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Effects of high temperature on floral development and flowering in spray chrysanthemum

Kouju Nozaki and Seiichi Fukai*

Horticultural Science, Faculty of Agriculture, Kagawa University, Miki, Kagawa 761-0795, Japan.
**E-mail: fukai@ag.kagawa-u.ac.jp*

Abstract

Delayed flowering of chrysanthemum under high temperature conditions is a serious obstacle for all year round cut chrysanthemum flower production in southern temperate and subtropical zones. To clarify the causes of flowering delay in spray chrysanthemum, two different genotypes of spray chrysanthemum (*Dendranthema grandiflorum* (Ramat.) Kitam. syn. *Chrysanthemum morifolium*) were grown under high-temperature conditions: summer-to-autumn flowering type (SA type, high temperature tolerant) and autumn flowering type (A type, high temperature sensitive). Their flower-bud initiation and development were subsequently compared. Results clarify that two independent events caused by high temperatures occur in the shoot apex of spray chrysanthemum under short-day conditions. First, high temperatures slowed floral development in inflorescence, thereby increasing the number of florets in both SA and A chrysanthemum genotypes. Secondly, high temperatures slowed the developmental speed of inflorescence after the budding stage, and the time to reach the bud break stage was prolonged, thereby delaying flowering, especially in A chrysanthemum genotypes.

Key words: Chrysanthemum (*Dendranthema grandiflorum* (Ramat.) Kitam. syn. *Chrysanthemum morifolium*), floral development, high temperature.

Introduction

Chrysanthemum (*Dendranthema grandiflorum* (Ramat.) Kitam. syn. *Chrysanthemum morifolium*) is one of the most globally important ornamental species. The effects of temperature, especially sub-optimal temperature, on growth and flowering of chrysanthemum have been studied intensively (van der Ploeg and Heuvelink, 2006). However delayed flowering of chrysanthemum as a result of high temperatures is still a serious problem, not only in southern temperature zones such as Japan, but also in tropical zone countries like Malaysia, Thailand and Indonesia, where production of cut chrysanthemum flowers has increased recently. Chrysanthemum is a short-day plant; consequently, its flowering can be controlled by changing the day length (Okada, 1963). Short-day treatment is essential to produce cut chrysanthemum flowers in areas where the natural day length is longer than the critical day length in summer. The greenhouse often has high temperatures when it is shaded for this purpose. It has been reported that high temperatures engendered delayed flowering in chrysanthemum (Cockshull, 1979; Cockshull and Kofranek, 1994; Nishio *et al.*, 1988; Whealy *et al.*, 1987). Nevertheless, a few studies have been done to clarify the relationship between floral development and flowering delay. It remains unclear how the delay is reflected in the development of inflorescence. Most genotypes of spray chrysanthemum grown in Europe have a critical day length of about 13.5 h. The genotypes are designated as autumn flowering (A) type. Kawata *et al.* (1987) found the absolute short-day genotypes of chrysanthemum with longer critical day length (16-19 h), for flowering in summer under natural day length in Japan. The genotypes are designated as summer-to-autumn flowering (SA) type. Heat-tolerant cultivars were bred based on the SA genotypes (Shibata and Kawata, 1987). The SA genotypes show only a little flowering delay in summer, but they often show insufficient stem elongation in winter. Because of the defect of SA genotypes, year-round production of spray chrysanthemum is established by combining SA with A genotypes in Japan (Shibata *et al.*, 1988; Koyama *et al.*, 1996). It will be valuable to reveal differences in floral development of both SA and A types under high temperature conditions for breeding programs of heat tolerant year-round producible spray chrysanthemums.

This study was intended to elucidate the causes of flowering delay under high temperature conditions in terms of floral initiation and development. In this study, both SA and A genotypes were grown under high temperature conditions. Their respective floral development characteristics were compared at various developmental stages.

