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Effects of Temperature and Illuminating Conditions on Regeneration and Development of Bulblets in Scale Culture of Seven *Lilium* Spp.

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Summary

Excised scales of lily bulbs were kept at 15 ℃ and 25 ℃, and under continuous light or dark to study the regeneration and development of bulblets. The seven species were examined: *Lilium rubellum* Baker, *L. speciosum* Thunb. 'Uchida', *L. nobilissimum* Makino, *L. formosanum* Wallace, *L. longiflorum* Thunb.'Hinomoto', *L. maculatum* Thunb., and the Asiatic hybrid *L.* X 'Benisugata'.

1. Generally, more bulblets were regenerated at 25 ℃ than at 15 ℃ in all *Lilium* spp: bulblets of *L. rubellum* and *L.* X 'Benisugata' were formed equally well at 15 ℃ and 25 ℃. Regardless of temperatures, more bulblets of *L. formosanum*, *L. longiflorum* 'Hinomoto', and *L.* X 'Benisugata' regenerated in the light more than they did in the dark.

2. Regenerated bulblets grew better under light at 25 ℃ than at 15 ℃ and the light stimulated the formation of scaly leaves from bulblets of all species and cultivars, except in *L. nobilissimum*. In *L. nobilissimum*, bulblets failed to form scaly leaves under any cultural conditions. Growth of bulblets of *L. formosanum*, *L. longiflorum*'Hinomoto', and *L. maculatum* was promoted in darkness, whereas the bulblets of *L. rubellum* and *L. nobilissimum* grew best under light at 25 ℃.

3. Bulblets regenerated at 15 ℃ tended to rot during cold treatments compared with those regenerated at 25 ℃, and the latter bulblets sprouted more frequently than the former ones after transplantation in a greenhouse.

Key Words: bulblet growth, cultural conditions, *Lilium* spp., scale culture, scaly leaves

Introduction

We previously reported that during in vitro propagation of *Lilium rubellum*, a continuous light stimulated bulblet regeneration in scale segments cultured at 25 ℃, but the fresh weight of bulblets was lighter than that of those formed in darkness (Niimi, 1985). Secondly, the growth of bulblets excised from scales was better in continuous light than in darkness (Niimi, 1984a). In scale culture of *L. longiflorum* 'Ace', bulb number and size increased in the dark, whereas the formation of bulbs was suppressed under a 16-h photoperiod. The suppression is attributed to the emergence of leaves and gain in the fresh weigh of root and callus under light (Stimart and Ascher, 1978). Leaf emergence on scale bulblets was also promoted in scale cultures of *L. speciosum* (Aguettaz et al., 1990) and *L. japonicum* (Yamagishi, 1995) when the explants were maintained under a 16-h photoperiod. Whereas Stimart and Ascher (1978), Aguettaz et al. (1990), and Yamagishi (1995) reported that the development of leaves on scale bulbs of three species was enhanced by light, we extended the research by investigating the effects of ambient temperatures and continuous light or darkness on the regeneration and development of bulblets in scale cultures of seven *Lilium* spp., including *L. longiflorum*.

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Materials and Methods

1. Plant materials

Aseptic bulbs obtained as previously described (Niimi, 1984b) were used in the present study. Bulbs of *L. rubellum* Baker, *L. speciosum* Thunb., *L. nobilissimum* Makino, *L. formosanum* Wallace, *L. longiflorum* Thunb.'Hinomoto', *L. maculatum* Thunb., and the Asiatic hybrid *L.* X 'Benisugata' were cultured at 24 ± 1 ℃ in the dark on a basal medium consisting of Murashige and Skoog's inorganic salts (1962), 2mg · liter^{-1} glycine, 100mg · liter^{-1} myo-inositol, 0.1mg · liter^{-1} thiamine hydrochloride, 0.5mg · liter^{-1} nicotinic acid, 0.5mg · liter^{-1} pyridoxine hydrochloride, 0.1mg · liter^{-1} NAA, 0.001mg · liter^{-1} BA, 5% sucrose, and 0.8% agar, and adjusted at pH 5.7.

