Meiosis and Pollen Fertility in Higo Chrysanthemum (*Dendranthema* × *grandiflorum* (Ramat.) Kitam.)

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Summary

To understand the cytogenetic behaviors and pollen resource potentialities, meiosis and pollen fertility were examined in the 16 cultivars of Higo chrysanthemum (*Dendranthema* × *grandiflorum* (Ramat.) Kitam.).

Bivalent formation was highly regular at metaphase I in the pollen mother cells of all the cultivars although univalents and quadrivalents were also sporadically distributed. Considerable abnormalities such as lagging chromosomes and chromosome bridges at telophase I and II, and unequal sizes and abnormal numbers of microspores at tetrad stage were observed in the succeeding stages of microsporogenesis in all the cultivars. Pollen fertility varied from 0.4 to 97.7% among the cultivars and they could be grouped into 3: high (71~100%), 8 cultivars; intermediate (31~70%), 5 cultivars; and, low (0~30%), 3 cultivars.

It is indicative from the above results that majority of the cultivars of Higo chrysanthemum are potential pollen resources for the improvement of modern chrysanthemums.

Introduction

Higo chrysanthemum (*Dendranthema* × *grandiflorum* (Ramat.) Kitam.), Higo-giku in Japanese, is a peculiar group of chrysanthemum cultivars which has been cultivated exclusively in Higo (the old name of Kumamoto Prefecture) for more than 200 years (Murayama, 1974). This group of chrysanthemum is in nature a bedding flower, and its techniques of arrangement and cultivation are unique (Ninaki, 1982). Nevertheless, the chances to cultivate and aesthetically appreciate these cultivars are limited to Kumamoto Prefecture despite continuous cultivation.

The cultivars of Higo chrysanthemum displayed variations on the size and color of the inflorescence, petal shape and chromosome number (Miyazaki et al., 1982). These cultivars are hexaploid, yet embrace aneuploids ($2n = 52 \sim 56$). Further, a high degree of polymorphisms were manifested in the isozymes of glutamate-oxaloacetate transaminase, phospho-gluco isomerase and peroxidase of these cultivars (Roxas et al., 1993).

Isozyme analysis is useful for the identification of the cultivars even at the early stages of the plant growth. In addition to the above studies, cytogenetic examinations are necessary to utilize these cultivars as breeding materials for modern chrysanthemums.

In the present study, chromosome pairing and the succeeding stages of microsporogenesis were examined to understand the cytogenetic behaviors of the cultivars of Higo chrysanthemum. Pollen fertility was also investigated in order to distinguish the cultivars with pollen resource potential to be used as a breeding material for the improvement of modern chrysanthemums.

Materials and Methods

Sixteen greenhouse-grown cultivars which represent the typical characteristics (size and color of inflorescences, petal shape, and chromosome number) of Higo chrysanthemum were selected from the 29 cultivars used in the previous study (Roxas, et al., 1993). At the early emergence of inflorescences immature tubular florets were used for the microscopic observations in metaphase I, telophase I, telophase II and tetrad stages of the

pollen mother cells (PMCs). Metaphase I was mainly observed with fresh anthers, and the anthers fixed with Carnoy's fluid or Newcomer's fluid (Sharma and Sharma, 1980) were used for additional analysis. At the early stage of flower blooming, the mature tubular florets were fixed with Carnoy's fluid and were used for the observation of the morphology and stainability of the pollen grains. Observation was made with a minimum of 500 pollen grains per capitulum in at least 3 capitula. PMCs and pollen grains were stained with 1% aceto-carmin, applying the smear method.

Results

Metaphase I

In the 16 cultivars examined, 6 kinds of chromosome configurations were observed: hexavalent, pentavalent, quadrivalent, trivalent, bivalent and univalent (Figs. 1-2, Table 1). A high frequency of bivalents (25.06~26.70/cell) and a low frequency of univalents (0.15~1.34/cell) and quadrivalents (0.13~0.49/cell) were observed in all the cultivars. Hexavalents (0~0.06/cell) and trivalents (0~0.06/cell) were rare, and pentavalents were very rare.