Materials and methods

Cultivation outline: This study used four genotypes of summer-to-autumn flowering type (SA) and five genotypes of autumn flowering type (A) spray chrysanthemums. Mother plants were grown in a greenhouse maintained at a minimum temperature of 15°C under long day conditions (night break). Compost with a mixture of Masa soil (granite) and manure (3:1) was used for this study. All plants were fertilised with 1,000-times diluted Hyponex® (a complete soluble fertiliser, $N:P_2O_5:K_2O$=6:10:5, Hyponex Co. Ltd., Japan, Osaka) once a week during the experiment. For daylength regulation, the short-day treatment (light period 8:00–18:00) (SD) was given by blacking-out to extend the daily dark period; the long-day treatment (LD) was made by a 4 h night break (22:00-2:00) with incandescent lamps at 3 μmol m^{-2} s^{-1}. Budding was defined as visible terminal flower bud appearance. Bud break was defined as a developmental stage of inflorescence in which the top of involucres opened with 3-mm

diameter in terminal inflorescence. The vertical petal was defined as a state in which petals of ray florets extended a vertical state. Flowering was defined as the state in which petals of ray florets opened completely to a horizontal state.

Effects of temperature on floral initiation and development (Experiment I): Two genotypes of spray chrysanthemum were used in this experiment: 'Sei-Monako' (SA type) and 'Sei-Maria' (A type). Cuttings were provided from these mother plants on 26 April in 2001. Eleven rooted cuttings of each genotype were planted in containers (20 x 60 x 15 cm); they were decapitated at the uppermost leaf on 14 May. All lateral shoots were allowed to grow. On 15 June, the plants were transferred to growth chambers that were controlled at a constant 20 or 30°C; SD was given until flowering. For scanning electric microscopic observation (SEM, S-2150; Hitachi Ltd., Tokyo), four shoot apexes of each treatment (20 or 30°C) were collected at 5, 10, 15, 20, 25, 30 and 45 days after the start of SD. Collected samples were fixed immediately with FAA (formalin: acetic acid: 70% ethanol, 5: 5: 90). After fixation, leaves and bracts were removed from the shoot apex under a binocular microscope. The samples were then dehydrated in the ethanol – acetone – isoamyl acetate series and dried in a critical point drier (HCP-1; Hitachi Ltd.). After coating with Pt, the samples were observed using SEM. The remaining shoots (5 shoots per treatment) were allowed to continue cultivation until flowering to provide a measurement of the number of florets.

Effects of high temperature exposed immediately after the start of SD on flowering (Experiment II): Rooted cuttings of 'Sei-Monako' and 'Sei-Maria' were transplanted on 15 July in 2002 in 9 cm-diameter plastic pots. They were decapitated at the uppermost leaf on 29 July. After 4 weeks of growth in a greenhouse under LD, the plants were planted into 21 cm-diameter clay pots (five plants per pot, two replications in each treatment). One lateral shoot per plant was allowed to grow; the others were removed. Then SD treatment started in the growth chambers that were controlled at a constant 20 or 30°C. Treatments consisted of five groups: plants were exposed to 30°C in the period from the start of SD to 5, 10 or 15 days, and were then transferred and grown at 20°C until flowering; plants of the other two groups were grown at 20 or 30°C from the start of SD to flowering. The number of days from the start of SD to budding and flowering, the number of leaves and florets, and the diameter of inflorescence at flowering were recorded.

Genotype related difference in development of inflorescence (Experiment III): This experiment used eight genotypes of spray chrysanthemum: 'Sei-Monako', 'Sei-Snow', 'Yellow-Shoes' and 'Sei-Suffle' (SA type), 'Sei-Alps', 'Sei-Liese', 'Chatoo' and 'Sei-Pino' (A type). Rooted cuttings of eight genotypes were transplanted on 5 May in 2003 in 9 cm-diameter plastic pots. They were decapitated at the uppermost leaf on 19 May. After 4 weeks of growth under LD, the plants were planted into 21 cm-diameter clay pots (five plants per pot) on 19 June. Then SD was given until flowering in the growth chambers controlled at 20°C. One lateral shoot per plant was allowed to grow. For five plants of each genotype, the days from the start of SD to budding, bud break and anthesis were determined, as were the respective diameters of inflorescence at budding, bud break and flowering.

Effects of high temperature on flowering after the visible bud stage (Experiment IV): This experiment used four genotypes of spray chrysanthemum: 'Sei-Snow' and 'Sei-Suffle' (SA type), and 'Sei-Alps' and 'Sei-Pino' (A type). Rooted cuttings of four genotypes were planted on 7 April in 2004 in 9-cm-diameter plastic pots. They were decapitated at the uppermost leaf on 21 April. One lateral shoot per plant was allowed to grow. After 4 weeks of growth in a greenhouse that was maintained at minimum temperature of 15°C under LD, SD was begun on 22 May. They were transferred to growth chambers controlled at 20 or 30°C, and kept under SD until flowering when the plants began the visible bud stage. The number of days from the start of SD to budding, bud break, vertical petal and anthesis, and the diameter of inflorescence at the flowering of five plants per genotype were recorded. The size of inflorescence in terminal inflorescence was measured every day for a period of budding to vertical petal.