2. Scale culture

Four outermost scales were excised from in-vitro grown bulbs which weighed 300 to 400mg. From this population four scales were selected randomly and transferred to a 50-ml Erlenmeyer flask, containing 20 ml of the basal medium with 0.7% agar and cultured for

10 weeks in the following four environmental regimes: a) continuous darkness at 15 ℃ and 25 ℃ ; b) continuous light condition with cool white fluorescent lamps, 1000 to 1200 lx, at 15 ℃ and 25 ℃ .

Bulblets, regenerated on bulb scales, were excised from the explants after 10 weeks and washed with tap water. The number of bulblets was recorded for each flask, and the bulblets were classified into two types: a) bulblets consisting of only scales (referred to as BTP); b) those composed of both scales and scaly leaves which consist of a small basal scales and an upper foliar part on scaly leaves, namely hypogenous type plant (HTP) (Matsuo and Van Tuyl, 1984). The fresh weight of each bulblet was recorded after removal of both roots and an upper scaly leaf.

3. Cold treatment and transplantation of bulblets

All bulblets from each cultural treatment were mixed with moist vermiculite (tap water: vermiculite = 1 : 4, v/v), placed into a polyethylene bag and stored at 4 ℃ for 8 weeks. After the cold treatment, the bulblets were washed with tap water. The number of rotten bulblets in each cultural treatment was recorded and these were discarded.

Twenty healthy bulblets were transplanted per pot (15cm in diameter and 7cm in height), 2 to 3cm in depth, potting mixed soil of paddy soil: sand: leaf mold (1 : 2 : 2, v/v/v). They were grown in a greenhouse where the night / day temperatures, 10~20 ℃ / 15~25 ℃ , respectively, which fluctuated depending on the weather. All bulblets were harvested 6 weeks after transplanting and washed with tap water. Numbers of sprouting and rotting bulblets were recorded for each cultural treatment.

Results

1. Regeneration and growth of bulblets from scale culture

Table 1 shows the genotype, cultural temperature, and illuminating conditions, and their interaction on regeneration and growth of bulblets.

1) Number of regenerated bulblets

More bulblets regenerated at 25 ℃ than they did at 15 ℃ in all *Lilium* spp. (Table 2).

Scale explants which were cultured at 15 ℃ responded to light conditions, depending on the genotype. Explants of *L. formosanum*, *L. longiflorum* 'Hinomoto', and *L. maculatum* regenerated more bulblets under light than in

Table 1. Combined analyses of variance in the number of regenerated bulblets and mean fresh weight of regenerated bulblets in scale cultures of 7 *Lilium* spp. as affected by genotype (G), cultural temperature (T) and illuminating conditions (I) [z].

Source of variation	df	No. of regenerated bulblets		Mean fresh weight of bulblets	
		MS	F-value	MS	F-value
G	6	12229	82.4**[y]	42046	56.2**
T	1	3072	124.2**	96460	773.7**
I	1	469	18.9**	1452	11.6**
G × T	6	261	1.7NS	33376	44.6**
G × I	6	592	3.9**	9717	12.9**
T × I	1	5	0.2NS	1156	9.2**
G × T × I	6	271	1.8NS	10048	13.4**
Error	392	9691		48868	

[z] Values are shown in Tables 2 and 3.

[y] NS and ** indicate nonsignificant and significant at $P = 0.01$, respectively.

Table 2. Effects of temperature (T) and illuminating conditions (I) on the number of bulblets regenerated from cultured scale segments in 7 *Lilium* spp.[z]

Temperature (℃)	Illuminating conditions[y]	Number of regenerated bulblets (flask^{-1})						
		L. rubellum	*L. speciosum*	*L. nobilissimum*	*L. formosanum*	*L. longiflorum* 'Hinomoto'	*L. maculatum*	*L.* X 'Benisugata'
15	Dark	13.2a[x]	11.3a	1.4a	0a	2.1a	0.7a	10.8a
	Light	18.1a	10.3a	0a	2.4b	5.3b	4.3b	15.2ab
25	Dark	15.4a	18.1b	7.9b	4.3c	6.7b	9.8d	16.3ab
	Light	23.4b	16.2b	10.7c	6.4d	10.3c	7.1c	18.3b
Significance[w]								
T		NS	**	**	**	**	**	*
I		**	NS	NS	**	**	NS	NS
T × I		NS	NS	**	NS	NS	**	NS

[z] Four scales were inoculated in each flask and cultured for 10 weeks. Values represent the mean of 15 flasks.