'Hatsu Shigure' and 'Mado No Yuki' showed a slightly lower frequency of bivalents and a higher frequency of quadrivalents among the cultivars. Although 'Shiranui' was also observed to have a slightly lower frequency of bivalents, this cultivar possessed 53 chromosomes. Univalents were comparatively higher in 'Tennyō No Mai', 'Kinyō', 'Mado No Yuki', 'Shiranui', 'Mine No Matsu' and 'Nowake'. All of these cultivars except 'Mado No Yuki' were aneuploid.

Telophase I

Normal PMCs which had 2 equal-sized nuclei but without lagging chromosome nor chromosome bridge ranged from 35.5 to 81.6% of the PMCs observed (Fig. 3, Table 2). 'Zuisei' and 'Beni Kosode' were of high percentage while 'Hatsu Shigure', 'Kuni No Hikari' and 'Tagoto No Tsuki' were of low percentage of normal PMCs. Abnormal PMCs with unequal sizes of nuclei ranged from 0.6 to 16.3% of the PMCs observed and were comparatively high in 'Kuni No Hikari' and 'Shiranui'. On the other hand, those with lagging chromosome ranged from 9.9 to 62.6% and were comparatively

high in 'Hatsu Shigure' and 'Tagoto No Tsuki' whereas low in 'Beni Kosode'. In addition, those with chromosome bridges were sporadically observed in some PMCs ranging from 0 to 5.5% and were comparatively high in 'Mine No Matsu'.

Telophase II

Normal PMCs which had regular number (4) and equal-sized nuclei but without lagging chromosome nor chromosome bridge ranged from 11.9 to 70.7% of the PMCs examined (Fig. 4, Table 3). These were high (70.7%) in 'Zuisei', whereas comparatively low (11.9~31.4%) in 'Hatsu Shigure', 'Kuni No Hikari', 'Shiranui', 'Tagoto No Tsuki', 'Mine No Matsu' and 'Nowake'.

Abnormal PMCs with irregular numbers of nuclei ranged from 0 to 6.4% of the PMCs observed and were comparatively high in 'Mine No Matsu' and 'Nowake'. Those with unequal sizes of nuclei ranged from 2.4 to 18.2% and were comparatively high in 'Inkunshi', 'Mado No Yuki' and 'Nowake'. On the other hand, those with lagging chromosomes ranged from 21.0 to 85.7% and were high in 'Hatsu Shigure', 'Kuni No Hikari', 'Shiranui', 'Tagoto No Tsuki' and 'Mine No Matsu'. In addition, those with chromosome bridges ranged from 0 to 5.3% and were comparatively high in 'Nogio'.

Tetrad

Although the number of microspores per PMC varied from 1 to 7, majority of the PMCs possessed 4 nuclei (normal number) ranging from 85.5 to 98.0% of the PMCs examined (Fig. 5, Table 4). The highest frequency of irregular number of microspores in a PMC was 3 in almost all the cultivars and PMCs with 3 microspores were highly detected in 'Hatsu Shigure' and 'Nowake'. Cultivars with the highest variation on the number of microspores in a PMC were 'Inkunshi' (2, 3, 4, 5, 6), 'Mine No Matsu' (2, 3, 4, 5, 6), 'Mado No Yuki' (2, 3, 4, 5, 7) and 'Nowake' (1, 3, 4, 5, 6) while 'Kuni No Hikari', 'Tagoto No Tsuki' and 'Takaragasa' obtained the lowest variation (3, 4).

At tetrad stage, PMCs which had 4 equal-sized microspores and without mini-microspore (Fig. 5) nor micronucleus ranged from 27.3 to 68.8% of the PMCs observed. A high frequency of normal tetrads were observed in 'Takaragasa' while low in 'Hatsu Shigure' and 'Shiranui'.