Results

Effects of temperature on floral initiation and development (Experiment I): Both 'Sei-Monako' and 'Sei-Maria' showed the same sequence of events in floral initiation and development at 20 and 30°C (Fig. 1). No genotypic differences were apparent in the time required from dome formation to complete floret formation. In both genotypes, however, inflorescences developed slowly at 30°C in comparison with those at 20°C. Each developmental stage of chrysanthemum inflorescence was defined according to Fukai *et al.* (1997). Shoot apexes were vegetative in both genotypes and temperatures until 5 days after start of SD (DASD). Shoot apexes of both genotypes at 20°C reached to the latter stage of involucre formation in 5-10 DASD. They reached the latter stage of floret formation, and corolla formation started in the florets at the bottom of the dome in 15 DASD. Shoot apexes of both genotypes at 20°C completed floret formation by 25 DASD. Flowering of 'Sei-Monako' and 'Sei-Maria' at 20°C was observed at 48 and 55 DASD, respectively. On the other hand, the shoot apexes of both genotypes at 30°C did not produce floret primordia until 15 DASD. Floret formation started in 15-20 DASD at 30°C, and a corolla appeared in the florets at the bottom of dome at 25 DASD. Shoot apexes of both genotypes at 30°C finished floret differentiation by 55 DASD. Flowers of 'Sei-Monako' and 'Sei-Maria' at 30°C were observed at 62 and 94 DASD, respectively.

Table 1. Effects of temperature on the number of florets in spray chrysanthemum

Types	Cultivars	Treatments	Number of florets[z]	
			Ray florets	Disk florets
Summer-to-autumn flowering type	'Sei-Monako'	20°C	23.5 ± 2.5**	253.5 ± 16.4**
		30°C	33.8 ± 0.4	455.6 ± 47.2
Autumn flowering type	'Sei-Maria'	20°C	21.6 ± 1.1 *	152.0 ± 7.1**
		30°C	23.3 ± 1.0	360.0 ± 33.3

[z]Mean ± SD. ** and * denote significant difference by t-test at $P < 0.05$ and $P < 0.01$, respectively.

