Flower Growth, Coloration and Petal Pigmentation in Four Lisianthus Cultivars

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Summary

Floral flavonoid content in relation to petal color before and after anthesis in four cultivars of lisianthus [*Eustoma grandiflorum* (Raf.) Shinn.] were determined. 'Bridal Violet' and 'Asuka no Asa', 'Azuma no Yosooi', and 'Mickey Rose' were classified into delphinidin, pelargonidin, and cyanidin major types, respectively, from HPLC profiles; peonidin and malvidin existed as minor components. Anthocyanin synthesis began before anthesis; total anthocyanins tended to increase after anthesis. Whereas flavonol content reached its maximum before anthesis in all cultivars, as the lisianthus petals unfurled, other anthocyanidin(s) appeared, resulting in changes in anthocyanidin ratios. However, those ratios remained nearly constant after anthesis; flower color did not change during flowering. With respect to pigment constitution, it was the first case that 'Mickey Rose' was found to be cyanidin dominant. Results on flavonol contents suggest that the copigment effect was not present in lisianthus cultivars.

Key Words: anthocyanidin, *Eustoma grandiflorum*, flavonol, flower color.

Introduction

Lisianthus [*Eustoma grandiflorum* (Raf.) Shinn.], an important new ornamental plant, which belongs to the family Gentianaceae, originated along the eastern slope of Rocky Mountains (USA). However, commercial cultivars were intensively developed in Japan (Halevy and Kofranek, 1984).

Anthocyanins, common plant pigments, are part of the very large and widespread group of water-soluble plant constituents collectively known as flavonoids and are part of the natural beauty of the plant world (Kuhnau, 1976). Changes in colors depend on the degree of acidity as well as on the type of anthocyanidin pigments in the cells and the structure of their substituents (Brouillard and Dangles, 1994; Amic and Trinajstić, 1991). Such modifications are known to be controlled in the flowers by single gene substitutions (Forkmann, 1994).

Biosynthesis of floral anthocyanins and flavonols has been studied intensively in *Petunia hybrida* (Weiss and Halevy, 1991) and *Antirrhinum majus* (Sang et al., 1991). For lisianthus cultivars, Asen et al. (1986) characterized the flavonoids of purple and pink lisianthus flowers based on anthocyanin and flavonol structures. Flavonoid pigments and factors, influencing their expression in flower color, were demonstrated in lisianthus (Oren-shamir et al., 1999; Griesbach, 1992; Markham and Ofman, 1993). However, detailed studies on antho-

cyanidin development during flowering have not yet been determined although anthocyanidins are the most responsible factor on flower color. Thus, there has always been an interest in anthocyanidin synthesis in association with diverse flower colors among floricultural crops.

In this paper, flower coloration of four lisianthus cultivars, which were pink, reddish-purple, violet, and purple, was studied in relation to their anthocyanidin characteristics during their flowering periods. The findings would be a step in breeding new varieties of lisianthus with desirable flower colors on the basis of their anthocyanidin phenotypes.

Materials and Methods

Plant materials

Four cultivars of lisianthus, 'Bridal Violet' (violet edge), 'Azuma no Yosooi' (pink edge), 'Mickey Rose' (reddish-purple) and 'Asuka no Asa' (purple) were examined for their daily growth pattern and flower pigment constituents before and after anthesis. Seeds (Sakata Seed Co., Yokohama, Japan) were planted and seedlings of each cultivar grown in seed trays using standard greenhouse practices established for lisianthus (Roh and Lawson, 1984). Seedlings were transplanted in a polyethylene house 110 days after sowing, when they formed four to six true leaves. Flower bud growth was recorded from seven days prior to full bloom. In late May 1999, plants began to flower when the plastic house attained 20–35 °C (min. –max.). Three flowers from each cultivar were collected from the day they

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unfurled up to the seventh day for color notation and chemical analyses.

Anthocyanin and flavonol extraction

Slices of fresh petals (only the colored portions) were macerated in 5 ml of 1% HCl methanolic solution with a glass homogenizer and a homogenate was allowed to stand 36 hrs at 4 °C. After filtering, a 2-ml aliquot of filtrate was heated with 4 ml of 2 N HCl at 100 °C for 2hr in the heating block. On cooling, the sample was refiltered through a Millipore disk (0.45 μ m) and the filtrate analyzed by high-performance liquid chromatography (HPLC).

