Response of Oriental Hybrid Lily (*Lilium oriental* cv. Sorbonne) Flowers to Exogenous Fluridone and Absciscic Acid Application and Responses of Endogenous Absciscic Acid and Gibberellic Acid 3

Liu Yang

Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 320 West Donggang Road Lanzhou, Gansu, 730000, China; and the University of Chinese Academy of Sciences, No.19A Yuquan Road, Beijing 100049, China

Zhongkui Xie¹

Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 320 West Donggang Road Lanzhou, Gansu, 730000, China

Zhijiang Wu

Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 320 West Donggang Road Lanzhou, Gansu, 730000, China; and the University of Chinese Academy of Sciences, No.19A Yuquan Road, Beijing 100049, China

Yajun Wang, Zhihong Guo, Yubao Zhang, and Ruoyu Wang

Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 320 West Donggang Road Lanzhou, Gansu, 730000, China

Additional index words. oriental hybrid lily, fluridone, ABA, GA₃, height, flower number, flower diameter

Abstract. The oriental hybrid lily (*Lilium oriental* cv. Sorbonne) is an economically important flower noted for its pink petals. Flower quality is determined by plant height, number of flowers per plant, and flower diameter. The commercial value can be increased by improving flower quality through cultural practices such as exogenous application of hormones; however, information on this practice is unavailable for this lily hybrid. In the present study, we soaked lily bulbs for 24 hours in one of four concentrations of absciscic acid (ABA) or one of three concentrations of the ABA biosynthesis inhibitor fluridone before subjecting the bulbs to a cold storage treatment at 4 °C. During cold storage, bulbs were sampled and buds were collected every 10 days for 80 days (that is, lasting eight times). The ABA and gibberellic acid 3 (GA₃) contents of buds of treatments that showed a significant difference with the control were measured in a 10-day interval. Greenhouse experiments with different cold storage durations of bulbs that measured height, flower number per plant, and flower diameter were conducted. The interaction of hormone treatments and cold storage duration played nonsignificant roles in parameters of flower quality. Exogenous fluridone application to bulbs at 12 mg·L⁻¹ improved flower quality: height and flower number increased significantly compared with the control, but flower diameter did not change. ABA had no effect on flower quality. Because the fluctuation of endogenous GA₃ is more remarkable than ABA after the application of fluridone that led to the improvement of flower quality, it can be inferred that this influence on flower quality is achieved through fluridone's regulation on the content of endogenous GA₃. A low endogenous GA₃/ABA ratio was associated with improved flower quality: 12 mg·L⁻¹ fluridone decreased the GA₃/ABA ratio in most times of the cold treatment. In addition, cold storage duration affected flower quality; the 50-day cold storage can achieve the highest height, the most flower number, and bigger flower diameter simultaneously. The results of the present study suggest that soaking bulbs in 12 mg·L⁻¹ fluridone before cold treatment followed by 50 days of cold storage before planting will increase plant height and flower number per plant.

The oriental hybrid lily (*Lilium* spp.) is one of the most popular ornamental plants worldwide. The Sorbonne cultivar is an economically important flower noted for its fragrance and pink petals. It has auspicious implications in Chinese culture and is favored by Chinese customers; as a result, it is one of the three most popular lily cultivars in China (Yamagishi and Akagi, 2013). The flower quality is mainly related to plant height, flower number per plant, and flower diameter (Lindsay et al., 1998; Savvas et al., 2002; Sohn et al., 2003). Improved flower quality is important in commercial production to improve market competitiveness and grower revenues.