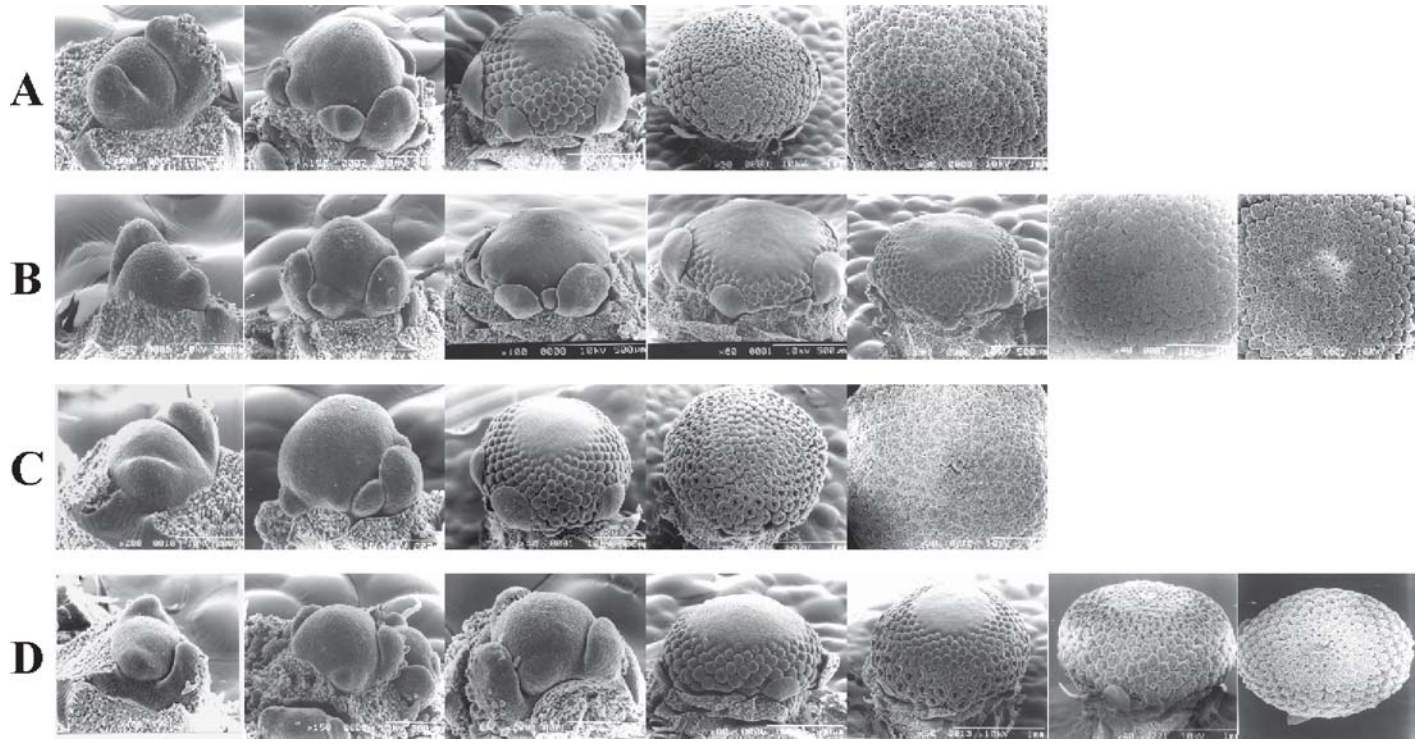

Fig. 1. Effects of temperature on morphological changes in the shoot apex. A: 20°C 'Sei-Monako', B: 30°C 'Sei-Monako', C: 20°C 'Sei-Maria', D: 30°C 'Sei-Maria'. These photographs represent the 5, 10, 15, 20, 25, 30 and 45 days after SD from the left of the line.

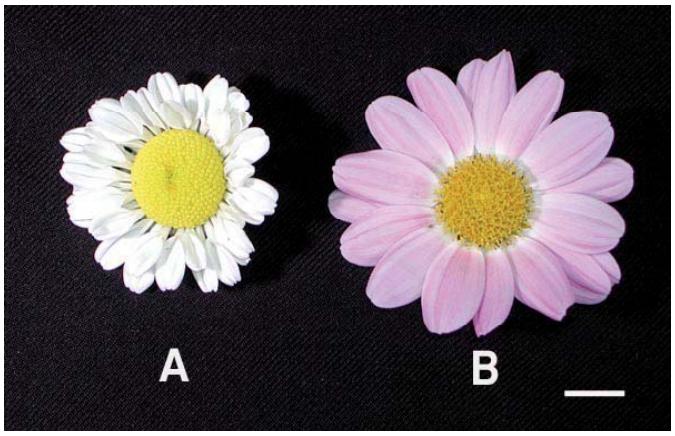

Fig. 2. Effects of temperature on the aspect of inflorescence at the flowering. A: 30°C 'Sei-Monako', B: 20°C 'Sei-Monako'. This photograph was taken 68 days after SD.

The size of inflorescence at 20°C was much larger than that at 30°C in both genotypes. Inflorescences at 20°C had shorter petals of ray florets with pale colour and a larger central part consisting of disk florets (Fig. 2). Considerably more ray florets and disk florets were apparent in plants grown at 30°C than in those grown at 20°C in both genotypes (Table 1).

Effects of high temperature exposed immediately after start of SD on flowering (Experiment II): The numbers of days to budding and flowering were slightly influenced by high temperature exposure immediately after the start of SD, whereas the number of florets increased considerably as a result of exposure to high temperature (Table 2). In 'Sei-Monako', no significant differences in the number of days to budding and flowering were apparent among the three treatments in which 5-15 days of high temperature were given during floral initiation to early development of inflorescence. All parameters of the three