[y] Cultures were maintained under continuous light and dark conditions.

[x] Values in the same column not followed by the same letter are significantly different at $P = 0.05$ following Duncan's new multiple range test.

[w] NS, * and ** indicate nonsignificant, significant at $P = 0.05$ and 0.01, respectively.

Table 3. Effects of temperature (T) and illuminating conditions (I) on the fresh weight of bulblets regenerated from cultured scale segments in 7 *Lilium* spp.[z]

Temperature (℃)	Illuminating conditions[y]	Fresh weight of regenerated bulblets (flask^{-1})						
		L. rubellum	*L. speciosum*	*L. nobilissimum*	*L. formosanum*	*L. longiflorum* 'Hinomoto'	*L. maculatum*	*L.* X 'Benisugata'
15	Dark	19.7a[x]	30.1b	7.6a	0a	9.2a	3.1a	6.9a
	Light	13.2a	1.2a	0a	4.2b	1.5a	4.4a	4.3a
25	Dark	28.9b	56.6c	50.0b	29.6c	60.6c	18.1c	21.5b
	Light	39.5c	49.7c	84.4c	18.2d	40.1b	10.9b	20.1b
Significance[w]								
T		**	**	**	**	**	**	*
I		NS	**	**	NS	**	*	NS
T × I		**	**	**	**	NS	**	NS

[z] Four scales were inoculated in each flask and cultured for 10 weeks. Values represent the mean of 15 flasks.
[y] Cultures were maintained under continuous light and dark conditions.
[x] Values in the same column not followed by the same letter are significantly different at $P = 0.05$ following Duncan's new multiple range test.
[w] NS, * and ** indicate nonsignificant, significant at $P = 0.05$ and 0.01, respectively.

the dark; no bulblets were formed from scales of *L. nobilissimum* under light condition and none from *L. formosanum* in the dark.

When scale explants were cultured at 25 ℃ , more bulblets were regenerated in *L. maculatum* scales held in the dark than in those kept in the light. There were no statistically significant differences between bulblets grown in the light or dark in *L. speciosum* and *L.* X 'Benisugata'. Bulblet regeneration was promoted by light in other four species.

2) Growth of regenerated bulblets

Whereas growth of regenerated bulblets was promoted at 25 ℃ in all *Lilium* spp., bulblets of *L. rubellum* and *L. nobilissimum* grew better under light. Contrarily, bulblets of *L. formosanum*, *L. longiflorum* 'Hinomoto', and *L. maculatum* grew better in the dark. Bulblets of *L. speciosum* and *L.* X Benisugata' grew equally well in the light and dark (Table 3).

3) Scaly Leaf emergence

Temperature and illuminating conditions affected scaly leaf emergence from developing bulblets, namely formation of HTP in all *Lilium* spp., except *L. nobilissimum* whose bulblets formed no scaly leaves under any cultural conditions (Table 4). The number of HTP increased under continuous light at 15 ℃ and 25 ℃ , particularly at 15 ℃ ; More than 90% of bulblets in *L. speciosum*, *L. longiflorum* 'Hinomoto', and *L.* X 'Benisugata' and 40% in *L. rubellum* under light condition at 15 ℃ developed to HTP; whereas only 16% of bulblets in *L. rubellum* and more than 47% in other *Lilium* spp.

Table 4. Effects of temperature (T) and illuminating conditions (I) on scaly leaf formation from bulblets (bulblets with scaly leaves)[z] in scale cultures of 7 *Lilium* spp.[y]

Temperature (℃)	Illuminating conditions[y]	Percentage of HTP*						
		L. rubellum	*L. speciosum*	*L. nobilissimum*	*L. formosanum*	*L. longiflorum* 'Hinomoto'	*L. maculatum*	*L.* X 'Benisugata'
15	Dark	0	1 ± 1	0	0	8 ± 4	0	30 ± 5
	Light	40 ± 5	91 ± 2	0	40 ± 12	99 ± 1	41 ± 8	90 ± 3
25	Dark	0	0	0	65 ± 8	26 ± 6	80 ± 5	16 ± 7
	Light	16 ± 7	47 ± 7	0	82 ± 7	76 ± 5	90 ± 3	83 ± 2
Significance[w]								
T		NS	*	NS	*	NS	*	NS
I		*	*	NS	*	*	*	*
T × I		*	*	NS	NS	*	*	NS