PMCs with mini-microspores ranged from 14.5

to 53.9% and were high in 'Tenny No Mai', 'Shiranui' and 'Mine No Matsu', while low in 'Chihiro No Umi'.

Pollen

The percentage of stained pollen grains varied from 0.4 to 97.7% among the cultivars and they could be grouped into 3: high (71~100%), 8 cultivars; intermediate (31~70%), 5 cultivars; and, low (0~30%), 3 cultivars (Figs. 6-8, Table 5). 'Chihiro No Umi', 'Takaragasa', 'Nogio', 'Zuisei' and 'Beni Kosode' exhibited more than 90% of pollen stainabilities. On the other hand, 'Hatsu Shigure' and 'Mado No Yuki' were observed to have

less than 10% of pollen stainabilities. The well-stained pollen grains were tricolporate (Fig. 6) which easily separated from each other, while unstained pollen grains were amorphous which clumped together (Fig. 8).

Discussion

Quadrivalents, bivalents and univalents were common among all the cultivars examined but the frequency of quadrivalents and univalents were relatively low. Univalent formation was comparatively high in 6 cultivars (5 were aneuploid), which seems to be related to their aneuploidy. However, bivalent formation was highly regular in all the

Table 1. Chromosome pairing in the pollen mother cells of Higo chrysanthemum.

Cultivar name	Chromosome number	Number of PMCs observed	Number of chromosome pairings ²					
			VI	V	IV	III	II	I
Chihiro No Umi	54	39	0	0	0-2 (0.30)	0	23-27 (26.31)	0-2 (0.15)
Chiyo No Kotobuki	52	39	0-1 (0.03)	0-1 (0.03)	0-1 (0.13)	0	22-27 (26.49)	0-2 (0.23)
	53							
	54							
Hatsu Shigure	54	41	0	0	0-2 (0.49)	0-1 (0.03)	23-27 (25.77)	0-4 (0.41)
Kuni No Hikari	54	46	0	0	0-1 (0.28)	0	24-27 (26.33)	0-2 (0.61)
Tenny No Mai	55	32	0-1 (0.03)	0	0-1 (0.13)	0-1 (0.06)	24-27 (26.44)	0-3 (1.25)
Inkunshi	54	30	0	0	0-1 (0.10)	0	24-27 (26.70)	0-2 (0.20)
Kinyo	55	32	0	0	0-2 (0.38)	0-1 (0.06)	23-27 (26.19)	0-1 (0.94)
Mado No Yuki	54	33	0	0	0-2 (0.42)	0	22-27 (25.64)	0-2 (1.03)
Shiranui	53	32	0-1 (0.03)	0	0-3 (0.31)	0-1 (0.03)	21-26 (25.06)	0-3 (1.34)
Tagoto No Tsuki	54	47	0	0	0-1 (0.26)	0-1 (0.02)	23-27 (26.08)	0-2 (0.74)
Takaragasa	54	53	0	0	0-4 (0.13)	0	19-27 (26.57)	0-6 (0.34)
Mine No Matsu	55	32	0	0	0-2 (0.25)	0-1 (0.03)	23-27 (26.31)	0-3 (1.28)
Nogio	54	32	0-1 (0.06)	0	0-2 (0.19)	0-1 (0.03)	21-27 (26.25)	0-2 (0.28)
Nowake	55	31	0	0	0-2 (0.19)	0-1 (0.03)	23-27 (26.55)	0-2 (1.03)
Zuisei	54	36	0-1 (0.06)	0	0-1 (0.19)	0	23-27 (26.31)	0-2 (0.44)
Beni Kosode	54	41	0	0	0-2 (0.22)	0-1 (0.03)	23-27 (26.34)	0-2 (0.37)

² Range (Mean) of the number of chromosome pairings per PMC are shown.

Figs. 1-2. Chromosome pairings at metaphase I in the PMCs of Higo chrysanthemum cultivars. Fig. 1. 'Chihiro No Umi'. 27 II. Fig. 2. 'Kinyo'. 1 IV + 25II + 1I. Arrows indicate a quadrivalent (IV) and a univalent (I). x ca. 1000.