HPLC analyses

Anthocyanidin compositions were qualitatively and quantitatively determined by profiles of HPLC (GUL-LIVER CO-966 Intelligent Column Thermostat). The linear flow-gradient conditions were; 1.5 % H_3PO_4 as A eluent and H_3PO_4 : HCOOH : CH_3CN : H_2O (1.5 : 20 : 25 : 53.5) as B eluent; A : B = 70 : 30 to 30 : 70 (v/v%), 60 min.; column, TSKgel ODS-80Ts QA, Toso Co.; column temperature, 40 °C ; flow rate, 0.8 ml $\cdot$ min $^{-1}$; wave length, 525 nm and an injection volume, 10 μ l/sample. Anthocyanidins detected in HPLC profiles were identified by matching their retention times to those of authentic anthocyanidins from sweet pea petals (Sakata and Uemoto, 1976; Hong and Wrolstad, 1990). Each anthocyanidin, pelargonidin (Pg), cyanidin (Cy), delphinidin (Dp), peonidin (Pn), and malvidin (Mv), was expressed as peak area percentage of whole areas of the respective anthocyanidins in HPLC profiles (Fig. 1).

Total anthocyanins (TA) and flavonols (TF) in petals

The above filtrates of acidic methanolic extracts were analyzed for TA and TF without acid hydrolysis. Optical

Fig. 1. HPLC profiles of 'Mickey Rose' and 'Bridal Violet'. The retention times of anthocyanidins are as follows: Dp, 14.6; Cy, 19.9; Pg, 25.6; Pn, 30.5; and Mv, 34.3 (min.).

densities (O.D.) of TA and TF in the filtrates were measured at 525 nm and 370 nm, respectively, with a UV spectrophotometer (Toshiba, Spectra; Model SPM-60A). Copigment indices (CI) were calculated by the equation; $\text{CI} = \text{TF}/\text{TA}$ as a logarithmic function. The concentrations were calculated quantitatively from a simple linear regression using cyanin (cyanidin 3,5-di-

Fig. 2. Growth patterns of lisianthus flower buds in 'Bridal Violet', 'Azuma no Yosooi', 'Mickey Rose', and 'Asuka no Asa' measured daily for 7 days before anthesis (DBA). (A) diameter, (B) length, and (C) fresh weight. Vertical lines are SD, $n=5$.

O-glucoside) for TA and rutin (quercetin 3-*O*-rutoside) for TF as authentic standards, according to Hashimoto et al. (2000) and presented as mg/100 mg fresh petal (mg%).

Petal color measurement

Petal color at the three different parts of an individual flower was measured immediately after harvest with a color analyzer (Nippon Denshoku, NR-3000) as CIE-LAB (CIE, 1986) to obtain its correlation with total petal anthocyanin contents. A luminance or lightness component (L^*), and two chromatic components, a^* and b^* were determined (Voss, 1992). C^* value (saturation of color) and hue angle (h) were calculated by the equations: $C^* = (a^{*2} + b^{*2})^{0.5}$ and $h = \tan^{-1} (b^*/a^*)$ (Gonnet, 1998).

Statistical analysis

An analysis of variance (SAS, 1995, $P < 0.05$) was conducted to specify the significant chromatical and chemical characteristics of lisianthus petals. The mean and standard deviations were calculated for each sample in triplicate.

Results and Discussion

Flower bud growth and pigment synthesis before anthesis

Among the four lisianthus cultivars, flower bud diameters differed significantly with days before anthesis (DBA). The diameter of 'Bridal Violet' (min.) and

'Mickey Rose' (max.) were 18.8 and 26.6 mm, respectively, just prior to anthesis (Fig. 2). Bud length of 'Asuka no Asa' was longest of the cultivars through the bud growth stage. Bud length in descending order by cultivar is: 'Azuma no Yosooi', 'Mickey Rose' and 'Bridal Violet'. Varietal variations of fresh weight of buds were recorded on different DBA. Buds of 'Mickey Rose' were the heaviest, whereas those of 'Bridal Violet' were the lightest.

