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Effects of Low Temperature on Dormancy Release in Lily Bulbs

Hong-Mei Sun[1] • Jaime A. Teixeira da Silva[2] • Yun-Fei Li[1] • Tian-Lai Li[1*]

[1] College of Horticulture, Shenyang Agricultural University, Key Laboratory of Protected Cultivation, LiaoNing Province 110161, Shenyang, China
[2] Faculty of Agriculture, Department of Horticulture, Kagawa University, Ikenobe, Miki cho, Kita gun, Kagawa, 761-0795, Japan

Corresponding author: * ltl@syau.edu.cn

ABSTRACT

The mechanism of dormancy and dormancy release in lily (*Lilium* spp.) bulbs is still incomplete and ambiguous. Based on a summary of dormancy characteristics, we review the effects of low temperature on dormancy release. This paper highlights the metabolic changes in carbohydrates, endogenous hormones, free amino acids and phenols during low temperature storage, and the key stages in dormancy release as well as the effects of different parts of the lily bulb. The possible physiological mechanism of low temperature on dormancy release in lily bulbs and some problems which should be investigated in this field are also discussed in this review.

Keywords: carbohydrates, endogenous hormones, free amino acids, *Lilium*, phenol
Abbreviations: ABA, abscisic acid; **GA_3**, gibberellic acid; **GC/SIM**, gas chromatography-selected ion monitoring; **HPLC/MS**, high-performance liquid chromatography-mass spectrometry; **PAL**, phenylalanine ammonia-lyase; **Phe**, phenylalanine

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INTRODUCTION

For bulb crops, dormancy is an important and complex physiology process (Lang 1987; Dole 2003). Most lily bulbs generally are characterized by spontaneous dormancy and the key technology during commercial production consists in breaking and prolonging dormancy. However, research outcomes on bulb dormancy in *Lilium* are highly deficient up to now, with poor and non-specific definitions about dormancy and dormancy release (Niimi 1985). There are still many problems which should be resolved about practical technology in regulating bulb dormancy (Gude *et al*. 2000), for example, how to judge whether the bulbs are mature or dormancy-released; how to control dormancy or sprouting during cultivation; what kinds of conditions are necessary for normal growth of bulb. Except for low temperature treatment, other technologies have not been industrialized because the mechanism of dormancy has not yet been clarified. The effects that *in vitro* culture conditions on bulblet formation and dormancy, such as inorganic salts (Lim *et al*. 1998), illumination (Haruki *et al*. 1999), temperature and growth regulators (Kim *et al*. 2000; Hidehiro *et al*. 2001), have been reported largely since the 1960s, but studies on the mechanism of metabolism in the bulb, especially commercial bulbs, are still at an elementary stage. This review sums up the results about effects of low temperature on dormancy of lily bulbs and we hope to serve as a reference for research in the mechanism of dormancy.

DORMANCY AND SIGNS OF DORMANCY RELEASE

Because of inadequate work in *Lilium*, the rudimental concepts of growth biology are still ambiguous. The markers of dormancy and dormancy release are always expected by the producers and researchers (Hertogh 1996). Low temperature is necessary for the sprouting of lily bulbs after harvest (Shin *et al*. 2002; Langens-Gerrits *et al*. 2003), but the effects and scope of low temperature change greatly depend on species or varieties, cultural conditions or patterns, even different sizes within the same variety. Usually, dormancy can be released when bulbs are stored at 0-8°C for 60 to 120 d (Gude *et al*. 2000). However, for some Asiatic hybrids such as 'Cordelia', 12°C is a low enough temperature to break dormancy (Sun *et al*. 2003). This complexity results in many disputes about the correct mechanism of dormancy in lily bulbs. For most varieties of lily, the different harvest time will induce diverse effects of low temperature (Erwin *et al*. 1998). If the bulbs are harvested too early, chilling injury will occur during cold storage, whereas late harvesting will result in rotting of bulbs. Actually the optimum harvest stage of lily bulbs has not yet been defined. Usually planters

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decide whether to harvest according to the state of plant withering, but senescence progress in different species are diversified (Gude H *et al*. 2000).