Fig. 3. Chromosome bridges and lagging chromosomes at telophase I in the PMCs of Higo chrysanthemum 'Nowake'. Arrows indicate chromosome bridges (b) and lagging chromosomes (1). x ca. 500.

Fig. 4. Chromosome bridges and lagging chromosomes at telophase II in the PMCs of Higo chrysanthemum 'Shiranui'. Arrows indicate chromosome bridges (b) and lagging chromosomes (1). x ca. 500.

Fig. 5. Normal PMC (right) and abnormal PMC with 2 mini-microspores (left) at tetrad stage of Higo chrysanthemum 'Mine No Matsu'. Arrows indicate mini-microspores. x ca. 1000.

Figs. 6-8. Pollen grains of Higo chrysanthemum cultivars. Fig. 6. 'Zuisei'. All pollen grains show high stainability. Fig. 7. 'Kuni No Hikari'. Four pollen grains display high stainability while the remaining show low stainability. Three well-stained pollen grains are larger than others. Fig. 8. 'Mado No Yuki'. All pollen grains are without protoplasm. x ca. 200.

Table 2. Percentages of normal and abnormal PMCs at Telophase I in Higo chrysanthemum cultivars.

Cultivar name	Number of PMCs observed	Normal PMCs (%)	Abnormal PMCs (%)		
			Unequal sizes of nuclei	Lagging chromosomes	Chromosome bridges
Chihiro No Umi	367	54.8	11.2	29.8	4.4
Chiyo No Kotobuki	279	68.8	5.7	25.4	0
Hatsu Shigure	155	35.5	0.6	62.6	1.3
Kuni No Hikari	300	40.3	14.7	44.0	1.0
Tenno No Mai	316	52.2	1.6	42.4	3.8
Inkunshi	448	72.1	3.6	21.7	2.7
Kinyo	336	52.4	10.4	34.2	3.0
Mado No Yuki	327	62.7	9.5	26.9	0.9
Shiranui	584	55.3	16.3	27.6	0.9
Tagoto No Tsuki	310	36.5	11.0	52.3	0.3
Takaragasa	357	72.5	3.1	23.2	1.1
Mine No Matsu	310	60.0	2.6	31.9	5.5
Nogio	366	69.4	4.9	24.3	1.4
Nowake	392	52.0	11.5	33.2	3.3
Zuisei	537	78.6	2.8	17.7	0.9
Beni Kosode	332	81.6	6.6	9.9	1.8

Table 3. Percentages of normal and abnormal PMCs at Telophase II in Higo chrysanthemum cultivars.

Cultivar name	Number of PMCs observed	Normal PMCs [*] (%)	Abnormal PMCs (%)			
			Irregular numbers of nuclei	Unequal sizes of nuclei	Lagging chromosomes	Chromosome bridges
Chihiro No Umi	262	63.0	0.4	5.3	31.3	0
Chiyo No Kotobuki	147	49.0	2.7	13.6	34.7	0
Hatsu Shigure	126	11.9	0	2.4	85.7	0
Kuni No Hikari	240	15.0	0	4.2	80.8	0
Tenno No Mai	186	53.8	1.6	8.1	35.5	1.1
Inkunshi	109	58.7	0.9	16.5	23.9	0
Kinyo	115	61.0	0	12.2	25.2	1.7
Mado No Yuki	143	49.0	1.4	17.0	32.2	0.7
Shiranui	442	34.4	1.1	14.0	50.0	0.5
Tagoto No Tsuki	235	24.3	0	8.9	66.4	0.4
Takaragasa	174	62.6	0	3.4	32.2	1.7
Mine No Matsu	156	31.4	5.1	10.3	52.6	0.6
Nogio	190	51.1	1.6	12.6	29.4	5.3
Nowake	110	30.9	6.4	18.2	40.9	3.6
Zuisei	229	70.7	1.3	7.0	21.0	0
Beni Kosode	243	54.7	2.9	6.2	35.8	0.4