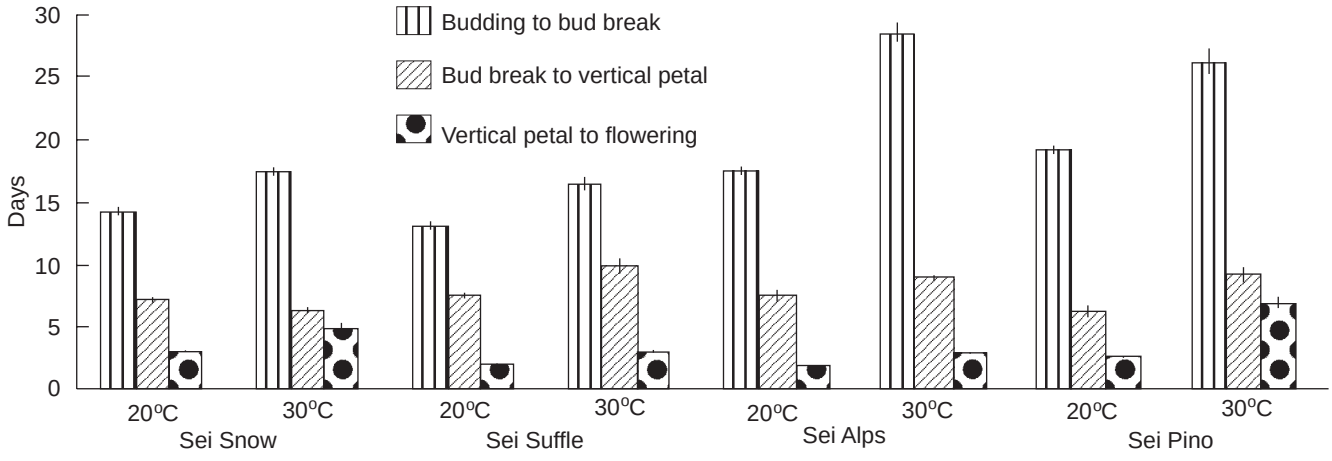

Fig. 3. Effects of temperature after budding on the days to flowering. 0 of the vertical axis denotes the budding day. Vertical bars represent SD.

