Cytogenetic Studies on the Origin of *Camellia vernalis*

I. On the Meiotic Chromosomes in Some Related *Camellia* Forms in Hirado Island

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Summary

In Hirado island, which is situated at the north-western part of Kyushu in Japan, both species of *C. japonica* and *C. sasanqua* are distributed together. Recently, certain new forms were found there by Kumazawa and Oda (21), suggesting that some of them could be regarded as varieties of *C. vernalis* originating in Hirado as natural hybrids between *C. sasanqua* and *C. japonica*. In order to approve such a consideration, the authors carried out morphological and cytological surveys in *C. vernalis* comparing it with *C. sasanqua* and with *C. japonica*.

As a result, the authors could recognize one tetraploid and two triploid forms originating in Hirado. The tetraploid form was considered to be the primary hybrid between *C. sasanqua* (hexaploid) and *C. japonica* (diploid). One triploid form was considered to be the secondary hybrid between the tetraploid variety and *C. japonica*, and the other triploid one was supposed to be an auto-triploid form of *C. japonica*.

Introduction

The first taxonomic description of *C. japonica* var. *vernalis* was done by Makino in 1905 (24) using the cultivated variety 'Ginryu'. In 1915, he also came to regard it as an intermediate hybrid species, *C. vernalis* (Haru-sasanqua), raised between the two parental species, *C. sasanqua* and *C. japonica*, because characteristics such as leaf size and flowering time of 'Ginryu' took a somewhat intermediate position relative to the above two species (25). Thereafter, about thirty varieties regarded as those of *C. vernalis* had been discovered in Japan by Kirino (13, 14) and Hakoda *et al.* (8). Many varieties regarded as *C. vernalis* had already appeared at the Edo-period (1603~1868) in Japan, and some old varieties were named after the local towns in Kyushu, for example; 'Hirado', 'Kokaji' and 'Koisahaya' (8). The northernmost geographic distribution of wild *C. sasanqua* is limited to the northern part of Kyushu where *C. japonica* also grows wild with overlapping of flowering

time, so that one of the original localities of *C. vernalis* should be duly pointed out to be in Kyushu.

On the other hand, cytogenetic studies on chromosome behaviours in *Camellia* have made an advance recently (1, 2, 6, 7, 10, 11, 12, 15, 16, 17, 18, 19, 20, 22, 23, 26, 30) and *C. vernalis* was discovered to include two groups of forms, one with 60 and the other with 45 chromosomes, both of which showed the intermediate numbers composed of *C. japonica* ($2n=30$) and *C. sasanqua* ($2n=90$). From cytological and morphological standpoints, Tashiro and Iwasa (30) considered *C. vernalis* as a hybrid species raised between *C. sasanqua* and *C. japonica*, and assumed, moreover, that the tetraploid group would belong to the primary hybrid and the triploid group to the secondary one (11).

Recently, Kumazawa and Oda (21) have been surveying on the distribution of *Camellia* varieties in Hirado and found some original stock plants which may be reckoned as *C. vernalis*. From a historical point of view, they suggested that those stock plants of *C. vernalis* had originated through the natural crosses between wild types of *C. sasanqua* and *C. japonica*, and certain red flowering plants

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of *C. sasanqua* had also originated in Hirado from *C. vernalis*. The earlier flowering characteristic and higher chromosome number of *C. sasanqua* could be assumed to be the cause of genetic isolation from *C. japonica*. Moreover, according to Parks *et al.* (29), closely related species with the overlapping distributions are more prone to have been provided with much stronger barriers against inter-specific hybridization than the allopatric species of similar relationship. In fact, the crossings between both species had been tried out by many workers such as Hilsman (9), Parks *et al.* (29) and Ackerman (1), but, except for certain special cases, there usually occurred certain difficulties in obtaining hybrid individuals between them.

If many stock plants, which are considered to have been related with the creation of some forms of *C. vernalis*, had originated in Hirado spontaneously as was suggested by Kumazawa and Oda (21), they will duly suffice to give us an interesting idea not only about the origin of *C. vernalis* but also concerning the evolution of the genus *Camellia*. The authors have investigated the chromosome numbers and the meiotic behaviours of chromosomes in PMCs with certain stock plants of *C. vernalis* which were considered to have originated exclusively in Hirado and with their parental stock plants distributed in the same locality.

Materials and Methods

All the materials used for the study of mi-

Table 1. List of *Camellia* in Hirado.