Regulation of plant growth and development by hormone application is an effective way to improve flower quality, but little knowledge is available on how to achieve this for the hybrid lily. Previous research suggests that ABA application inhibits plant height growth or stem elongation in Imperial Japanese Morning Glory at 25 and 50 mg·L⁻¹ (Pharbitis nil; Nakayama and Hashimoto, 1973), apple with 5 mL ABA at 50 μM (*Malus hupehensis* and *M. sieversii*; Ma et al., 2008), and pepper at 250 mg·L⁻¹ by drench with different frequency and timing (*Capsicum annuum* 'Aristotle'; Biai et al., 2011). Exogenous ABA reduced (0.1 mg·L⁻¹) or completely inhibited (1.0 mg·L⁻¹) in vitro formation of leaves generated from the scales of oriental hybrid lily (*Lilium* cv. Siberia; Zhao et al., 2010). However, in some species, ABA plays a positive role; it increases shoot length in yerba mate (*Ilex paraguariensis*; Sansbero et al., 2004) and flower formation in Blue Torenia (*Torenia fournieri*; Tanimoto and Harada, 1981) and sacred Tulsi (*Ocimum sanctum*; Nair et al., 2009). In addition, ABA increases floral bud initiation, the number of inflorescences, and the number of flowers per inflorescence. High endogenous ABA levels increase the percentage of leafless inflorescences and the number of flower buds per node in Satsuma mandarin (*Citrus unshiu* 'Okitsu'; Koshita et al., 1999) and apple (*M. domestica* cv. Redchief; Cao et al., 2000). On the other hand, flower bud formation in explants of tobacco (*Nicotiana tabacum* 'Samsun') was inhibited by ABA application at 10, 100, and 1000 μM (Barendse et al., 1985).

Fluridone {1-methyl-3-phenyl-5-[3(trifluoromethyl)-phenyl]4-[1H]pyridone} inhibits the production of phytoene desaturase, and therefore blocks the carotenoid biosynthesis pathway and indirectly inhibits the biosynthesis of ABA in plants (Arias et al., 2005; Chae et al., 2004; Harvey et al., 1994; Hoffmann-Benning and Kende, 1992; Kusumoto et al., 2006). Therefore, fluridone influences many physiological processes through its effect on the ABA level. For example, fluridone application at 25 or 125 μM for 24 h decreased the number of buds of a hybrid between Japanese bunching onion and shallot (*Allium wakegi* cv. Kiharabansei No.1; Yamazaki et al., 1999), decreased mesocotyl length of rice (*Oryza sativa* cv. JC 91) at 10 μM (Watanabe et al., 2001), and

decreased the growth rate of broadbean (*Vicia faba*) at 10 μM (Popova, 1995). However, fluridone (10 μM or 100 μM) plus sucrose increased the shoot numbers and greatly increased the total fresh weight of potato (*Solanum tuberosum* 'Arran Banner') under in vitro culture (Harvey et al., 1994). Application of fluridone to flowers of cocoa (*Theobroma cacao* 'Amelonado') at 172 $\text{mg}\cdot\text{L}^{-1}$ (Aneja et al., 1999) and Chinese Hibiscus (*Hibiscus rosa-sinensis* 'La France') at 10 μM (Trivellini et al., 2011) prevented senescence and extended longevity. However, information is not available on the effect of fluridone application on the quality of lily flowers.

Although individual hormones affect plant physiology, the interactions among hormones also play important roles, and in some cases, the interaction may be more important than the individual hormones. Therefore, the balance of hormones is a critical factor in physiological regulation by plants (Ross and O'Neill, 2001; Zentella et al., 2002). The interaction between gibberellins (GAs) and ABA determines the growth rate of deep-water internodes in rice (*Oryza sativa* cv. M-9; Hoffmann-Benning and Kende, 1992) and the developmental transition from dormancy to germination in barley (*Hordeum vulgare* cv. Himalaya; Zentella et al., 2002). An appropriate GA/ABA ratio is needed for germination and maturation of maize (*Zea mays*; White et al., 2000). A low ratio of GA/ABA is required under short-day conditions to promote tuber formation in potato (*S. tuberosum*), whereas a high ratio is required for night-break (1 h white light in the middle of the dark period) and long-day conditions to promote flowering (Macháková et al., 1998).