[z] A bulblet with leaves corresponds to a hypogenous type plant, HTP (Matsuo and Van Tuyl, 1984)
[y] Four scales were inoculated in each flask and cultured for 10 weeks.
[x] Cultures were maintained under continuous light and dark conditions.
[w] (total number of HTP/total number of regenerated bulblets) × 100. Values represent the mean ± standard error of 15 flasks.
[u] NS, * and ** indicate nonsignificant, significant at $P = 0.05$ and 0.01, respectively.

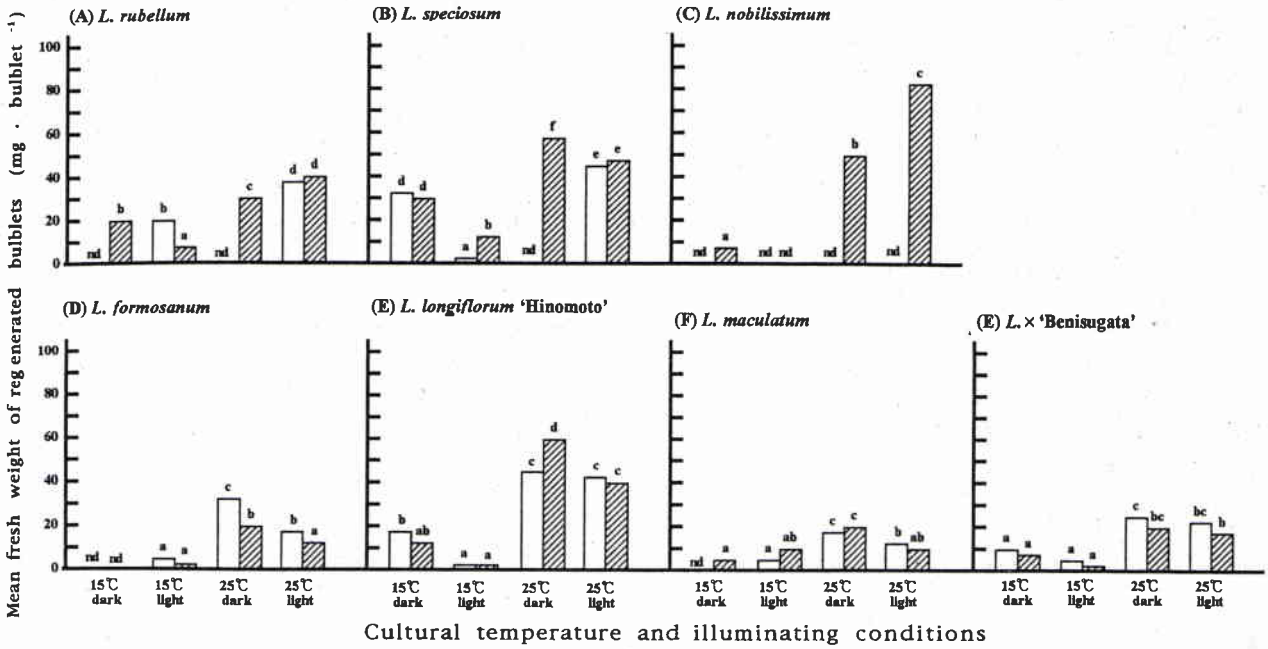

Fig. 1. Comparison of the fresh weight between regenerated bulblets without scaly leaves (BTP) (▨) and those with scaly leaves (HTP) (□) in scale cultures of 7 *Lilium* spp. affected by temperature and illumination. Values in each species not followed by the same letter are significantly different at $P = 0.05$ following Duncun's new multiple range test; nd = not determined.

formed HTP when their scale explants were cultured at 25 ℃ under light.

Differences in the mean fresh weight between BTP and HTP were observed under each combination of genotype and cultural conditions (Fig. 1): HTP bulblets were heavier than those of BTP when scale explants of *L. rubellum* were cultured under light at 15 ℃ . Similar weight differences occurred between HTP and BTP of *L. formosanum* grown in the light and dark. Contrarily, BTP of *L. speciosum* and *L. longiflorum* 'Hinomoto' grown under dark at 25 ℃ were heavier than those of HTP. No significant differences in fresh weight between BTP and HTP were observed in the other combinations of genotypes and cultural conditions.