Sun *et al*. (2004a, 2005a) studied the metabolic activities such as changes in carbohydrates and endogenous hormones as well as morphological changes of both plants and bulbs of *Lilium davidii* var. *unicolor*, whose bulbs have a long dormancy and development period; the Asiatic Elite hybrid bulbs, in contrast have a shorter dormancy period and period of development. The results indicate that maturity and dormancy are different physiological phenomena in bulbs. The bulbs harvested at the whole plant withering stage are dormant, but the terminal bud of new bulbs show obvious development (Sun *et al*. 2004a); specifically, the whole plant withering stage is not the beginning of bulb dormancy. Starch content (Sun *et al*. 2004a), endogenous abscisic acid (ABA) level (Sun *et al*. 2006a), and nitrogen, phosphorus, and potassium content (Sun *et al*. 2004b) in the bulb all reached maximum levels half-way through the withering stage, but the fresh and dry weights peaked only following complete withering. Bulbs harvested halfway through the withering stage are more insensitive to low temperature from 2 to 12°C.

From the 1950s, many technologies for breaking dormancy have been reported in succession, but the results are not unanimous. This owes, on one hand, to the complexity of the experimental materials and dormancy itself. On the other hand, it is as a result of the subjective judgment on dormancy release as assessed by each researcher. In most situations, bulbs which can sprout after various treatments are broadly categorized as dormancy release. Moreover, some reports measure the degree of dormancy release in *Lilium speciosum* with the required days from planting to plantlet formation (Aguettaz *et al*. 1990). Sun *et al*. (2004a, 2006b) investigated the sprouting difference among various varieties after low temperature treatment, and plant growth and bulb yield were also studied. The results showed that dormancy release in lily bulbs could be divided into four phases: terminal bud development in bulbs, sprouting, plantlet emergence, and plant formation. The rapid elongation of buds and their normal growth were probably the most suitable markers for dormancy release rather than sprouting or plantlet emergence (Sun *et al*. 2004a).

METABOLIC CHANGES IN BULBS DURING LOW TEMPERATURE STORAGE

Changes in carbohydrates

During low temperature storage, there are the phases in which starch decomposes and soluble sugars accumulate significantly, which is accompanied by the synthesis of related enzymes (Miller *et al*. 1989, 1990a, 1990b, 1993; Shin *et al*. 2002; Sun *et al*. 2004a; Xu *et al*. 2006). It was found that the content of sucrose, mannose, fructose and oligosaccharides in the scales of *Lilium longiflorum* Thunb. 'Nellie White' increased as starch content declined when the bulbs were stored in moist peat for 85 d (Miller *et al*. 1989). Furthermore, the change extent of carbohydrate in bulbs stored at -1°C is bigger than bulbs stored at 4.5°C. Miller *et al*. (1989) considered that glucomannan was another storage carbohydrate in lily bulbs because of the increase in mannose content and also reported the breaking down of glucomannan and starch in the bulbs of *L. longiflorum* Thunb. 'Nellie White' (Miller *et al*. 1990a, 1993). Sucrose is an essential soluble sugar and it serves as the primary transport carbohydrate in lily bulbs (Shin *et al*. 2002; Sun *et al*. 2005a) while the glucose or fructose content is comparatively much lower (**Table 1**). In *Lilium rubellum*, storage at 4-8°C for 14 weeks induced a 1.5-, 1.8- and 1.9-fold increase in sucrose, glucose and fructose concentrations, respectively (Xu *et al*. 2006). Sucrose steadily increased up to 10 weeks of cold storage and decreased afterwards. Glucose and fructose both increased as the chilling continued for 14 weeks. Chen *et al*. (1986) reported that carbohydrate content was related with the sprouting competence of cormels of *Gladiolus* X *gandavensis* 'Van Houtte'. Sun *et al*. (2004a) found that there were extremely significant positive correlations between the sprouting of terminal buds and the total soluble sugar content (r = 0.7382) or the amylase activity (r = 0.7276), but a negative correlation with starch content (r = -0.7024). This result illustrated that carbohydrates in the bulb diverted into an available form depending on the level of sprouting of the bulb. The significant interaction between storage temperature and storage duration affected carbohydrate metabolism and the sprouting of bulbs (Sun *et al*. 2004a). Soaking bulbs in gibberellic acid (GA) cannot to-

Table 1 Changes of sucrose and reducing sugar content in different parts of lily bulb during bulb development (adopted and modified from data in Sun *et al*. 2005a).