The three anthocyanidins, Pg, Cy, and Dp, were identified in floral buds of four lisianthus cultivars by the retention times in the HPLC profiles (Fig. 1). Their compositions differed among four cultivars (Table 1): in 'Bridal violet' only Dp appeared 2 DBA, whereas in 'Azuma no Yosooi', only Pg was present in 1 DBA. In 'Mickey Rose', Pg and Cy were found 2 DBA; the percentage of Cy 6-fold greater than Pg. Markham and Ofman (1993) noted an existence of Cy glycosides with the major acylated Dp glycosides in lisianthus flower pigments. However, 'Mickey Rose' is the first cultivar containing Cy as a dominant anthocyanidin. 'Asuka no Asa' differed slightly in that only Dp was present 5 DBA, followed by Cy 3 DBA; Cy concentration was 1/9th that of Dp.

Anthocyanin synthesis started slowly 2-, 1-, 2- and 5- DBA in 'Bridal Violet', 'Azuma no Yosooi', 'Mickey Rose' and 'Asuka no Asa', respectively. Flavonol synthesis also started before anthesis and reached their maximum amount at the bud stage (Fig. 3). Davies et al. (1993) and Oren-shamir et al. (1999) reported similar

Table 1. Daily changes in the proportions of individual anthocyanidins (%) in petals of four lisianthus cultivars before and after anthesis.^z

Cultivar	Anthocyanidin ^y	Days before anthesis							Days after anthesis						
		6	5	4	3	2	1	0	1	2	3	4	5	6	7
Bridal Violet	Pg	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Cy	-	-	-	-	-	-	3	6	4	2	1	3	1	2
	Dp	-	-	-	-	100	100	91	90	90	94	99	91	97	97
	Mv	-	-	-	-	-	-	6	5	6	3	-	6	2	1
Azuma no Yosooi	Pg	-	-	-	-	-	100	86	92	90	90	92	80	89	91
	Cy	-	-	-	-	-	-	14	8	10	10	8	19	11	8
	Dp	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mickey Rose	Pg	-	-	-	-	8	13	22	23	22	20	21	22	21	23
	Cy	-	-	-	-	92	87	74	73	74	74	73	71	73	73
	Dp	-	-	-	-	-	-	4	4	4	4	4	4	4	4
	Pn	-	-	-	-	-	-	-	-	-	2	2	3	2	1
Asuka no Asa	Pg	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Cy	-	-	-	11	10	10	7	7	4	8	7	6	4	4
	Dp	-	100	100	89	90	90	88	90	91	90	92	93	96	96
	Pn	-	-	-	-	-	-	5	3	4	3	1	1	-	-

^z Fresh petals (n=3) were collected each day from six days before anthesis to seven days later. Flowers opened at day 0.

^y Pg, pelargonidin; Cy, cyanidin; Dp, delphinidin; Mv, malvidin; and Pn, peonidin. Retention time of each anthocyanidin in HPLC analysis is referred to Fig. 1.

Fig. 3. Total anthocyanin (TA) and flavonol (TF) in lisianthus flower buds of (A) 'Bridal Violet', (B) 'Azuma no Yosooi', (C) 'Mickey Rose', and (D) 'Asuka no Asa' prior to anthesis (DBA). Vertical lines are SD, $n=5$. mg% = mg/(100 mg fresh bud). ND, not detected.

results on floral anthocyanin biosynthesis in lisianthus. Petals at the bud stage are white or light green until they begin to unfurl. Anthocyanin synthesis is then initiated and the pigments begin to accumulate.

Pigment synthesis after anthesis

During 7 days after anthesis (DAA), in 'Bridal Violet', Dp which accounted for over 90% of the TA, was a major anthocyanidin with Cy and Mv as minor aglycones (Table 1). In 'Azuma no Yosooi', Pg made up over 80% of the TA after anthesis with only a trace of Cy. In 'Mickey Rose', Cy and Pg were the major anthocyanidins with Dp and Pn as minor components. Pn synthesis started 3 DAA. In 'Asuka no Asa' Dp was the major pigment, coexisting with Cy and Pn after anthesis. Pn diminished on 6 DAA. With respect to methylated anthocyanidins, mapping the pathway of the hydroxylation of the B-ring of anthocyanidin skeleton and their methylation of each pigment genotype will be important steps in breeding lisianthus for new flower colors.