Species	Variety	G. B.*	H.**
<i>C. japonica</i>	Chinshin	45	4
	Hirado-oyabu	58	10
<i>C. sasanqua</i>	H-5	37	3
<i>C. vernalis</i>	Gaisen	140	8
	Sayohime	55	6

* Girth at base (cm).

** Height of tree (m).

crosporogenesis had been collected in Hirado. Those stock plants including *C. sasanqua*, *C. japonica* and *C. vernalis* are listed in Table 1. In Hirado, the authors were able to recognize not only 4 varietal forms of *C. vernalis* introduced from other districts of Japan but also 5 varietal forms originating in Hirado and their offspring populations.

Flower-buds collected were fixed and preserved with Newcomer's solution (27). Smear preparations of meristematic anthers were practiced in 1% aceto-carmin. The chromosome pairing behaviours at diakinesis and at early first metaphase of meiosis were observed. The meiotic data were based on the detailed observations of the chromosome behaviours in PMCs.

Results and Discussion

As reported by many workers (5, 6, 7, 11, 15, 16, 17, 22, 23, 26, 30), the wild forms of *C. japonica* in Hirado, excepting one stock plant, were also of diploid nature ($2n=30$) and in their meiotic cells fifteen bivalent chromosomes were usually observed. In the stock

Table 2. Characteristics of certain species in genus *Camellia* in Hirado.

	<i>C. japonica</i>	<i>C. japonica</i>	<i>C. vernalis</i>	<i>C. vernalis</i>	<i>C. sasanqua</i>
Variety name	wild type	Hirado-oyabu	Sayohime	Gaisen	wild type
Somatic chromosomes (2n)	30	45	45	60	90
Flower color	red	red	red	red	white
Flower form	single	single	single	single	single
Stamen form	regular	regular	regular	spreading	spreading
Hairs on ovary	glabrous	glabrous	pubescent	pubescent	pubescent
Leaf size (cm ²)	19.58	38.86	9.76	9.20	7.86
Hairs on petiole	glabrous	glabrous	pubescent	pubescent	pubescent
Dots* (/cm ²)	84.58	41.56	60.86	32.83	0
Pollen fertility	99.4 (528)**	39.9 (1,031)	11.7 (614)	84.7 (1,238)	88.7 (791)
Seed set-ability	high	none	none	low	high
Blooming period	Mar.-Apr.	Mar.-Apr.	Nov.-Apr.	Nov.-Mar.	Oct.-Nov.

* Number of brown dots on the under surface of leaves.

** Number of pollen grains observed.

Table 3. Chromosome pairings at meiotic division in PMCs of *C. japonica* 'Chinshin'.

Configurations	Frequency of PMCs (%)		Total (%)
	Diakinesis	Metaphase-1	
15 _{II}	119 (99.2)	50 (100)	169 (99.4)
14 _{II} +2 _I	1 (0.8)	1 (0)	1 (0.6)
Total	120 (100)	50 (100)	170 (100)

Table 4. Chromosome pairings at meiotic division in PMCs of *C. sasanqua*, stock number 'H-5'.

Configurations	Frequency of PMCs (%)		Total (%)
	Diakinesis	Metaphase-1	
45 _{II}	6 (85.7)	13 (92.9)	19 (90.5)
44 _{II} +2 _I	1 (14.3)	1 (7.1)	2 (9.5)
Total	7 (100)	14 (100)	21 (100)

plant 'Chinshin' of *C. japonica* originated in Hirado, the pairing behaviour of meiotic chromosomes was also found to be quite normal ($2n=15_{II}$) at both stages of diakinesis and metaphase-1 (Table 3, Fig. 1). The pollen fertility of these plants was very high and the seed set ability was relatively high (Table 2).

The data concerning chromosome associations of *C. sasanqua* (stock number 'H-5') at both stages of diakinesis and metaphase-1 in PMCs are given in Table 4. Though this stock plant was not taken as a real wild type of *C. sasanqua*, as shown in Fig. 2, 45 bivalent chromosomes were recognized at both stages of diakinesis and metaphase-1 of meiosis in this plant. The chromosome numbers of certain cultivated forms of *C. sasanqua* have hitherto been reported to be $2n=75$, 90, 105 and 120 by Ito *et al.* (10) and by Kondo (17). But most of the wild forms in Japan have been considered, in turn, to have exclusively 90 chromosomes in somatic cells. Therefore, so far as this form ($2n=90$) is concerned, *C. sasanqua* may be well assumed to be an allo-hexaploid form consisting of three genomes though it is rather difficult to judge from this result only how these genomes are different from each other. Moreover, as reported by Kondo (15, 18), *C. sasanqua* might be a segmental allo-hexaploid in which a large number of homologous segments were distributed throughout the genomes.

