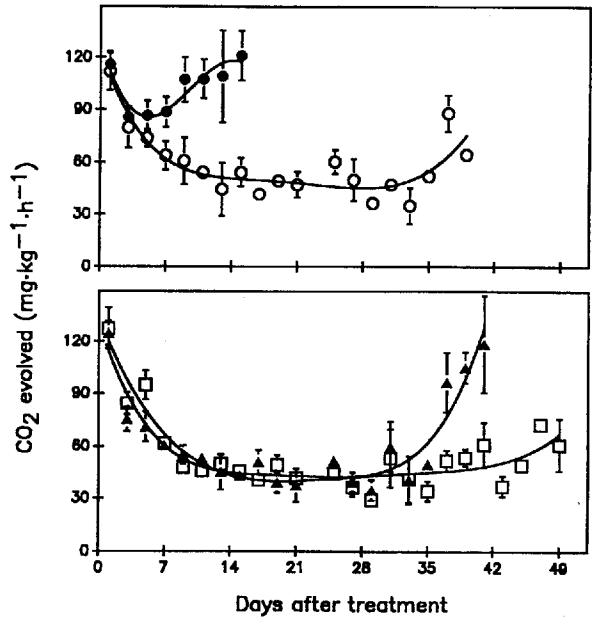

Fig. 4. Changes in respiration rates of excised Easter lily leaves treated with deionized water (●), 500 mg·L^{-1} GA_3 (○), 500 mg·L^{-1} BA (▲), or 500 mg·L^{-1} each of BA and GA_3 (❑). Leaves were kept in deionized water in a 20 °C dark growth chamber. Data were collected until leaf area became 50% yellow. The means ± standard errors of five replicate leaves are reported.

were maintained. There was no difference in respiratory rates between those treated on the seventh or tenth day.

Delaying treatment of Easter lily leaves until visual detection of leaf yellowing did not lessen the effectiveness of the growth regulators. In cocklebur, treatment of yellowing leaves with cytokinin appeared to have a regreening effect (Leshem, 1986). The effect was attributed to the reorganization of the disassembled grana with cytokinin treatment observed in transmission electron micrographs.

Results of the present study indicate that GA_3 and BA delay foliar chlorosis of excised Easter lily leaves that have or have not been cold stored. Furthermore, these growth regulators are effective when applied after visual detection of yellowing. Physiologically, GA_3 and BA lower the respiration rate and delay the rise of respiration.

Declining endogenous levels of cytokinins and gibberellins have been associated with foliar senescence (Nooden et al., 1990; Smart et al., 1991; van Doorn and van Lieburg, 1993), and exogenous application of these growth regulators delay leaf senescence in various plant species (Beevers, 1966; Hicklenton, 1991; Maclean and Dedolph, 1962; Nooden, 1986). Although the responses of Easter lily leaves to treatment with GA_3 or BA are similar, the actions of the two growth regulators on delaying leaf senescence may not be the same. The yellowing pattern of BA-treated leaves is different from that of GA_3-treated leaves. Yellowing of BA-treated leaves initiates at the margins, whereas the pattern of yellowing in GA_3-treated leaves occurs uniformly across the leaf. In addition, the synergistic effects of GA_3 and BA in delaying foliar chlorosis of Easter lily (Han, 1995) and soybean (Nooden, 1986) indicates that the actions of the two growth regulators in delaying leaf yellowing may be different. Treatment with solutions of 1 or 5 mM of chloramphenicol or streptomycin, inhibitors of chloroplast protein synthesis, did not delay chlorophyll loss in Easter lily leaves (data not shown) or rice leaves (Okada et al., 1992), while treatment with cycloheximide, an inhibitor of cytoplasmic protein synthesis, and kinetin prevented the synthesis of two proteases in oat leaves and significantly delayed chlorophyll loss (Martin and Thimann, 1972). The effects of cytokinin on leaf yellowing may therefore be via its effect on the protein synthesis in the cytoplasm.

The actions of GA_3 are less clear. In the presence of light, GA_3 increased the activity of sucrose phosphate synthase in *Glycine max* L. (Cheikh and Brenner, 1992), increased phloem loading of sucrose in *Vicia faba* L. (Aloni et al., 1986), and delayed the decrease in photosynthetic rate in leaves of cut alstromeria stems (Jordi et al., 1994). None of the theories applies to this study since the Easter lily leaves were maintained in a dark environment. The marked inhibition of respiration rate in the GA_3-treated leaves of Easter lily, on the other hand, suggests that GA_3 may affect leaf senescence via its effect on the preservation of the carbohydrate levels in the leaves. Other studies suggest that lower levels of endogenous GA_3 in presenescent leaves may facilitate the onset of leaf senescence and that application of exogenous GA_3 may simply compensate for the low levels of endogenous GA_3 and, thus, delay senescence (Aharoni and Richmond, 1978; Mattoo and Aharoni, 1988).