Cultivars	Parts of bulb	Variety of sugar	Soluble sugar content (%) during different growth stages							
			Planting	Plantlet	Visible bud	Anthesis	20 d after anthesis	40 d after anthesis	Half withered	Withered
Lilium davidii var. *unicolor*	Exterior scales	Sucrose	8.64	8.47	7.1	9.01	8.34	7.05	10.17	8.66
		Reducing sugar	1.26	1.38	2.49	2.36	1.42	2.37	2.58	2.34
	Middle scales	Sucrose	8.62	8.76	7.04	7.21	8.72	8.85	9.95	7.36
		Reducing sugar	1.29	1.77	1.27	1.47	1.39	1.41	2.47	1.24
	Interior scales	Sucrose	8.91	7.04	6.48	6.99	7.17	9.61	8.76	6.34
		Reducing sugar	1.18	1.43	0.67	0.99	1.71	2.27	2.41	1.98
	Daughter bulb	Sucrose	-	-	4.29	5.48	6.23	7.53	6.43	6.77
		Reducing sugar	-	-	0.67	0.56	1.15	1.59	1.96	1.93
	Basal plate	Sucrose	3.74	2.7	2.5	3.67	3.59	5.21	2.61	2.49
		Reducing sugar	0.31	1.37	1.99	1.84	1.66	2.16	1.34	1.43
Asiatic hybrids Elite	Mother bulb	Sucrose	10.54	2.19	4.18	5.01	7.37	6.05	6.48	4.53
		Reducing sugar	0.51	1.77	2.79	1.35	0.51	0.37	1.01	1.55
	Daughter bulb	Sucrose	-	-	2.04	5.58	7.34	6.25	5.88	7.03
		Reducing sugar	-	-	0.79	0.3	0.36	0.3	0.49	0.46
	Basal plate	Sucrose	4.44	1.82	2.29	1.16	2.57	2.4	2.66	3.12
		Reducing sugar	0.45	0.36	0.63	0.84	0.81	0.58	0.9	0.74

Table 2 Correlation analysis between substance changes and endogenous hormone content in different parts of *Lilium davidii* var. *unicolor* bulb.

Tissue of bulb	Factor	Linear regression	Correlation coefficient	Reference
Terminal bud	Amylase	$Y=274.05-2.09X_1+20.31X_2+15.24X_4$	0.9912**	
	Total soluble sugar	$Y=9.13-0.07X_1+0.82\ X_2+0.46\ X_4$	0.9733**	
	PAL	$Y=5.41-0.02X_1+0.15\ X_2+0.18\ X_4$	0.9440**	Sun *et al*. 2006c
	Phenols	$Y=577.75-1.97X_1+28.05X_2+28.61X_4$	0.9761**	
	Arginine	$Y=8.85+0.16X_1$	0.7130**	
Exterior scales	Amylase	$Y=239.32-0.18X_1+32.95X_2-15.86X_4$	0.9250***	
	Total soluble sugar	$Y=82.86+4.6X_2-0.01X_3$	0.9339***	
	PAL	$Y=1.89+0.13X_2-0.06X_4$	0.7531*	Sun *et al*. 2006a
	Phenols	$Y=322.38+12.01X_2+0.03X_3-2.98X_4$	0.8921**	
	Arginine	$Y=2.54-0.003X_1+0.43X_2$	0.7954*	
Middle scales	Amylase	$Y=83.30+11.66X2+0.01X3$	0.9726**	
	Total soluble sugar	$Y=113.65-0.06X1+5.37X2$	0.9587**	
	PAL	$Y=224.86+7.84X2$	0.7956**	Sun *et al*. 2005b
	Phenols	$Y=1.10+0.08X2$	0.7115**	
	Arginine	$Y=9.95+0.02X1$	0.6096*	
Interior scales	Amylase	$Y=270.50-0.61X_1$	0.9488***	
	Total soluble sugar	$Y=162.53-0.32X_1-4.53X_2$	0.8133**	
	PAL	$Y=3.95-0.01X_1-0.05X_2-0.07X_4$	0.9693***	Sun *et al*. 2006a
	Phenols	$Y=390.42-3.46X_2-12.48X_4$	0.9438***	
	Arginine	$Y=4.91+0.09X_1+4.38X_2$	0.7199*	