Several new stock plants regarded as *C. vernalis* were discovered in Hirado by Kumazawa and Oda (21). Among these plants, a

Table 5. Chromosome pairings at meiotic division in PMCs of *C. vernalis* 'Gaisen'.

Configurations	Frequency of PMCs (%)		Total (%)
	Diakinesis	Metaphase-1	
30 _{II}	37 (75.5)	8 (61.5)	45 (72.6)
29 _{II} +2 _I	11 (22.4)	4 (30.8)	15 (24.2)
28 _{II} +4 _I	1 (2.0)	1 (7.7)	2 (3.2)
Total	49 (100)	13 (100)	62 (100)

certain stock plant named 'Gaisen' was found to be tetraploid. The general tendency of configuration of 'Gaisen' at diakinesis and metaphase-1 of meiosis in PMCs was 30_{II}, and some univalent chromosomes were observed (Table 5, Fig. 3). As the fertility of this stock plant was rather high, some seedlings from this plant were able to be gained and to keep alive in a vigorous state. American research workers of *Camellia* (28) regarded tetraploid varieties as *C. hiemalis*, but in Japan tetraploid varieties such as 'Egao', 'Umegaka' and others were regarded as *C. vernalis*. In the present paper, the authors define that *C. vernalis* is a species of hybrid origin between *C. sasanqua* and *C. japonica*, including not only triploid species but also tetraploid species. It may be assumed from the following facts that 'Gaisen' is a primary hybrid raised between *C. sasanqua* and *C. japonica* in Hirado, viz.; 1) Some morphological characteristics of 'Gaisen' were intermediate between *C. sasanqua* and *C. japonica*; 2) One of the stock trees of 'Gaisen' in Hirado was considered to be the oldest tree of *C. vernalis* in Japan, being about 400 years old; 3) In Hirado, the authors were able to find a number of flowers of *C. japonica* in late November when *C. sasanqua* were still blooming, so that it had been considered that the procedures of primary hybridization between them had been done there; 4) In an oldest book titled 'Chika-Zufu', the old cultivated variety 'Hirado-sasanqua' which could be regarded as *C. vernalis* was described; 5) Furthermore, judging from the chromosome number, 'Gaisen' ($2n=60$) was considered to be a primary hybrid raised between *C. sasanqua* ($2n=90$) and *C. japonica* ($2n=30$).

Triploid plants of two different species were also discovered in Hirado. One was named 'Sayohime' which showed some intermediate

Figs. 1~6. Meiotic chromosomes in PMCs of *Camellia* ($\times 600$). a : by microphotography; b : by drawing
 Fig. 1. *C. japonica* 'Chinshin' at early metaphase-1, $2n=15_{II}$.
 Fig. 2. *C. sasanqua* stock number 'H-5' at early metaphase-1, $2n=45_{II}$.
 Fig. 3. *C. vernalis* 'Gaisen' at diakinesis, $2n=30_{II}$.
 Fig. 4. *C. vernalis* 'Sayohime' at diakinesis, $2n=17_{II}+11_I$.
 Fig. 5. *C. vernalis* 'Sayohime' at anaphase-1, 13 lagging chromosomes are observed.
 Fig. 6. *C. japonica* 'Hirado-ōyabu' at diakinesis, $2n=9_{III}+6_{II}+6_I$.

Table 6. Chromosome pairings at meiotic division in PMCs of *C. vernalis* 'Sayohime'.

Configurations	Frequency of PMCs (%)		Total (%)
	Diakinesis	Metaphase-1	
$1_{III}+16_{II}+10_I$	0 (0.0)	1 (5.9)	1 (3.4)
$1_{III}+14_{II}+14_I$	2 (16.7)	0 (0.0)	2 (6.9)
$1_{III}+11_{II}+20_I$	0 (0.0)	1 (5.9)	1 (3.4)
$19_{II}+7_I$	0 (0.0)	1 (5.9)	1 (3.4)
$18_{II}+9_I$	1 (8.3)	1 (5.9)	2 (6.9)
$17_{II}+11_I$	0 (0.0)	2 (11.8)	2 (6.9)
$16_{II}+13_I$	3 (25.0)	5 (29.4)	8 (27.6)
$15_{II}+15_I$	5 (41.7)	1 (5.9)	6 (20.7)
$14_{II}+17_I$	1 (8.3)	4 (23.5)	5 (17.2)
$13_{II}+19_I$	0 (0.0)	1 (5.9)	1 (3.4)
Total	12 (100)	17 (100)	29 (100)

Table 7. Chromosome pairings at meiotic division in PMCs of *C. japonica* 'Hirado-ōyabu'.