In the present study, our objective was to determine the effects of exogenous hormone ABA or its biosynthesis inhibitor fluridone application of cold storage before planting on flower quality and the response of endogenous hormones (ABA, GA₃) to exogenous hormone application and measured endogenous GA₃/ABA ratio to investigate how it was influenced by ABA and fluridone applications. By understanding the optimal concentrations of ABA and fluridone, the response of endogenous hormones to exogenous ABA and fluridone and the optimal cold-storage duration, it will provide a basis for the use of exogenous ABA

and fluridone, thus making it possible to improve flower quality in lily production.

Materials and Methods

Plant material. We selected bulbs of the oriental hybrid lily (cv. Sorbonne) that had been propagated in Longde (Ningxia Autonomous Region, China) for the study. On 25 Oct. 2012, bulbs (14 to 16 cm in diameter) were treated with 1 $\text{g}\cdot\text{L}^{-1}$ imazalil (a fungicide) for 30 min and were then treated with various concentrations of one of two hormones with the concentrations chosen based on the results of preliminary tests (data not shown): ABA at 0.1, 1.0, 10, or 100 $\text{mg}\cdot\text{L}^{-1}$ or fluridone at 0.01, 0.1, or 12 $\text{mg}\cdot\text{L}^{-1}$. Water was used as the control. The bulbs were immersed in the hormone solutions and kept there for 24 h, after which the bulbs were stored at 4 °C (± 0.5 °C) in pored polythene bags that were padded with peat at a water content of 75% (w/w); the relative indoor humidity was maintained at 75%. Sampling of bulbs of all treatments began on the 10th day after the cold treatment and occurred every 10 d thereafter for 80 d. Our preliminary tests revealed that the highest hormone contents occurred in the buds of the bulbs, so we collected the buds for chemical analysis. After collection, the buds were frozen in liquid nitrogen and stored at -80 °C until analysis. The bulbs were maintained in cold storage conditions up to the day of planting in the greenhouse; starting on the 30th day of cold storage, 30 bulbs from each treatment were planted in the greenhouse in a split-plot design lasting five times in a 10-d interval; cold storage duration was the main plot and hormone treatment was the subplot. The plants were exposed to natural light in the greenhouse, the planting medium was peat, and the nutrient and water needs were met by supplying nutrient solution of improved Hoagland (116N-29P-106K-97Ca-51S-22Mg-1B-8Mn-3Zn-18Fe) every 5 d. Plant height (measured with a ruler to a precision of 1 mm) was measured when the first flower opened, but flower number per plant and flower diameter (measured with a ruler to a precision of 1 mm) were recorded at harvest time for all 30 plants in each treatment.

Determination of hormone levels. ABA and GA₃ of treatments that showed a significant difference with the control in flower quality in the greenhouse experiments were extracted and measured according to the methods of An et al. (2010) and Xu et al. (2006) with the following modifications: 2 g of frozen buds were homogenized with a mortar and pestle in 10 mL of 80% (v/v) methanol with 50 μL of 30 $\text{mg}\cdot\text{mL}^{-1}$ sodium diethyldithiocarbamate (an antioxidant) and 0.1 g polyvinylpyrrolidone (to absorb pigments). The mortars, pestles, and reagents were precooled to 4 °C; all operations were conducted on ice and the extraction process was conducted in the dark. The extraction solution was subjected to ultrasonication (KQ-300E; Kunshan, Jiangsu Province, China) for 30 min and then stored at 4 °C overnight. After

centrifugation at 48,000 g at 4 °C for 15 min, the supernatant was removed and stored, and then 5 mL 80% (v/v) methanol was added to resuspend the precipitate. The solution was held at 4 °C for 4 h and then centrifuged again at the same intensity, and the supernatant was mixed with the previous supernatant. The combined extraction solution was centrifuged again at the same intensity and the precipitate was discarded.