X_1: ABA; X_2: GA_3; X_3: IAA; X_4: ZR; * $P<0.05$, ** $P<0.01$, *** $P<0.001$

tally substitute low temperature for breaking dormancy (Langens *et al*. 1997; Niimi *et al*. 1998) because decomposition of starch in outer scales would be inadequate or too late compare to low temperature treatment (Langens 1997). Some studies proved that the lower the temperature, the earlier the break down of starch (William 1989; Sun *et al*. 2004a), which may lead to dissimilar results among different storage temperatures.

Changes in endogenous hormones

It was reported that endogenous hormone levels in bulbs are associated with dormancy development and release, but the results are not identical. Lin *et al*. (1975) reported that the ABA content increased somewhat and the gibberellic acid (GA_3) content did not change during the storage of *L. longiflorum* bulbs at 4.5°C up to 80 d. Gude *et al*. (2000) investigated the changes in ABA content during dormancy development in the bulbs of Asiatic hybrids, oriental hybrids and *L. longiflorum*. The results showed that the development of dormancy was related with the content of endogenous ABA except for *L. longiflorum*. Xu *et al*. (2006) reported that the concentration of endogenous ABA level in *L. rubellum* bulbs decreased as storage duration increased. However, Takayama *et al*. (1993) concluded through GC/SIM (gas chromatography-selected ion monitoring) analysis that there was little difference in ABA level between dormancy and dormancy-released bulbs. Djilianov *et al*. (1994) also considered, by using HPLC/MS (high-performance liquid chromatography-mass spectrometry), that there was no relation between ABA content and dormancy in bulblets of *Lilium speciosum* regenerated *in vitro*. Some studies explained that other uncertain factors other than ABA might also be involved in the dormancy of lily bulbs (Kim *et al*. 1994). It was suggested that the development of dormancy and dormancy release under low temperature storage is regulated mainly by endogenous GA_3 and ABA (Sun *et al*. 2005b, 2006a, 2006c), and that the effects of GA_3 and ABA were not isolated. Regression analyses of the metabolism showed that the metabolic mechanism in different tissues of the bulb differed markedly during bulb development and storage at low temperature during dormancy release. For terminal buds, the principal organ of bulb dormancy (Sun *et al*. 2004a), endogenous ABA was the key inhibitor of sprouting (Sun *et al*. 2006c). However, substance changes in exterior scales and middle scales were regulated mainly by endogenous GA_3, but mostly by endogenous ABA in the interior scales (Sun *et al*. 2005b, 2006a; **Table 2**).

Changes in category and content of free amino acids

Free amino acids are important intermediate products of nitrogen metabolism and the initial products of carbon assimilation in plants (Xia *et al*. 1998). Sun *et al*. (2004c) reported that free amino acids in lily bulbs mostly existed in young tissues such as terminal buds and inner scales. Furthermore, the content of free amino acids changed evidently at an early stage, i.e. at 34 d during low temperature storage of up to 101 d. Accompanied by significant changes of free amino acids, the terminal buds developed promptly in the bulbs, implying that the changes of free amino acids might also be involved in releasing dormancy. Arginine is the most frequently found amino acid, which accounts for more than 50% of total free amino acids (Sun *et al*. 2004c). Amino acids belonged to the glutamic acid family such as arginine, glutamine and proline play important roles (Sun *et al*. 2004c) during dormancy release by low temperature. To fully understand the mechanism of dormancy in lily bulbs, it will be necessary to study thoroughly the metabolism of free amino acids.