2. Bulblet rot during cold treatment

Bulblets in all *Lilium* spp., regenerated at 15 ℃ rotted more frequently during cold treatment than did those regenerated at 25 ℃ (Table 5): all bulblets of *L. nobilissimum*, which were regenerated at 25 ℃ , survived; on the other hand, none of the bulblets of *L. formosanum*, *L. longiflorum* 'Hinomoto', and *L. maculatum*, which were regenerated at 15 ℃ under light or dark, survived.

3. Sprouting and bulblet rot after transplanting in a greenhouse

Bulblet rot occurred in all *Lilium* spp. after transplanting to the greenhouse (Fig.2). More than 80% of the bulblets of *L. speciosum*, regenerated at 15 ℃ under

Table 5. Effects of temperature and illuminating conditions during scale culture on the frequency of rotting of regenerated bulblets 8 weeks after cold treatment in 7 *Lilium* spp.[z]

Temperature (℃)	Illuminating conditions[y]	Percentage of bulblets rotten during chilling[x]						
		L. rubellum	*L. speciosum*	*L. nobilissimum*	*L. formosanum*	*L. longiflorum* 'Hinomoto'	*L. maculatum*	*L.* X 'Benisugata'
15	Dark	12.1	2.9	47.6	–[w]	100	100	30.2
	Light	57.0	92.3	–	100	100	100	4.4
25	Dark	13.4	4.4	0	3.1	8.5	18.4	4.9
	Light	19.7	3.3	0	6.7	22.1	8.4	8.7

[z] Regenerated bulblets were removed from each scale 10 weeks after culture and treated at 4 ℃
[y] Scale cultures were maintained under continuous light and dark conditions.
[x] (number of rotten bulblets after cold treatment/number of cold-treated bulblets) × 100.
[w] Not determined.