The methanol in the supernatant was evaporated under flowing nitrogen, the remaining aqueous phase was frozen at -80 °C, and the sample was then freeze-dried. The residue was dissolved in 5 mL of ultrapure water, and then C₁₈ Sep-Pak columns (Waters, Milford, MA) were used to collect the hormones. The columns were pretreated with 10 mL of methanol and 80 mL of ultrapure water, the hormones were extracted from the samples by the columns, then the columns were eluted with 6 mL of 60% (v/v) methanol to extract the hormones. The eluate was passed through a 0.45- μm filter membrane (Merck Millipore, Billerica, MA) as the last step of the extraction procedure.

Determination of hormone levels. The analysis was performed with an Agilent 1200 high-performance liquid chromatograph (Agilent, Santa Clara, CA). The analytical procedure was as follows: we used an Eclipse XDB-C18 reverse-phase column (Agilent; 4.6 $\times$ 150 mm, 5 μm) at 20 °C. The mobile phase was a mixture of methanol (A), acetonitrile (B), and 0.05% (v/v) acetic acid (C) in a gradient elution (An et al., 2010) as follows: 0 min, 25% A, 4% B, 71% C; 11 min, 41% A, 9% B, 50% C; 25 min, 80% A, 20% C; and 35 min, 25% A, 4% B, 71% C. The flow rate was 0.6 $\text{mL}\cdot\text{min}^{-1}$. The hormones were detected using the following absorption wavelengths and times: 0 min, 270 nm; 7 min, 200 nm (for GA₃); and 14 min, 270 nm (for ABA). Data were acquired with an Agilent chromatography workstation [Rev. B. 04. 02 (96)]. Endogenous GA₃ and ABA were identified by their retention time in comparison with external standards.

Results

The hormone treatment had significant influences on the height and flower number per plant but not on the flower diameter. Cold-storage duration had significant influences on the height and flower diameter but not on the flower number per plant. The interaction between hormone treatment and cold-storage duration played a nonsignificant role in regulating all three parameters of flower quality (Table 1).

Impact of hormone applications on flower quality. Our results (Table 2) suggest that fluridone increases the quality of the flowers. Fluridone application at 12 $\text{mg}\cdot\text{L}^{-1}$ significantly improved the plant height (by 8.6 cm to 61.1 cm) and number of flowers (by 0.8 per plant to 3.8) compared with the control but had no significant effect on the flower diameter. The percentage increases of plant height and flower number in comparison with

Received for publication 1 Aug. 2014. Accepted for publication 22 Jan. 2015.

We thank the Ningxia Agricultural Comprehensive Development Office (NTKJ2014091), the Natural Science Foundation of China (31370447), and the Hundred Talents Program of the Chinese Academy of Sciences "Molecular mechanism of biological control of plant diseases" program for funding this research. We also thank Liang Zhao (Lanzhou Institute of Chemical Physics, the Chinese Academy of Sciences) for help in the hormone level determination and Randy Kutcher (University of Saskatchewan) for suggestions about an early version of this manuscript.

¹To whom reprint requests should be addressed; e-mail wxhcas@lzb.ac.cn.

Table 1. The variance analysis of hormone treatment, cold-storage duration, and their interaction on height, flower number per plant, and flower diameter across the experiment process.^z

Source	Ht (cm)				Flower number (per plant)				Flower diam (cm)			
	df	Mean square	F	Significance	df	Mean square	F	Significance	df	Mean square	F	Significance
Corrected model	39	38.97	1.57	0.05	39	0.47	2.41	0.00	39	2.38	1.29	0.17
Intercept	1	366,174.91	14,769.49	0.00	1	1,226.88	6,329.57	0.00	1	34,510.21	18,719.94	0.00
Hormone treatment	7	125.10	5.05	0.00	7	1.37	7.06	0.00	7	2.33	1.26	0.28
Cold-storage duration	4	91.81	3.70	0.01	4	0.55	2.85	0.03	4	14.15	7.67	0.00
Hormone treatment*cold-storage duration	28	9.89	0.40	1.00	28	0.23	1.18	0.28	28	0.71	0.39	1.00
Error	80	24.79			80	0.19			80	1.84		
Total	120				120				120			
Corrected total	119				119				119			