Changes in phenol content

Phenols have been considered as one of the main growth inhibitors in plants (Chen *et al*. 1997). Konoshima *et al*. (1973) reported that phenols and ABA together restrained the sprouting of gladiolus corms. However, opposing opinions emerged over time and certain authors considered that phenolic compounds promote the germination of seeds (Reigosa *et al*. 1999; Sfendiyaro *et al*. 2001). For lily bulbs, the total phenolic content decreased obviously during dormancy development and increased during chilling storage (Sun *et al*. 2004d); furthermore, in sprouting bulbs the content was significantly more than in dormant bulbs. In the first 34 d of storage, total phenols accumulated markedly and increased 60.5% at 2°C than the first day of storage as the terminal bud developed in the bulb. Therefore, we initially proposed that phenols in lily bulbs might not be inhibitors of sprouting (Sun *et al*. 2004d). But due to the diversity and complexity in the category and structure of phenols, it is clear that the detailed component related to bulb dormancy and acting mechanism have significance to both theory and practice.

Table 3 Substances content and relative enzymes activity in different parts of *Lilium davidii* var. *unicolor* bulbs stored at 2°C for 101 d (based on findings and data from Sun *et al*. 2004a, 2004d, 2005a, 2006c).

Parts of bulb	Amylase activity ($\mu g \cdot min^{-1} \cdot g^{-1} \cdot FW$)	Phenol content ($\mu g \cdot g^{-1} \cdot FW$)	PAL activity ($0.01\ OD \cdot g^{-1} \cdot FW \cdot min^{-1}$)	ABA content ($pmol \cdot g^{-1} \cdot FW$)	GA_3 content ($nmol \cdot g^{-1} \cdot FW$)	IAA content ($pmol \cdot g^{-1} \cdot FW$)	ZR content ($nmol \cdot g^{-1} \cdot FW$)	Starch conten ($mg \cdot g^{-1} \cdot FW$)	Soluble sugar ($mg \cdot g^{-1} \cdot FW$)
Terminal bud	362.7	750.7	6.2	35.3	3.2	175.2	5.8	38.1	116.5
Basal plate	613.5	1200.0	15.0	80.6	68.4	191.4	37.5	22.4	108.5
Exterior scales	495.3	435.3	3.4	52.3	5.6	480.5	2.4	38.7	95.3
Middle scales	220.1	325.7	1.9	20.3	11.6	1010.7	9.1	191.7	164.1
Interior scales	293.5	370.9	3.7	10.1	6.5	1800.3	0.7	136.5	148.6

KEY STAGES IN DORMANCY RELEASE OF LILY BULBS

During chilling storage, the contents of carbohydrate (Sun *et al*. 2004a), phenol (Sun *et al*. 2004d), free amino acid (Sun *et al*. 2004c) and endogenous hormones including ABA and GA_3 (Sun *et al*. 2005b, 2006a, 2006c) in lily bulbs all changed significantly. Especially in the first 34 d, starch degradation closely coincided with an increase of soluble sugar, phenols and endogenous GA_3 content. At the same time, buds developed rapidly in bulbs (Sun *et al*. 2004a). These results suggested that this metabolism was involved in dormancy release of bulbs. However, bulbs stored only for 34 d sprouted slowly and grew so poorly that they never emerged into plantlets after planting. One or two plantlets formed a rosette (Sun *et al*. 2004a). Therefore, storage for 34 d at a low temperature cannot provide an answer for the need of dormancy release. The above metabolic mechanisms were essential to physiologically prepare bulbs for sprouting. Buds of bulbs stored at 10°C developed in the bulbs at first, but the sprouting speed was not as good as bulbs stored at 2°C or 6°C (Sun *et al*. 2004a). Within 101 d, the regularity of both sprouting and harvesting improved and biomass increased with the decline of storage temperature and also with prolonged storage, which was coherent with the metabolic changes under different storage temperatures. According to the sprouting of bulbs and plant growth, it was concluded that storage at 2°C for 101 days was the best treatment for the dormancy release of mature *L. davidii* var. *unicolor* bulbs (Sun *et al*. 2004a).