Configurations	Frequency of PMCs (%)		Total (%)
	Diakinesis	Metaphase-1	
$1_{IV}+13_{III}+1_{II}$	0 (0.0)	1 (5.6)	1 (4.5)
$14_{III}+3_I$	0 (0.0)	1 (5.6)	1 (4.5)
$13_{III}+3_{II}$	1 (25.0)	1 (5.6)	2 (9.1)
$13_{III}+2_{II}+2_I$	0 (0.0)	4 (22.2)	4 (18.2)
$12_{III}+13_I+3_I$	1 (25.0)	0 (0.0)	1 (4.5)
$11_{III}+5_{II}+2_I$	0 (0.0)	1 (5.6)	1 (4.5)
$11_{III}+4_{II}+4_I$	0 (0.0)	3 (16.7)	3 (13.6)
$11_{III}+3_{II}+6_I$	1 (25.0)	0 (0.0)	1 (4.5)
$10_{III}+5_{II}+5_I$	0 (0.0)	4 (22.2)	4 (18.2)
$9_{III}+7_{II}+4_I$	0 (0.0)	1 (5.6)	1 (4.5)
$9_{III}+6_{II}+6_I$	1 (25.0)	0 (0.0)	1 (4.5)
$8_{III}+8_{II}+5_I$	0 (0.0)	1 (5.6)	1 (4.5)
$8_{III}+7_{II}+7_I$	0 (0.0)	1 (5.6)	1 (4.5)
Total	4 (100)	18 (100)	22 (100)

characteristics between 'Gaisen' (*C. vernalis*) and a certain wild form of *C. japonica*. The other one was *C. japonica* 'Hirado-ōyabu' named by Kumazawa which had larger leaves and flowers than the typical *C. japonica*. The

comparative study of chromosome pairings at meiosis revealed a significant difference between these two triploid plants. In the for-

Table 8. Average configurations at meiotic division in PMCs of different species of genus *Camellia* in Hirado.

Species	Variety	2n	Configurations	PMCs*
<i>C. japonica</i>	Chinshin	30	14.99 _{II} + 0.01 _I	170
	Hirado-oyabu	45	0.05 _{IV} + 11.18 _{III} + 3.91 _{II} + 3.45 _I	22
<i>C. vernalis</i>	Sayohime	45	0.14 _{III} + 15.34 _{II} + 13.90 _I	29
	Gaisen	60	29.69 _{II} + 0.61 _I	62
<i>C. sasanqua</i>	H-5	90	44.90 _{II} + 0.19 _I	21

* Number of PMCs observed.

mer, considerably many univalent chromosomes were observed at meiosis (Table 6, Fig. 4) and the most common configuration at diakinesis in PMCs was 15_{II} + 15_I. Thus, 'Sayohime' was assumed to be an allo-triploid consisting of a pair of similar but somewhat different genomes. Judging from the number of chromosomes and the morphological characteristics of the plant, it was considered that 'Sayohime' was a secondary hybrid between *C. vernalis* 'Gaisen' and a wild type of *C. japonica* in Hirado. So, it was considered that 'Sayohime' was understood to be a form belonging to the triploid group of *C. vernalis*. At stages of anaphase-1 and telophase-1, some laggards and chromatid bridges were observed (Fig. 5), and also this stock plant showed high pollen sterility, never obtaining any seed. Conversely, 'Hirado-Ōyabu' displayed more than eight trivalent formation (Table 7, Fig. 6) at diakinesis and metaphase-1 of meiosis in PMCs, and the pollen fertility was rather high (39.9%). From this data, 'Hirado-ōyabu' was considered to be an autotriploid of *C. japonica*. In Hirado, no tetraploid varieties have been met with so far in *C. japonica*, so that the origin of this triploid *C. japonica* will presumably be traceable to the rare conjugation of a diploid gamete with an ordinary haploid one (6, 7).