^zThe hormone treatment including four concentrations of abscisic acid (ABA) and three concentrations of fluridone (biosynthesis inhibitor of ABA), treatment procedure was soaked the bulbs of lily 'Sorbonne' in hormone solution for 24 h and then stored in 4 °C. Cold storage of bulbs for different times (from 10th day in 10-d interval lasting for five times) and then planted in the greenhouse. $P \leq 0.05$.

the control were 16.4% and 26.7%, respectively. The 0.01 mg·L⁻¹ fluridone treatment significantly improved plant height (by 4.5 cm to 57.0 cm) but had no effect on the other two parameters. The 0.1 mg·L⁻¹ fluridone treatment had no effect on all three parameters of flower quality. None of the four ABA concentrations caused a significant difference in comparison with the control for the three parameters (Table 2). None of the treatments increased flower diameter in comparison with the control.

The cold-storage duration also affected flower quality. The plant height and flower number per plant decreased with increasing cold-storage duration, and the difference became significant after 60 to 70 d of storage (Table 3). In contrast, flower diameter increased with increasing storage duration, and the difference became significant after 50 d (Table 3). In other words, the bulbs stored for 30 d produced the highest plants and the most flowers per plant but with the lowest flower diameter; cold storage for 70 d produced the shortest plants and the fewest flowers per plant but with the highest flower diameter. Fluridone treatment at 12 mg·L⁻¹ has an application prospect in production. For the bulbs treated with 12 mg·L⁻¹ fluridone, the highest plants, the most flowers per plant, and the highest flower diameter were achieved simultaneously at 50 d of cold storage (Table 4).

Hormone analysis. The ABA level in the buds decreased significantly starting from the 40th day of cold storage at 4 °C when the lily bulbs were treated with 12 mg·L⁻¹ of exogenous fluridone (Fig. 1A). When the bulbs were treated with 100 mg·L⁻¹ of exogenous ABA, the level of endogenous ABA in the buds also decreased significantly at 20th days and 50th to 80th days of cold storage (Fig. 1A). These results suggest that the application of both ABA and its biosynthesis fluridone at high concentrations would decrease ABA levels in the buds. Exogenous application of 12 mg·L⁻¹ fluridone or 100-mg L⁻¹ ABA also decreased the level of GA₃ (Fig. 1B). The endogenous GA₃ level was consistently significantly lower than in the control after the application of 12 mg·L⁻¹ fluridone; after exogenous application of 100 mg·L⁻¹ ABA, the level of GA₃ became

Table 2. The impact of the exogenous hormones on the parameters of flower quality across all cold-storage durations.^z

Treatment	Ht (cm)	Flower number (per plant)	Flower diam (cm)
Control	52.5 ± 4.6 c	3.0 ± 0.5 bc	17.3 ± 0.8 ab
0.1 mg·L ⁻¹ ABA	55.4 ± 4.4 bc	3.3 ± 0.4 b	16.8 ± 1.6 ab
1.0 mg·L ⁻¹ ABA	55.8 ± 4.7 bc	3.3 ± 0.5 b	16.5 ± 1.4 b
10 mg·L ⁻¹ ABA	53.8 ± 4.4 bc	3.3 ± 0.4 b	16.8 ± 1.2 ab
100 mg·L ⁻¹ ABA	52.2 ± 4.2 c	2.8 ± 0.3 c	16.8 ± 1.5 ab
0.01 mg·L ⁻¹ fluridone	57.0 ± 5.3 b	3.1 ± 0.4 bc	17.7 ± 1.2 a
0.1 mg·L ⁻¹ fluridone	54.1 ± 3.9 bc	3.1 ± 0.4 bc	16.7 ± 1.4 ab
12 mg·L ⁻¹ fluridone	61.1 ± 6.7 a	3.8 ± 0.7 a	17.2 ± 1.9 ab