EFFECTS OF DIFFERENT PARTS OF LILY BULB ON DORMANCY RELEASE

Previous reports mostly paid attention to scales or the whole bulb, and the difference among various parts of the bulb were largely ignored. It was once reported that inhibitors were produced in new scales of *L. longiflorum* (Wang *et al*. 1970), and discarding new scales would promote sprouting and flowering. Sun *et al*. (2004a, 2004b, 2004c, 2004d, 2005a, 2005b, 2006a, 2006c) studied the metabolic changes in the terminal bud, mother bulb, daughter bulb and basal plate. Since the mother bulb in *L. davidii* var. *unicolor* is depleted less than other varieties in one growth cycle, it was divided further into exterior scales (scales in 1 and 2 layers), middle scales (scales in 3 and 4 layers) and interior scales (scales in 5 to 8 layers). All parts of bulb showed obvious changes in carbohydrates (Sun *et al*. 2004a), phenols (Sun *et al*. 2004d), free amino acids (Sun *et al*. 2004c) and endogenous hormones (Sun *et al*. 2005b, 2006a, 2006c) during bulb development and dormancy. However, the extent of change in the terminal bud and basal plate were greater, and lower in scales (Sun *et al*. 2004a, 2004c, 2004d, 2006a). Moreover, the exterior scale was the most active part compared to either middle or interior scales (Choi 1998; Sun *et al*. 2005a). This illustrated that the terminal bud was the main body and focus of dormancy in lily bulbs, but that the development of buds could not be independent of scales and basal plate. In particular, in the basal plate, amylase activity, the ratio of reducing sugar to total soluble sugar (Sun *et al*. 2004a, 2005a), phenolic content, phenylalanine ammonia-lyase (PAL) activity (Sun *et al*. 2004d) and endogenous hormones content (Sun *et al*. 2006c) were evidently much higher than in other parts despite its lower carbohydrate content (**Table 3**). The basal plate is the insertion part not only for the terminal bud, but also for scales and basal roots. Thus, elements in the soil can be assimilated and utilized by lily plants and scales can provide energy and nutrition for the growth of the terminal bud, which may be the effect of the basal plate on metabolism and metabolite transfer. Whether some key enzymes or hormones are synthesized in this part should be studied to better elucidate the mechanism of lily bulb dormancy and development. Because of the diverse mechanisms in different parts of the bulb, the relationship between the terminal bud and basal plate or scales needs to be further investigated.

POSSIBLE PHYSIOLOGICAL MECHANISM OF LOW TEMPERATURE ON DORMANCY RELEASE IN LILY BULBS

Stepwise regression analyses were carried out among various metabolic pathways and the results of studies showed that endogenous ABA was the key inhibitor for the development of the terminal bud (Sun *et al*. 2006c). However, the metabolic mechanisms differed in different parts of the bulb. For the terminal bud, a lower temperature resulted in the decline of ABA level, and an increase in GA_3 content and GA_3 to ABA ratio, which were the keys to bulb sprouting. At the same time, low temperature brought about an increase in amylase activity which resulted in the rapid degradation of starch. In addition, sufficient soluble sugar was vital for inducing bud elongation. Moreover, increased PAL activity produced more phenols, which may have also promoted the development of buds. For scales (Sun *et al*. 2005b, 2006a), at a lower temperature, ABA content declined while GA_3 content and the ratio of GA_3 to ABA increased initially; these reactions induced an increase in amylase activity and PAL activity other than by low temperature directly. Plenty soluble sugars arising from the degradation of starch provided energy for the growth of the terminal bud. Moreover, the soluble sugars were a large carbon pool for the synthesis of amino acids, producing more arginine and phenylalanine (Phe). PAL acts on Phe and results in the production of many phenols, which favor the sprouting of bulbs. The basal plate, the hinge of buds and scales, provided an important source of substances such as GA_3, amylase and PAL. Sprouting of the bulb and the metabolism of these substances differed significantly between various storage temperatures. A higher consumption of substances and inadequate soluble sugars led to faint sprouting capacity of bulbs stored at higher temperature (Sun *et al*. 2006c). In summary, sprouting of lily bulbs demand that the substance stream achieves certain levels in order to stimulate the normal growth of bulbs (Sun *et al*. 2006c).

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