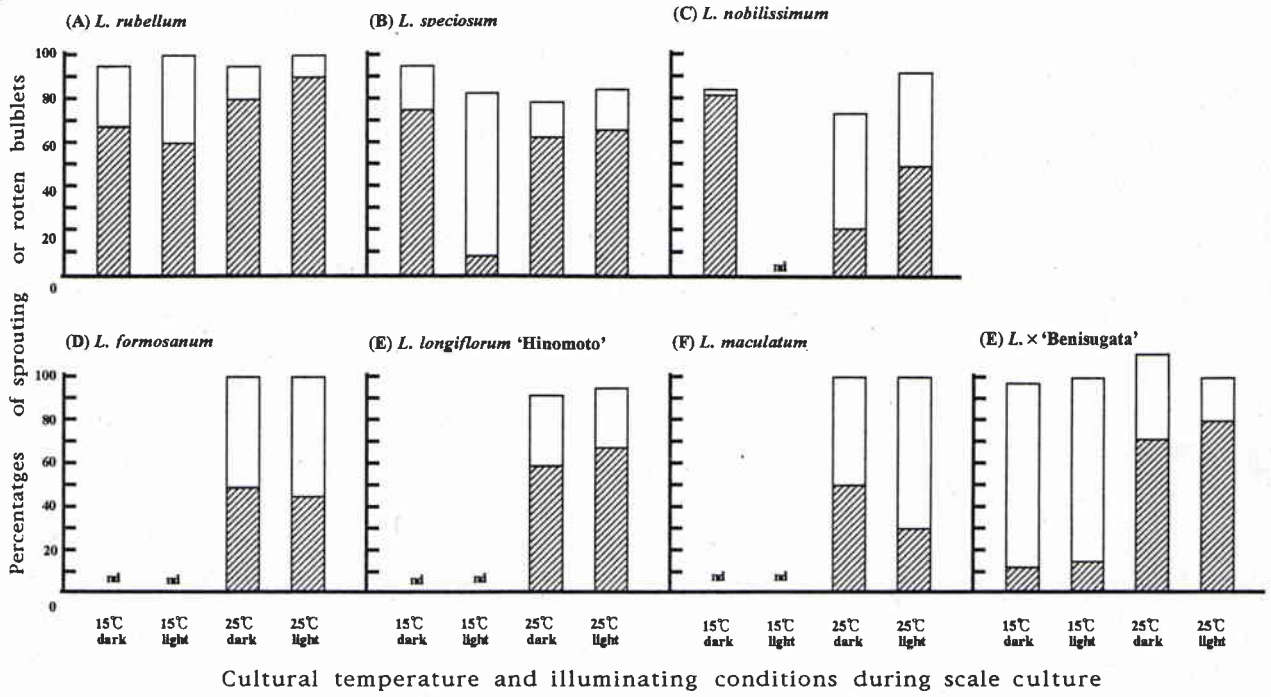

Fig. 2. Effect of cultural temperature and illuminating conditions during scale culture on the percentages of sprouting (▨) and rotting (□) bulblets 6 weeks after transplanting in a greenhouse in 7 *Lilium* spp. Scale cultures were maintained under continuous light and dark conditions at 15 ℃ and 25 ℃, respectively. After cold treatment the healthy bulblets were transplanted to a greenhouse. nd = not determined

light and those of *L.* X 'Benisugata' regenerated at 15 ℃ in the light or dark rotted. Generally, the percentage of sprouting after transplanting in a greenhouse was higher in bulblets regenerated at 25 ℃ than in those regenerated at 15 ℃. In *L. nobillissimum*, however, bulblets regenerated in darkness at 15 ℃ sprouted more frequently than those regenerated at 25 ℃.

Discussion

This study showed that temperature and light affected in vitro regeneration and development of bulblets from scale cultures of 7 *Lilium* spp. and that 25 ℃ was more favorable for survival than 15 ℃ (Table 2, 3). Our findings agree with the reports of Van Aartrijk and Blom-Barnhoor (1983) with *L. speciosum*, Niimi (1985) with *L. rubellum*, Stimart and Ascher (1981) and Higgins and Stimart (1990) with *L. longiflorum* 'Ace', and Stimart and Ascher (1981) with 'Nellie White' who found that bulblet regeneration and growth are promoted at 25 ℃. Similarly, the growth of new daughter bulbs attached to the mother bulb (Wang and Roberts, 1983) and scale bulbs in scaling (Shenk and Boontjes, 1970) were stimulated at 24 ℃ and 23 ℃, respectively. Why bulblets regenerated at 15 ℃ were more prone to rot than those regenerated at 25 ℃ during cold treatment and after transplanting in a greenhouse (Table 5; Fig. 2) is inexplicable. Niimi (1995) reported earlier that the small-sized bulblets of *L. japonicum* are more perishable in soil than are the larger ones. Perhaps, the incubation temperatures affect the nutrient uptake of bulblets from the medium leading to variances in composition and quality of the scale cells. Consequently, small-sized bulblets are doomed to be perishable during chilling and after transplantation to soil. Our present results indicate that temperature suitable for the differentiation and growth of bulblets in scale culture of *Lilium* spp. ranges from 20 ℃ to 25 ℃. This finding coincides with results in a previous paper (Niimi, 1985), although dormancy is readily induced in bulblets of *Lilium* spp. at tempratures greater than 20 ℃ (De Klerk and Paffen, 1995).

Bulblets, regenerated on scales which had been cultured under light and dark at 25 ℃, are categorized into four groups by morphology, BTP, HTP, and growth rates (Tables, 1, 2, and 3): In Group Ⅰ, when bulb scales are cultured under light and dark, no leaves emerge on bublets of *L. nobilissimum* or they rarely emerge on those of *L. rubellum*, and the growth of the bulblets is stimulated by light; Group Ⅱ, leaves emerge readily from regenerated bulblets when the scales are cultured under light, and the growth of the bulblet is stimulated only in the dark in *L. speciosum* and *L. longiflorum* 'Hinomoto'; Group Ⅲ, leaves emerge on bulblets at a high frequency in any cultural condition, but the bulblet growth is enhanced in darkness in *L. formosanum* and *L. maculatum*; and Group Ⅳ, both bulblet growth and leaf emergence are stimulated in both light and dark conditions in *L.* X 'Benisugata'. Based on the above, *Lilium* spp. as reported by Stimart