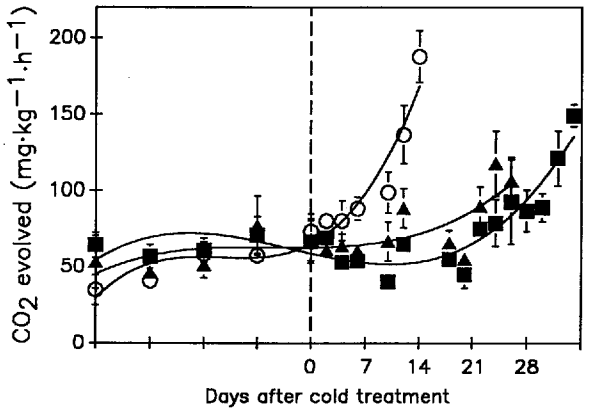

Fig. 5. Changes in respiration rates of excised Easter lily leaves during and after four weeks of storage in a 2 ± 0.7 °C cold room and treatment with deionized water (○), 500 mg·L^{-1} of BA (■) or GA_3 (▲) before cold storage. Leaves were kept in deionized water in a 20 °C dark growth chamber following the cold storage. Data were taken until the leaf area became 50% yellow. The means ± standard errors of five replicate leaves are reported. Dotted line indicates the day when leaves were removed from the cold storage.

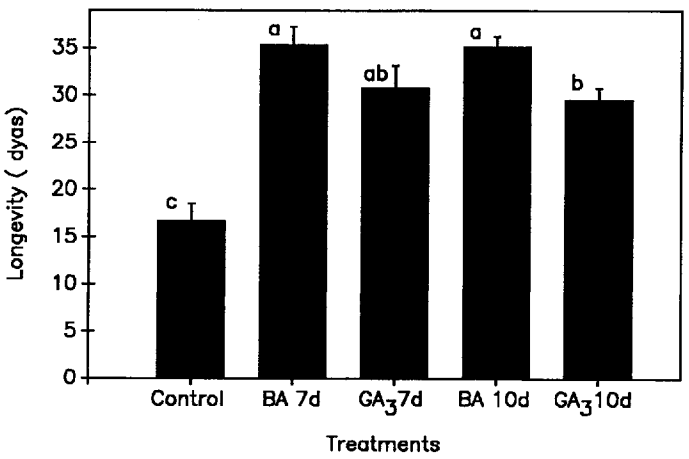

Fig. 6. Longevities of excised Easter lily leaves following treatments with deionized water, 500 mg·L^{-1} of BA or GA_3 at day 7 or at day 10. Leaves were kept in deionized water in a 20 °C dark growth chamber. The means ± standard errors of five replicate leaves are reported. Letters indicate significance among treatments determined with Duncan's multiple range test at $P = 0.05$.

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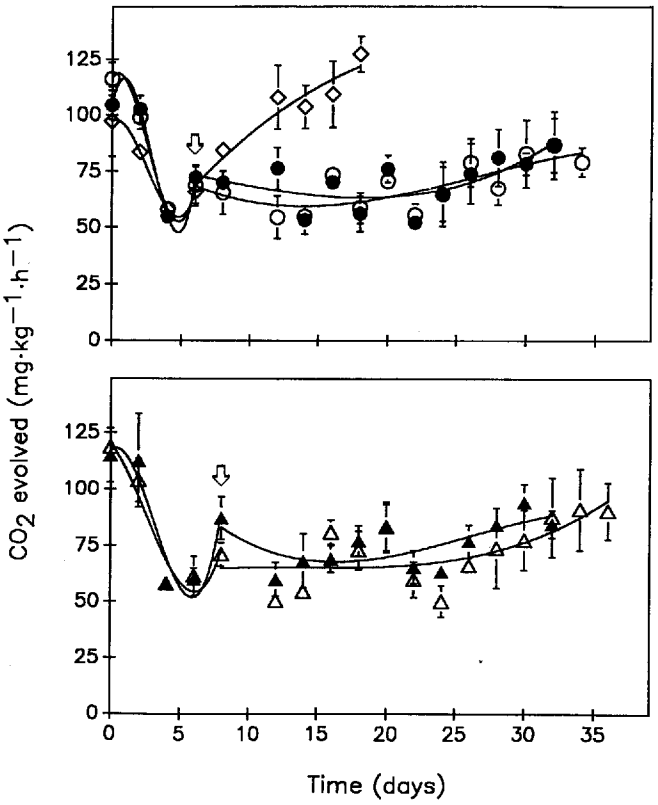

Fig. 7. Changes in respiration rates of excised Easter lily leaves treated with deionized water (◊), 500 mg·L^{-1} of BA (○) or GA_3 (●) on the seventh day or BA (Δ) or GA_3 (▲) on the tenth day. Leaves were kept in deionized water in a 20 °C dark growth chamber. The means ± standard errors of five replicate leaves are reported. Arrows indicate when leaves were treated with the growth regulators.

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