^zPlant height, flower number, and flower diameter of *Lilium* cv. Sorbonne after presoaking the bulbs in different concentrations of abscisic acid (ABA) or fluridone (an ABA biosynthesis inhibitor) for 24 h followed by storage at 4 °C lasting for 80 d. Untreated bulbs served as the control. Values of a parameter labeled with different letters differ significantly ($P \leq 0.05$). Data are the means ± SD of 150 bulbs (30 bulbs × 5).

Table 3. The impact of five cold-storage durations on the parameters of flower quality across all hormone treatments.^z

Duration of cold storage (days)	Ht (cm)	Flower number (per plant)	Flower diam (cm)
30	57.8 ± 5.2 a	3.3 ± 0.5 a	15.6 ± 1.3 d
40	56.4 ± 5.0 ab	3.3 ± 0.4 a	16.6 ± 1.2 cd
50	55.2 ± 6.6 abc	3.3 ± 0.7 a	17.0 ± 1.3 bc
60	54.1 ± 4.3 bc	3.1 ± 0.4 ab	17.4 ± 1.2 ab
70	52.7 ± 4.8 c	3.0 ± 0.4 b	18.0 ± 1.2 a

^zPlant height, flower number, and flower diameter of *Lilium* cv. Sorbonne under different cold storage (4 °C) durations after presoaking the bulbs in different concentrations of abscisic acid (ABA) or fluridone (an ABA biosynthesis inhibitor) for 24 h. Values of a parameter followed by different letters differ significantly ($P \leq 0.05$). Data are means ± SD of 240 bulbs (30 bulbs × 8).

Table 4. Simultaneous effects of fluridone treatment at 12 mg·L⁻¹ and cold-storage duration on plant height, flower number per plant, and flower diameter of *Lilium* cv. Sorbonne.^z

Duration of cold storage (day)	Ht (cm)	Flower number (per plant)	Flower diam (cm)
30	62.2 ± 3.2 ab	3.8 ± 0.6 b	16.6 ± 1.3 b
40	61.7 ± 1.6 ab	3.7 ± 0.5 b	16.5 ± 1.1 b
50	64.9 ± 1.4 a	4.7 ± 0.5 a	17.7 ± 1.4 ab
60	59.4 ± 1.3 ab	3.5 ± 0.2 b	16.9 ± 1.2 ab
70	57.2 ± 2.4 b	3.3 ± 0.6 b	18.0 ± 0.9 a

^zValues of a parameter followed by different letters differ significantly ($P \leq 0.05$). Data are means ± SD of 30 bulbs.

significantly lower than in the control at 20th days of cold storage and after 50 d of cold storage (Fig. 1B).

Treatment with 12 mg·L⁻¹ of exogenous fluridone decreased the ratio of GA₃ to ABA below that of the control, and the difference was significant at 20 d to 40 d and after 50 d of cold-storage durations (Fig. 2), whereas the ratio of treatment of 100 mg·L⁻¹ was the

same as the control except the significant difference occurred at the 60 d and 70 d of cold-storage duration (Fig. 2).

Discussion

The effect of exogenous application of hormones on the level of endogenous hormones is complex because there was positive or

Fig. 1. Changes in endogenous levels of (A) abscisic acid (ABA) and (B) gibberellic acid 3 (GA₃) after exogenous treatment of the bulbs of *Lilium* cv. Sorbonne with 12 mg·L⁻¹ of fluridone (FLU) or 100 mg·L⁻¹ of ABA for 24 h and then stored under 4 °C. Bulbs treated with water served as the control. Values labeled with * decrease significantly from the control ($P \leq 0.05$); values without label means that it has no significant difference with the control. Values are the means ($n = 5$ plants per replicate) $\pm$ SD.