^{*} PMCs with regular number (4) and equal-sized nuclei but without lagging chromosome nor chromosome bridge.

cultivars. This illustrates that Higo chrysanthemum cultivars behave more like amphiploids. In chrysanthemums, diploid-like meiosis were also observed in various garden cultivars [6x] (Dow-

rick, 1953; Endo and Kagawa, 1968; Nazeer and Khoshoo, 1985; Shimotomai, 1932), in polyploid taxa [4x, 6x, 8x, 10x] (Dowrick, 1952; Watanabe, 1977, 1981a, b, c) and in colchipooids [4x, 12x]

Table 4. Number of microspores in PMCs, percentages of normal and abnormal PMCs with mini-microspores at tetrad stage in Higo chrysanthemum cultivars.

Cultivar name	Number of PMCs observed	Percentage of PMCs							Normal tetrad (%)	With mini-microspores ^z (%)
		1	2	No. of microspores/PMC				7		
Chihiro No Umi	470	0	0.6	7.0	91.4	1.1	0	0	63.2	14.5
Chiyo No Kotobuki	170	0	0	5.3	94.1	0.6	0	0	52.9	35.9
Hatsu Shigure	169	0	0	10.7	87.7	1.8	0	0	31.9	33.1
Kuni No Hikari	296	0	0	2.0	98.0	0	0	0	46.0	23.0
Tenno No Mai	229	0	0.4	4.9	94.7	0	0	0	41.9	50.7
Inkunshi	348	0	0.3	2.9	95.2	1.4	0.3	0	55.5	34.2
Kinyo	193	0	2.6	1.5	94.5	1.0	0	0	59.1	35.8
Mado No Yuki	202	0	0.5	4.0	92.6	2.5	0	0.5	54.0	32.9
Shiranui	165	0	0	3.6	94.6	1.8	0	0	27.3	53.9
Tagoto No Tsuki	312	0	0	3.5	96.5	0	0	0	50.0	23.1
Takaragasa	154	0	0	3.9	96.0	0	0	0	68.8	26.0
Mine No Matsu	338	0	2.0	4.5	86.6	3.0	3.9	0	39.6	49.7
Nogio	350	0	0	2.0	97.2	0.8	0	0	52.8	34.8
Nowake	213	1.0	0	11.7	85.5	0.5	1.3	0	37.6	26.8
Zuisei	204	0	0	4.0	91.2	4.4	0.5	0	37.8	45.1
Beni Kosode	220	0	0	4.1	95.0	0.5	0.5	0	61.4	26.4

^z A mini-microspore possesses a minute nucleus formed by one or a few chromosomes and enclosed in a little cytoplasm.

Table 5. Pollen stainability in Higo chrysanthemum cultivars.

Cultivar name	Percentage of stained pollen grains ^z
Chihiro No Umi	91.1±1.4
Chiyo No Kotobuki	88.4±0.7
Hatsu Shigure	0.4±0.3
Kuni No Hikari	24.7±1.2
Tenno No Mai	69.3±4.8
Inkunshi	58.3±7.9
Kinyo	59.7±1.8
Mado No Yuki	6.6±2.4
Shiranui	78.0±3.3
Tagoto No Tsuki	42.2±3.4
Takaragasa	97.7±0.5
Mine No Matsu	85.4±1.6
Nogio	94.6±0.7
Nowake	58.7±6.2
Zuisei	95.1±1.6
Beni Kosode	92.7±0.7

^z Mean±standard error.

(Watanabe, 1983). There were multivalent suppressor systems in polyploid chrysanthemums and the degree of bivalent formation did not always agree with the degree of genic diploidization

(Watanabe, 1983). However, the complex meiosis in the PMCs of Higo chrysanthemum seems to exemplify its long history of seed or vegetative propagations and crossings. From the high frequency of bivalents at metaphase I in all the PMCs of all the cultivars, it is assumed that they hold a certain degree of pollen fertility. Nevertheless, a variation in pollen fertility among the cultivars is presumed since multiformity of univalents and multivalents were also observed.