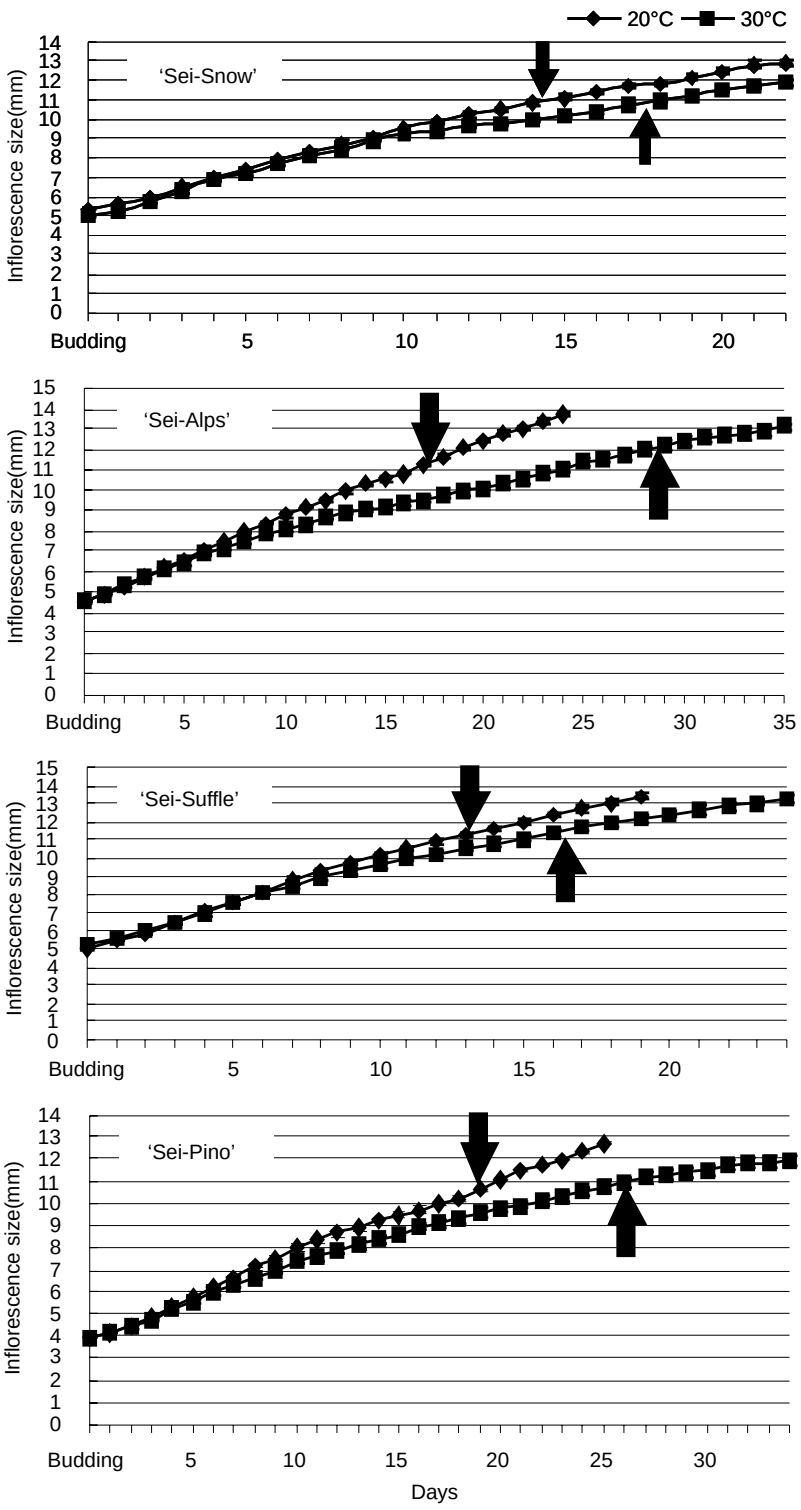

Fig. 4. Development situation of inflorescence from budding to vertical petals in the terminal flower bud. Arrows show the bud break period for each temperature.

treatments, except for the number of florets, were nearly equivalent to those of plants at 20°C. 'Sei-Maria' showed identical tendencies to those of 'Sei-Monako', but the days to flowering were slightly more in plants of the 15-day treatment. On the other hand, at 30°C, the days to budding were significantly more than those of other treatments in 'Sei-Maria'. In addition, the days to flowering at 30°C were many more than those of other treatments in both genotypes. No significant difference was found in the number of leaves, indicating that high temperatures had no effect on the transition from the vegetative phase to the reproductive phase. The inflorescence diameter was significantly smaller at 30°C in both genotypes. The number of disk florets increased in both genotypes when high temperatures were applied longer.

Genotypes difference in the development of inflorescence (Experiment III): All genotypes reached the budding stage in about 20 DASD, irrespective of flowering type SA and A (Table 3). On the other hand, the number of days to bud break varied from 29 days in 'Sei-Monako' and 'Chatoo' to 43 days in 'Sei-Alps'. 'Sei-Alps' and 'Sei-Liese' required more days to budding and showed more days to flowering. Diameters of inflorescences at bud break and flowering stage were significantly different depending on genotypes (Table 4). No constant relationship was observed in the diameter of inflorescence between the bud break and flowering stages.

Effects of high temperature after visible bud stage on flowering (Experiment IV): Plants grown at 30°C from budding to flowering showed delayed flowering compared with plants grown at 20°C. The flowering delay was remarkable in A genotypes (Fig. 3). The time required from budding to bud break at 30°C was much longer than that at 20°C in A genotypes, but the difference was small in SA genotypes. The time from bud break to the vertical petal stage and from vertical petal to flowering at 30°C was slightly longer than that at 20°C, except for 'Sei-Snow', for which the time from vertical petal to flowering at 30°C was longer than that at 20°C.

The time course of inflorescence development revealed a difference in the inflorescence size between at 20 and 30°C from 5 days after the budding stage in all genotypes. Differences between temperatures were small in SA genotypes and were large in A genotypes, in which the speed of inflorescence development slowed around 10 days after budding at 30°C. However, no big differences were apparent in the inflorescence diameter at the bud break stage in all genotypes. Flowering of SA genotypes at 30°C was almost identical to that at 20°C, but flowering at 30°C was particularly delayed in A genotypes.