The average configurations in PMCs of *Camellia* plants observed in this study are given in Table 8. It may be assumed that one pair of genomes of *C. sasanqua* was not so different from that of *C. japonica*, because the

configuration in PMCs of 'Gaisen', which was considered to be a primary hybrid between them from a viewpoint of characteristics and chromosome number, was composed of almost bivalents, and the configuration of 'Sayohime', a back cross hybrid with *C. japonica*, was composed of nearly the same number of bivalents and univalents. According to Kondo's reports (15, 19), in eight hybrid combinations of *Camellia* raised between diploid and hexaploid species, thirty bivalents were observed as the most common configuration at metaphase-1 and he supposed that hexaploid *C. sasanqua* would carry one genome like that of *C. japonica*. If the genome of *C. japonica* is presupposed as AA and that of *C. sasanqua* as A'A'BBB'B', the primary hybrid between them will have the genome constitution of AA'BB' and the back cross hybrid with *C. japonica* will have that of AAB-AA'B'. On the other hand, as *C. vernalis* 'Gaisen' displayed 30_{II} and 'Sayohime' displayed 15_{II} + 15_I, the genome constitutions of these cultivated varieties could be presumed as AABB and AAB respectively. Thus, *C. vernalis* 'Gaisen' will be a primary hybrid between *C. sasanqua* and *C. japonica*, and 'Sayohime' will be a secondary hybrid between *C. vernalis* 'Gaisen' and *C. japonica*. Origin or synthetic processes of these *C. vernalis* formulated from morphological and cytological viewpoints are reproduced in Fig. 7 as a schematic diagram.

In horticultural varieties regarded as *C. vernalis*, there are a number of triploid varieties such as 'Ginryu', 'Shokko-nishiki', 'Kyo-ni-

Fig. 7. Schematic diagram of probable origin of *C. vernalis* in Hirado.

shiki', 'Yamato-nishiki', 'Kamakura-shibori', 'Hisatomi' (unpublished) and so on. Recently, the authors have found some tetraploid cultivars allied to 'Gaisen' such as 'Showano-kagayaki', 'Yōkihi' and others. But in the other districts of Japan except Hirado, interrelationships between triploid and tetraploid species of *C. vernalis* have not yet been so clear.

Most varieties of *C. vernalis* have certain noticeable characteristics and they are duly expected to show much wider variations. But until now, no new artificial forms of *C. vernalis* have yet been raised, because it is not easy to breed up hybrid individuals between *C. sasanqua* and *C. japonica*, and also triploid *C. vernalis* has a rather rare seed set. The cultivated variety 'Gaisen' showed, however, rather high cross-compatibility with *C. sasanqua* and *C. japonica* (unpublished) and the flowering time of 'Gaisen' occurs during the period from November through March, so that it will become rather easy to cross with not only *C. sasanqua* but also with *C. japonica*. Furthermore, if the cultivated variety 'Gaisen' is a primary hybrid between *C. sasanqua* and *C. japonica* as is presumed in the present paper, its offsprings will be considered to be the segregating generation. Thus, 'Gaisen' will become an important variety as the seed parent for raising new forms of *C. vernalis*. The authors have been making further studies to make clearer the origin of *C. vernalis* using a large number of artificial cross combinations of *Camellia* forms.

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ハルサザンカの起原に関する細胞遺伝学的研究 (第1報)

平戸における数種ツバキ属植物の減数分裂染色体について

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摘 要

九州の北西部に位置する平戸島には、ヤブツバキとサザンカが野生的に共存しており、最近、熊澤及び小田(21)によって、それらの間の自然雑種と見られる数株が見出された。これらはいずれもハルサザンカの範ちゅうに入れられるべき諸形質を示している。著者らは、それらと同時に見出されたツバキの同質倍数体と考えられる株とともに、その成立過程を解明するため、形態的、また細胞遺伝学的調査を行った。

その結果、ツバキ属の倍数系列から見て4倍体1株と

3倍体2株を明らかにした。4倍体はサザンカ(6x)とヤブツバキ(2x)との間の一次雑種とみなされ、3倍体株のうち1株は、前記4倍体ハルサザンカとヤブツバキとの交雑に起因する2次雑種と考えられ、他の1株はヤブツバキの同質3倍体であった。それらは熊澤及び小田によって、それぞれ‘凱旋(がいせん)’、‘佐用媛(さよひめ)’及び‘平戸大藪(ひらどおおやぶ)’と命名されている。