Shimotomai (1932) and Endo and Kagawa (1968) detected abnormalities including lagging chromosomes, chromosome bridges and irregular number of microspores in the PMCs at the succeeding stages of microsporogenesis in garden chrysanthemums. Similar abnormalities were also observed in Higo chrysanthemum cultivars. In most of the cultivars, higher percentages of abnormal PMCs with lagging chromosomes were observed during telophase II (21.0~85.7%) than telophase I (9.9~62.6%). Similarly, in an induced autotetraploid of *C. coronarium* Linn. (Gupta and Gill, 1985), 6.7% of lagging chromosomes were observed at anaphase I/telophase I and 13.2% in anaphase II/telophase II. At tetrad stage, in an induced autotetraploid *C. coronarium* Linn. (Gupta

and Gill, 1985), abnormalities like polyads (7.3%) and tetrads with micropollens (14.7%) were encountered. In the case of Higo chrysanthemum, cultivars possessed higher percentage of PMCs with abnormal number of microspores and microspores with mini-microspores. Therefore, the irregular meiosis presumably led to the abnormalities in telophase I, telophase II and tetrad stages consecutively, and consequent genetic disharmony or unbalance may also disturb normal physiological processes both in induced autotetraploid and hexaploid chrysanthemums. These abnormalities are also possible to cause complex gene composition of the pollen and low pollen fertility.

Despite considerable abnormalities in meiosis and the succeeding stages of microsporogenesis, majority of the cultivars of Higo chrysanthemum exhibited high pollen fertility. On the other hand, there were 3 exceptional cultivars which carried the poorest pollen fertility. In this case, aneuploidy had not affected the pollen fertility of these cultivars. A survey conducted in the United States of America (Mulford, 1937), Japan (Kawase and Tsukamoto, 1977), and India (Nazeer and Khoshoo, 1985) revealed that the pollen fertility of garden chrysanthemum cultivars of these respective countries were 11.7~100.0%, 30.3~95.9%, and 15.6~95.6%. Variation in pollen fertility was also observed within the limits of 0.1~96.8% for edible and 3.8~97.2% for garnish chrysanthemums (Endo and Inada, 1990). In the same study, variation in pollen fertility was frequently dependent on season or individual difference of plants within the same cultivar or among the cultivars. Genic, cytoplasmic factors or both seem to cause the considerable variations of pollen fertility observed in various garden chrysanthemums above mentioned.

In this study, the cultivars with different sizes, colors and petal shapes of inflorescences and different chromosome numbers were examined and the results showed that the aforementioned characters has no relationship with the pollen fertility of Higo chrysanthemum.

From the above results, it is indicative that majority of the cultivars of Higo chrysanthemum are potential pollen resources for the improvement of modern chrysanthemums. Future studies on the pollen germination, seed fertility, and self and cross compatibilities in Higo chrysanthemum cultivars will further be explored.

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肥後ギクの減数分裂および花粉稔性

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摘 要

肥後ギクの細胞遺伝学的行動を明らかにし、交配用の花粉源としての能力を検討するために、16品種を供試して減数分裂および花粉稔性を調査した。

すべての品種の花粉母細胞の第一分裂中期において大部分の染色体は二価染色体を形成した。しかし、少数の一価および四価染色体の形成も観察された。また、すべての品種の第一分裂および第二分裂の終期において遅滞染色体および染色体橋が、四分子期において大

きさや数が異常な小胞子が観察された。花粉稔性は品種間差が大きく、0.4~97.7%の範囲で変異し、供試品種は高稔性(71~100%)の8品種、中稔性(31~70%)の5品種および低稔性(0~30%)の3品種に分けられた。

以上の結果から、肥後ギクの大部分の品種はキクの育種のための花粉親として利用できると考えられる。