negative feedback regulation. The results obtained in Chinese Hibiscus (*Hibiscus rosa-sinensis*) at 100 μM treated for 6 h (Trivellini et al., 2011) and apple (5 mL ABA at 50 μM) (*M. hupehensis* and *M. sieversii*; Ma et al., 2008) indicate that the endogenous ABA level increased when exogenous ABA was applied. However, in the present study, the endogenous ABA level in the buds decreased compared with the control when exogenous 100 mg·L⁻¹

ABA was applied, except at intermediate storage durations (30 and 40 d; Fig. 1A), demonstrating negative feedback in the response of ABA in buds to exogenous ABA.

The exogenous application of 12 mg·L⁻¹ of fluridone decreased the endogenous ABA level (Fig. 1A) because fluridone is an ABA biosynthesis inhibitor, and levels of endogenous ABA are negatively regulated by fluridone (Biddington et al., 1992; Chae et al., 2004;

Kusumoto et al., 2006). Treatment with 12 mg·L⁻¹ of fluridone as well greatly decreased the endogenous GA₃ level. In previous research, endogenous GA₃ at high levels decreased flower formation during the flower induction (1.53 $\mu\text{g g}^{-1}$) and initiation (3.88 $\mu\text{g g}^{-1}$) stages in olive (*Olea europaea*; Ulger et al., 2004). In this study we omitted determination of hormones in leaves after 12 mg·L⁻¹ of fluridone application, but in satsuma mandarin (*C. unshiu*), the leaves with high levels of endogenous GA_{1/3} after water stress led to fewer flowers (Koshita and Takahara, 2004). A lower endogenous GA level increased flower bud formation of apple (*M. domestica*; Cao et al., 2000). In the present study, the decreased GA₃ level observed after treatment with 12 mg·L⁻¹ fluridone (Fig. 1B) released the inhibitory effect of GA₃ on flower bud formation (Koshita et al., 1999) and therefore increased the flower number. We consider that the role of endogenous GA₃ on flower number and height is more important than endogenous ABA, 12 mg·L⁻¹ fluridone treatment promoting flower quality through lowered endogenous GA₃. Because the contents of hormones were variable in different species, the different extraction procedure also affected the final contents, so in this study, we compared the dynamic change trends of hormone, which is more significant than compared with the aspect of content.

The present results suggest clear effects of exogenous hormone application on hormonal regulation of plant growth and flowering. However, exogenous application of one hormone can lead to changes in metabolic processes related to other hormones, thereby affecting the content of those hormones. Thus, the ratio of two hormones is equally important as the level of a single hormone. In pea (*Pisum sativum*; Law and Hamilton, 1984) and tulip (*Tulipa gesneriana*; Xu et al., 2007), GA₃ application (0.45 μM by spray and 0.8 mg·mL⁻¹ by injection, respectively) increased the content of indoleacetic acid (IAA). In addition, IAA can promote the biosynthesis of GA₁ in pea (*P. sativum*; Ross et al., 2000). In lily cv. Sorbonne, treatment of the bulbs with 100 mg·L⁻¹ ABA decreased endogenous GA₃ during the cold-storage process (Fig. 1B), as was the case with the fluridone treatment. These results demonstrate the existence of interactions (crosstalk) between the two hormones.

The GA₃/ABA ratio changed after treatment with 12 mg·L⁻¹ fluridone or 100 mg·L⁻¹ ABA. The GA₃/ABA ratio after treatment with 12 mg·L⁻¹ fluridone was significantly lower than the control in most times of the study period but presented an increasing trend after 50 d of cold storage (Fig. 2). By combining this result with the results of the planting experiment, in which this treatment increased plant height and flower number (Table 2), we conclude that the lower GA₃/ABA ratio played a critical role in the regulation of plant growth and flower bud formation, leading to improved quality of the flowers. Similar results were obtained in