Our data reveal that during anthocyanidin synthesis in

lisianthus cultivars, methylated anthocyanidins appeared at the onset of anthesis with major anthocyanidins. Different biosynthetic pathways led to Dp or Pg—major cultivars with Cy as a minor component and, conversely, a Cy—major one with a small amount of Dp. It seems that a shift of biosynthesis might be involved because the individual anthocyanin ratio changes in each cultivar as well as the total anthocyanin content increases for several days after anthesis (Fig. 4).

The maximum anthocyanin (TA) in fresh petal was obtained 5 DAA in 'Bridal Violet' and 'Azuma no Yosooi', but at 3 and 4 DAA in 'Mickey Rose' and 'Asuka no Asa' cultivars, respectively (Fig. 4). The decline in TA as the petals senesced is attributed to the degradation and/or dilution of anthocyanins because no anthocyanin synthesis occurs in mature petals. Decreases in total flavonol (TF) in aging petals, especially those in 'Azuma no Yosooi' and 'Asuka no Asa', are attributed to decreases in TF synthesis. Likewise, flavonol and anthocyanin concentrations in mature petals could be ascribed to either decreased biosynthesis and/or increased degradation. To avoid the deleterious

Fig. 4. Total anthocyanin (TA) and flavonol (TF) for 7 days after anthesis (DAA) in lisianthus flower petals of (A) 'Bridal Violet', (B) 'Azuma no Yosooi', (C) 'Mickey Rose', and (D) 'Asuka no Asa'. Vertical lines are SD, $n=3$. $\text{mg}\% = \text{mg}/(100\text{mg fresh petal})$.

effects of UV radiation on cells TF synthesis reaches its optimum level before full bloom; subsequently, TF concentrations remain constant in lisianthus flowers (Uddin et al., 2001).

TA concentrations in the petals increased by nearly four-fold after unfurling in 'Azuma no Yosooi', whereas in three cultivars, TA increased 6- to 9-fold. The total amount of TF (TF $\times$ FW of petals) between DBA and DAA remained constant (data not shown) (Fig. 4). The decreasing concentration of flavonols after anthesis indicates that the decline in flavonol concentration in petals is due to rapid increases in cell number and size. Similar results were reported by Hung et al. (1997) who found that the cell division and elongation contribute to a decline in anthocyanin concentration in the periderm of a potato tuber.

Copigmentation is reported to be a formation of a certain stacked complex of anthocyanins and flavonols, which causes a bathochromical shift of an anthocyanin absorption spectrum (Robinson and Robinson, 1931; Asen et al., 1972). Our results show no significant relationship between copigment indices and b^* values

Fig. 5. Correlation between copigment index (CI) and total anthocyanin (TA) of lisianthus flowers: 'Bridal Violet', 'Azuma no Yosooi', 'Mickey Rose', and 'Asuka no Asa'. $\text{CI} = \text{TF}/\text{TA}$.

because no shift in the blue region in the absorption spectrum was detected.

Overall color perceived is also influenced by the copigment index (Joseph et al., 1998). However, in all cultivars, TAs were highly significant with respect to the copigment indices and negatively correlated with them ($r^2 = 0.85$, $n=32$) (Fig. 5). But the distribution along with

the correlation in the diagram differed from each other, e.g. 'Bridal Violet' with a lower CI was distributed into relatively a high TA area; conversely, 'Azuma no Yosooi' with a low TA had a high CI. The result was sufficient to indicate the lisianthus cultivar's characters. Furthermore, the strong logarithmic relationship between TA and CI is attributed to the relative constant

Table 2. Varietal variations in petal color after anthesis in four lisianthus cultivars.^z