Discussion

Effects of high temperature on chrysanthemum flowering have already been studied in relation to floral initiation (phase transition), flower-bud development, and other environmental factors (Cockshull, 1979; Cockshull and Kofranek, 1994; Karlsson *et al.*, 1989; Whealy *et al.*, 1987; Wilkins *et al.*, 1990). However, it remains unclear how the delay manifests itself in the processes of floral initiation and development in chrysanthemum. This study revealed that two independent phenomena occur in inflorescences under high temperature conditions: quantitative increase of florets and slow inflorescence development. Additionally, we emphasized the importance of the time required for development to a specific stage of inflorescence for flowering delay in chrysanthemum.

No difference was found in the sequence of floral initiation and development between the two genotypes at either 20 or 30°C in this study. The morphological changes in the process of floral development were almost

Table 2. Effects of high temperature during flower-bud initiation and development period on flowering

Cultivars	Treatments	Days to budding from the start of SD	Days to anthesis from the start of SD	Number of leaves	Diameter of inflorescence (mm)	Number of florets	
						Ray florets	Disk florets
'Sei-Monako'	20°C	20.7ab[z]	46.1a	19.1NS[y]	48.9b	27.5a	310.6a
	5 days	21.2ab	47.4a	18.1NS	49.8b	28.8a	316.3a
	10 days	20.1a	46.7a	17.7NS	49.4b	32.4b	386.7b
	15 days	21.9ab	48.8a	18.2NS	49.4b	32.9b	489.8c
	30°C	22.9b	60.5b	17.9NS	35.1a	33.8b	519.0c
'Sei-Maria'	20°C	20.8a	57.5a	23.2NS	60.7b	25.1NS	267.3ab
	5 days	21.4a	58.8ab	23.4NS	64.4b	25.6NS	258.1a
	10 days	21.1a	59.8ab	23.9NS	60.2b	23.3NS	262.6ab
	15 days	22.5a	61.8b	23.3NS	62.2b	25.4NS	287.2b
	30°C	25.6b	90.1c	23.3NS	35.9a	25.1NS	348.7c

z Different letters among treatments represent significant difference by Tukey's multiple range test ($P < 0.05$).
y NS: Not significant.

Table 3. Number of days from the start of SD to each development stage of inflorescence

Types	Cultivars	Days to budding from start of SD	Days to bud break from start of SD	Days to anthesis from start of SD
Summer-to- autumn flowering type	'Sei-Monako'	21.0ab[z]	29.0a	45.3ab
	'Sei-Snow'	19.6a	36.2b	46.4ab
	'Yellow-Shoes'	22.5b	34.0b	43.8a
	'Sei-Suffle'	19.3a	33.5b	45.5ab
Autumn flowering type	'Sei-Alps'	21.0ab	43.0c	51.8c
	'Sei-Liese'	19.4a	40.6c	50.6c
	'Chatoo'	20.8ab	29.0a	45.8ab
	'Sei-Pino'	19.2a	36.0b	48.0bc

Table 4. Diameter of inflorescence at different stages

Types	Cultivars	Diameter of inflorescence (mm)		
		Budding	Bud break	Flowering
Summer-to- autumn flowering type	'Sei-Monako'	5.23ab[z]	9.70ab	53.40bc
	'Sei-Snow'	5.24ab	11.24bc	41.72a
	'Yellow-Shoes'	5.93b	12.90cde	41.13a
	'Sei-Suffle'	5.48ab	13.10de	49.03b
Autumn flowering type	'Sei-Alps'	5.10a	14.37e	52.13bc
	'Sei-Liese'	5.42ab	14.48e	59.30c
	'Chatoo'	5.04a	8.76a	49.64b
	'Sei-Pino'	4.80a	12.20cd	38.52a

consistent with those of previous reports on floral development of chrysanthemums (Fukai *et al.*, 1997; Lee *et al.*, 2001; Okada, 1963; Yulian *et al.*, 1996; Zhang *et al.*, 1998). Present results showed that a morphological transition from a vegetative to reproductive shoot apex, *i.e.* dome formation, occurred during 5-10 DASD. Inflorescence development at 30°C was slower than that at 20°C, as described by Whealy *et al.* (1987). The period required from dome formation to completion of floret differentiation on the inflorescence was almost equal in both SA and A genotypes under identical temperature conditions. However, the number of days to flowering at 30°C in A genotype increased more than 30 days in comparison with the SA genotype. Results indicate that no direct relationship exists between flowering and completion of floret differentiation in inflorescence, suggesting that flowering delay is the result of high temperature effects on the latter developmental stages of the inflorescence.