Fig. 2. The ratio of endogenous gibberellic acid 3 (GA₃) to abscisic acid (ABA) after treatment of the bulbs of *Lilium* cv. Sorbonne with 12 mg·L⁻¹ of fluridone (FLU) or 100 mg·L⁻¹ of ABA for 24 h and then stored under 4 °C. Bulbs treated with water served as the control. Values labeled with * decrease significantly from the control ($P \leq 0.05$); values without label means that it has no significant difference with the control. Values are the means ($n = 5$ plants per replicate) $\pm$ SD.

potato (*S. tuberosum*; Macháček et al., 1998), for which the GA/ABA ratio increased during the night-break (1 h white light in the middle of the dark period) and long-day conditions, which were beneficial to flowering. In narrowleaf lupine (*Lupinus angustifolius* cv. Merrit), the declined cytokinin: IAA ratio was closely related to the strong growth of the main stem apex than the levels of either cytokinin or IAA alone (Emery et al., 1998). The low GA₃/ABA ratio observed during the early stages of the cold treatment in the present study (Fig. 2) decreased the metabolic rate but may have had the beneficial effect of increasing energy reserves during cold storage. The increased GA₃/ABA ratio after 50 d of cold treatment (Fig. 2) resulted from the increased level of GA₃ (Fig. 1B), which promoted plant growth. The dynamic changes in the GA₃/ABA ratio from lower levels during the first 50 d of storage to a higher level during the last 30 d of storage appears to be the key factor that regulated plant growth and flower bud formation, thereby directly affecting flower quality. These results suggest that 50 d is the optimal storage duration for increasing plant height and flower number, which is in alignment with the result based on analysis of cold storage duration (Table 4).

In addition to affecting plant growth and flower quality, exogenous hormone application potentially affected the endogenous hormone levels in the buds. Exogenous ABA had no significant effect on the growth and flower quality characteristics compared with the

control. In contrast, fluridone treatment in the present study affected plant growth and flower quality in a concentration-dependent manner; the two lower concentrations (0.01 and 0.1 mg·L⁻¹) had no significant effect on flower quality, whereas 12 mg·L⁻¹ fluridone significantly improved flower quality. Previous research demonstrated that the sensitivity of lily bulblets to exogenous ABA depended on the endogenous ABA level (Djilianov et al., 1994), which suggests that the effect of exogenous hormones will depend on their effects on levels of endogenous hormones. This regulation process also depends on temperature and is therefore influenced by the plant's dormancy status (Djilianov et al., 1994). In production environments, the dormancy status changes in response to temperature variations around harvest time. As a result, the sensitivity of bulbs to exogenous hormone application depends on the plant's environmental conditions and will be variable. The effect of applying the same concentration of hormones during different parts of the growing season will therefore vary and will depend on the plant's species, physiological status, endogenous hormone levels, and dormancy status and each of these characteristics must be determined before it will be possible to predict the plant's response.

Applying hormones to bulbs that have not broken their dormancy is an effective way to regulate the quality of flowers of the lily Sorbonne cultivar. In a production system, bulbs of this species that are soaked in

12 mg·L⁻¹ fluridone solution for 24 h before cold treatment should show increased height and flower number if all other conditions are suitable, thereby improving flower quality. Thus, this treatment should improve commercial flower production, thereby increasing the value of the flowers and revenue of the growers. However, fluridone is an herbicide that is often used to control submerged aquatic vegetation such as watermilfoil (*Myriophyllum spicatum*) and coontail (*Ceratophyllum demersum*) in lakes (Valley et al., 2006). Thus, its use should be carefully controlled to prevent its release into bodies of water, which would produce undesirable environmental impacts as a result of toxicity of fluridone on animals, especially aquatilia, that has been reported in the past (Hamelink et al., 1986; Paul et al., 1994). In the present study, most of the applied hormones would be taken up by the lily bulbs and removed from the peat during cold storage, and the remainder would likely degrade during subsequent plant growth (Netherland and Getsinger, 1995; Weber et al., 1986).

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