Cultivar	Color attribute ^y	Days after anthesis							
		0	1	2	3	4	5	6	7
Bridal Violet	C*	56.9	61.5	76.9	62.5	65.5	74.8	63.1	68.7
	<i>h</i>	−36.0	−35.5	−30.0	−30.6	−31.2	−28.2	−31.6	−26.2
Azuma no Yosooi	C*	38.3	40.2	43.4	37.7	34.4	38.9	36.2	37.9
	<i>h</i>	−6.1	−3.2	−4.8	−3.5	−3.3	−4.6	−2.8	−3.9
Mickey Rose	C*	39.9	40.5	38.1	38.5	39.6	42.5	36.6	41.0
	<i>h</i>	−22.7	−23.8	−22.7	−23.2	−22.4	−21.8	−22.2	−21.5
Asuka no Asa	C*	41.9	39.6	48.3	46.2	46.6	45.4	40.6	45.2
	<i>h</i>	−40.6	−40.7	−39.0	−37.7	−34.1	−37.9	−38.9	−35.5

^z Fresh petals ($n=3$) were collected daily for 7 days after anthesis.

^y C*, metric chroma; and *h*, hue angle.

Fig. 6. Variations in L*, a*, and b* values of lisianthus petals ($n=3$) for 7 days after anthesis (DAA) of (A) 'Bridal Violet', (B) 'Azuma no Yosooi', (C) 'Mickey Rose', and (D) 'Asuka no Asa'. Vertical lines are SD, $n=3$.

quantity of TF in petals. The high correlation supports the proposition that synthesis of flavonols and related glycosides remain in a constant equilibrium in lisianthus flowers.

CIELAB color notation of opened flowers

Different biosynthesis of anthocyanidins resulted in a different spectra of color attributes (C^* and h) in the flower petals (Table 2). Subsequent petal colors of lisianthus cultivars were dominated by three major anthocyanidins from the onset of anthesis. Dp dominant cultivars 'Bridal Violet' produced the highest C^* values at the unfurling stage and the hue angle which pointed clockwise at -36° , where the chromatic tonality of flower petal moved from purple to reddish-purple and extended the chromaticity by 2 DAA. The mature petals of Pg-, Cy-, and Dp-major cultivars, 'Azuma no Yosooi', 'Mickey Rose' and 'Asuka no Asa', displayed distinctly different hues, $-2.8^\circ \sim -4.6^\circ$, $-21.5^\circ \sim -22.4^\circ$ and $-35.5^\circ \sim -38.9^\circ$, respectively. Thus, the major anthocyanidins, control the color variation of petals and their cumulative quantities by extending chromas to individual color directions.

Although additional anthocyanidins, especially methylated ones, appeared late in lisianthus flowers, no distinctive changes in a CIEL*a*b* color coordinate occurred throughout DAA (Fig. 6). Similarly Griesbach (1992) reported that no change in color of lisianthus occurred during and after full bloom. But the data of CIEL*a*b* color indicate that the color of aging petals remained unchanged. Values of L^* , a^* and b^* fluctuated in 'Bridal Violet', whereas lightness of 'Azuma no Yosooi', 'Mickey Rose', and 'Asuka no Asa' tended to decrease after anthesis, but the difference was statistically insignificant. In this study no statistical relationship was found between b^* or a^* and CI (data not shown).

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トルコギキョウの開花に伴う花色と花弁色素構成の変化

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摘 要

開花前後の生育過程におけるトルコギキョウ [*Eustoma grandiflorum* (Raf.) Shinn.] 花弁中のフラボノイド色素と花色変化について調査した。供試品種は、‘ブライダルバイオレット’、‘あすかの朝’、‘あずまの粧’、‘ミッキーローズ’の4品種であり、高速液体クロマトグラフによる色素分析から、前二者はデルフィニジン主体型、‘あずまの粧’はペラルゴニン主体型、‘ミッキーローズ’はシアニン主体型であった。また、これらのアントシアニンに加え、ペオニンやマルビジンなどのメチル化アントシアニンも含まれていることが明らかとなった。

4栽培品種において、花弁アントシアニンの生成は開花前

に始まり、開花後その総含量は増加していく傾向が認められ、花弁フラボノール含量は、開花前には最高値に達することが確認された。また、開花日には、開花前のアントシアニン組成に加え、他のアントシアニンが新たに加わることが観察された。開花後は、アントシアニンの比率はほぼ一定に留まり花色は変化しなかった。‘ミッキーローズ’は、シアニンを花弁中の優勢色素とする品種として確認された初めての例である。なお、本研究に供試したトルコギキョウ品種では、花弁フラボノイド色素間のコピグメント効果は発現していないものと推察された。