Increased number of florets, especially disk florets, were observed in both SA and A genotypes at 30°C. Furthermore, increase was recognised when high temperatures were applied for only 5-15 days immediately after the start of SD. These facts indicate that the high temperature given in the early developmental stage of inflorescence determines the direction of differentiation in the inflorescence apex. In all cases, the increase of ray florets occurred even though a flowering delay did not take place, indicating that the increase of floret number and the delay of flowering under high temperature conditions are independent phenomena. Cockshull and Kofranek (1994) also described the increased floret number in chrysanthemum under high temperature conditions, but they did not recognize the independency of the increased flower number and delayed flowering. The reduced number of florets on the inflorescence or floral organs, particularly in petals, are recognised in many plants under high temperature conditions (Chimenti and Hall, 2001; Mito *et al.*, 1980). The reduced numbers of florets is inferred to have occurred because of faster growth under high-temperature conditions. In case of chrysanthemums, the increased number of florets can be attributed not only to the decreased development speed of inflorescence under high temperature conditions, but also some physiological changes in the inflorescence shoot apex.

The days to budding and flowering in both genotypes were almost equal for those grown at 20°C when high temperature was given only 5-15 DASD (Table 2). That fact implies that inhibition of inflorescence development in early stages that is caused by exposure to high temperature recovered rapidly after transferral to 20°C. These results indicate that the developmental speed of inflorescence is temperature dependent. In the same experiment, the number of leaves did not change among all temperature treatments. The high temperature given immediately after the start of SD did not greatly affect the phase transition from vegetative to reproductive. Observation by SEM, which showed that floral initiation occurred in the period of 5-10 DASD at 30°C, also supported this inference. Therefore, the delay of phase transition under high temperature conditions is very small even if it existed in genotypes used in this study. Nishio *et al.* (1988) reported no changes in the number of leaves in two genotypes of chrysanthemum when maintained at 27-30°C during the day time and at a range of 20-35°C night temperature in the first three weeks after start of SD. On the other hand, Wilkins *et al.* (1990) reported decreased leaf numbers from lower night temperatures when chrysanthemums were maintained at a minimum temperature of 21°C during the day and in a range of 13-21°C night temperatures in the first three weeks after starting SD. Cockshull and Kofranek (1994) also showed that high night temperatures of 32°C in the first 1-3 weeks after the start of SD increased the chrysanthemum leaf number. The differences of these results can be attributed to the fact that the phase transition from vegetative to reproductive phase is delayed under higher temperature conditions, but it is less delayed at night temperatures below 20°C (or mean daily temperature). Genotype differences in response to high temperature in terms of phase transition might also exist.

Inflorescence sizes at the budding stage were similar among genotypes used in this study when grown at 20°C, whereas differences in inflorescence size of genotype at the bud break stage were clear. The genotypes required a longer time to bud break at 20°C and required a longer time to flowering. In a genotypes, showing great delay of flowering under high temperature conditions, the time from budding to bud break stage was remarkably long at 30°C compared to that at 20°C (Fig. 3). The developmental speed of inflorescence in A genotypes at 30°C after the budding stage decreased considerably compared to those at 20°C, whereas the size of inflorescence at the bud break stage was not greatly different (Fig. 4). These results show that the inflorescence size at the bud break stage is genotype-dependent and that the time to reach this specific stage (size) is important to determine the flowering time. The time to reach the bud break stage was longer at 30°C, especially in A genotypes, showing the delay of flowering under high temperature conditions. The physiological explanation for such a phenomenon remains unclear. High photosynthetic capacity of SA genotypes under high temperature and high light intensity, as shown by Koyama *et al.* (2001), might be one reason for that difference. It can be concluded that high temperatures decreased the developmental speed of inflorescence in chrysanthemum after the budding stage. The time to reach the bud break stage was prolonged, engendering flowering delay.

Results of this study revealed that two independent events caused by high temperature occurred in the shoot apex of spray chrysanthemum under a short-day condition. First, the high temperatures decreased the floral development speed in inflorescence, thereby increasing the number of florets in both SA and A chrysanthemum genotypes. Secondly, as high temperatures decreased the developmental speed of inflorescence after budding stage, the time to reach the bud break stage was prolonged, thereby delaying flowering, especially in A chrysanthemum genotypes.

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