and Ascher (1978), Leshem et al. (1982), and Kim et al. (1996) might categorized: *L. lancifolium* and *L.* X 'Stargazer' (Kim et al., 1996) in Group Ⅰ ; *L. longiflorum* of 'Hinomoto' 'Georgia' (Kim et al., 1996), 'Ace' (Stimart and Ascher, 1978), and Osnat' (Leshem et al., 1982), *L.* X *formolongi* 'BS Super' and *L.* X 'Connecticut King' (Kim et al., 1996) in Group Ⅱ or Ⅲ . Response of these bulblets to different light conditions could probably be explained as follows: defferences in culture media which contain different exogenous growth regulators at various concentrations; genotypic and physiological differences in explants in which endogenous hormone levels and/or sensitivities to growth regulators are affected by light because it modifies endogenous levels of hormones in plant tissues (Evans, 1984; Rajagopal et al., 1986). The mechanism which influences scaly leaf emergence on bulblets mediated by light or other environmental factors will be clarified in a future work.

Regulating scaly leaf emergence on in vitro regenerated bulbs is a prerequisite for obtaining bulblets having the minimum size for transplanting in soil. Stimart and Ascher (1978) and Leshem et al. (1982) reported that bulblets cultured under a 16-h light photoperiod are small, probably due to scaly leaf emergence at a higher frequency, compared with those cultured in darkness. This study showed that in bulblets of *L. rubellum*, *L. speciosum*, *L. formosanum*, *L. longiflorum* 'Hinomoto', *L. maculatum*, and *L.* X 'Benisugata', scaly leaves emerged at a higher frequency at 25 ℃ in the light (Table 4), and that in *L. speciosum* and *L. longiflorum* 'Hinomoto', BTP was heavier than HTP when the scale segments were cultured at 25 ℃ in the dark (Fig. 1), and that in *L. formosanum*, *L. longiflorum* 'Hinomoto', and *L. maculatum*, the average weight of bulblets regenerated in darkness was greater than that in the light (Table 3). Based on our results and those of Stimart and Ascher (1978) and Leshem et al. (1982), cultural conditions which inhibit leaf emergence from in vitro developing bulblets seem to be favorable for the growth of bulblets regenerated on explants, probably because the leaves develop at the expense of bulbs (Stimart and Ascher, 1978). To obtain large, heavy bulblets, suitable for transplanting in soil, it is necessary to develop a method of stimulating the growth of bulblets without scaly leaves.

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7種類のユリのりん片培養における培養温度と光条件が子球の形成と発達に及ぼす影響

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摘　要

ヒメサユリ (*Lilium rubellum* Baker), カノコユリ (*L. speciosum* Thunb.), タモトユリ (*L. nobilissimum* Makino), タカサゴユリ (*L. formosanum* Wallace), テッポウユリ 'ひのもと' (*L. longiflorum* Thunb. 'Hinomoto'), イワユリ (*L. maculatum* Thunb.), およびアジアティックハイブリッド '紅姿' (*L.* X 'Benisugata') のりん片培養における培養温度 (15 ℃ あるいは 25 ℃) および光条件 (連続照明下あるいは暗黒下) が子球の形成および発達に及ぼす影響を調査した.

1. どのユリも 15 ℃ よりも 25 ℃ で培養した場合に多くの子球を形成し, ヒメサユリと '紅姿' では 15 ℃ でも 25 ℃ の場合と同程度に子球を形成した. そしてタカサゴユリ, テッポウユリ 'ひのもと' および '紅姿' の子球はいずれの培養温度でも暗黒下よりも連続照明下で促進された.

2. 形成された子球の生長はいずれのユリにおいても 15 ℃ よりも 25 ℃ で促進された. 25 ℃ の温度下ではタモトユリを除くすべてのユリでりん片葉の形成が明条件下促進された. そしてタカサゴユリ, 'ひのもと' およびイワユリでは暗条件下で子球の生長が促進され, ヒメサユリの子球は明条件下で促進された. 一方, タモトユリはいずれの培養条件下でもりん片葉を全く形成せず, 子球の生長は 25 ℃, 明条件下で最も促進された.

3. 15 ℃ で得られた子球は 25 ℃ で得られたものと比較して低温処理中に腐敗しやすかった. また, 温室に移植した子球の出葉は 25 ℃ の培養条件で得られた子球の方が 15 ℃ でものと比べて高く, 生育も良好であった.