Cytological Studies in Cultivated Species of *Camellia*

I. Diploid Species and their Hybrids¹⁾

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The diploid species and cultivars of *Camellia* studied showed complete and normal chromosome pairing at metaphase I in meiosis. Thirteen F₁ hybrid combinations between diploid species of *Camellia* showed similar patterns of meiotic chromosome configurations and chiasma frequencies at metaphase I. These hybrid combinations showed a single chromosome configuration of 15_{II}. In these hybrid combinations the chiasma frequencies deviated only slight from those of their parents. Metaphase chromosome pairing in meiosis I in hybrids of *Camellia* was not sufficient to assign distinct genome formulas for the properties of different chromosome sets in various species.

The presence of partial pollen sterility shown in many cultivated taxa of diploid *Camellia* was not correlated with chromosome configurations at metaphase I in PMC's. The sterility and partial sterility shown in diploid *Camellia* taxa might be due to either genetic differences or cryptic structural differences or chromosomal differences.

Since cultivated *Camellia* is longeval tree or shrub and is artificially selected for economic purposes, all genetical and cytological factors discussed have been accumulated and formed into more complicated genomic constitutions.

Introduction

The genus *Camellia* L., which is placed in the Theaceae Mirb., consists of eighty-two species grouped in twelve sections according to Sealy's monograph of the genus (1958). All the species of *Camellia* are distributed in southeastern Asia from Japan to the Himalayas and down to Java and Sumatra of Indonesia. Many species are sympatric in southeastern Indochina, China, Taiwan, and Japan. Since many *Camellia* species are economically useful plants, they have a rather long history of cultivation. Members of Sect. *Thea* (L.) Dyer [e.g., *Camellia sinensis* (L.) O. Kuntze and *C. irrawadiensis* P.K. Barua] are the tea plant. Seed oils have been extracted from members of Sect. *Theopsis* Cohen-Stuart, Sect. *Thea* (L.) Dyer, Sect. *Camellia* (L.) Dyer, and Sect. *Paracamellia* Sealy for centuries. Two Japanese camellias, *Camellia japonica* L. of Sect. *Camellia* and *C. sasanqua* Thunberg of Sect. *Paracamellia*, have been cultivated for many centuries as ornamental and decorative plants as well as for oil production (TUYAMA 1957, 1968; SEALY 1958).

It seems that among sympatric species of *Camellia* natural hybridization sometimes appear. Many naturally occurring forms intermediate between species have been discovered

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and deposited in various herbaria (SEALY 1958). Even intermediates between *Camellia sinensis* and *C. japonica* can be found in herbarium collections (TUYAMA 1966). In areas of sympatry, plants with intermediate morphological characters are so common as to obscure identification of such specimens (SEALY 1958). Many of these appear to be natural intersectional hybrids. Some herbarium specimens have not been determined as to species since they are morphologically interspecific or intersectional intermediates. Specimens morphologically resembling species in Sect. Theopsis are particularly a problem (SEALY 1958). SEALY's monograph (1958) includes a separate small section for "*Specimens not satisfactorily placed and doubtful, imperfectly known and excluded species.*"

The actual origin of the *Wabisuke* camellias remains a mystery (KITAMURA 1970). From a taxonomist's point of view (KITAMURA 1970), *Camellia uraku* is a form of *C. wabisuke* (Makino) Kitamura [= *C. wabisuke* form *uraku* (Kitamura) Kitamura]. Most clones of *Camellia wabisuke* do not set seeds; however, *C. wabisuke* form *uraku* is fertile. From this evidence and a consideration of a complex of taxonomic characters, KITAMURA (1970) is of the opinion that *Camellia wabisuke* might be a hybrid product of *C. sinensis* and *C. japonica*; and *C. wabisuke* form *uraku* have originated from *C. wabisuke* after several possible backcrosses to a parent of *C. wabisuke*. KATO and SIMURA (1970, 1971) found that in *Camellia wabisuke* cv. 'Kocho-Shiro-Wabisuke' irregularity of anthers and embryo sac occurred by the abnormal formation of their primordia and archesporial cells in anther primordia and young nucellus. This irregularity might be caused by two non-homologous chromosomes. They also noted that the karyotype of *Camellia wabisuke* cv. 'Kocho-Shiro-Wabisuke' had some similarities to that of *C. japonica* and *C. sinensis*; but it was closer to the karyotype of *C. japonica* than that of *C. sinensis*.

One of the first documented cases of artificial hybridization in *Camellia* in the Western hemisphere is that of *C. × williamsii* W.W. Smith taxonomically named in 1949 for the hybrid plants resulting from crosses between *C. saluenensis* Stapf ex Bean and *C. japonica*. Such a hybrid could also be found in Chinese gardens (SEALY 1958; with special reference to *C. saluenensis* f. *macrophylla* Sealy). *Camellia × williamsii* cv. 'J.C. Williams' is an early artificial hybrid raised from this combination. Since then a number of other hybrid cultivars of the same combination have been named such as *C. × williamsii* cv. 'Donation,' *C. × williamsii* cv. 'Mary Christian,' *C. × williamsii* cv. 'November Pink,' and so on (see *Camellia Nomenclature*: Ed. WOODROOF 1974). To the present time, a large number of various hybrid combinations have been raised, named, registered, and many of them are intersectional hybrids. As a result, introgression after artificial hybridization in *Camellia* under cultivation might occur.

PARKS and CASE (1969) and PARKS and KONDO (1974) demonstrated massive outcrossing of certain camellias in cultivation. The researches were done on plants from an artificially mixed population of *Camellia* species at Descanso Gardens, La Cañada, California. After a group of highly variable seedlings appeared naturally under a large planting of *Camellia saluenensis* at Descanso Gardens, open-pollinated seeds were systematically grown out from this planting. It was concluded that the improved forms of *Camellia saluenensis* which

occur spontaneously are largely a result of outcrossing with other species, mostly *C. japonica*. Although extensive hybridization can be demonstrated in collections such as those at Descanso Gardens, these gardens are very young—Descanso Gardens is about 40 years old (ROBERTS 1962). In Asia, on the other hand, camellias have been cultivated for centuries, and there has been much more opportunity for hybridization and introgression.

Excepting a few taxonomic works which show the natural distribution of species of *Camellia* found in nature, most systematic ranking of species, varieties, and cultivars named are shown under cultivated status; e.g., *C. euryoides* Lindley, *C. irrawadiensis* R.K.Barua, *C. japonica* L., *C. pitardii* Cohen-Stuart, *C. reticulata* Lindley, *C. sasanqua* Thunberg, *C. sinensis* (L.) O.Kuntz, *C. rosaeflora* Hooker, *C. maliflora* Lindley, *C. wabisuke* (Makino) Kitamura.

Information concerning the extent of the relationship between species is of prime importance from the taxonomic, evolutionary, and breeding points of view. A comparison of chromosome behavior in generic and species crosses can provide data for comparison of genetic and taxonomic relationships. Meiotic chromosome conjugation coupled with analyses of external chromosome morphology is studied in this paper with reasonable success in interpreting species relationships among the available cultivated, diploid species of *Camellia*.

Materials and methods

Table 1 lists the diploid clones of cultivated *Camellia* used for this study. The hybrid clones used in this study were chosen because they were intermediate between the parental species or cultivars in morphological characteristics. Most of the materials were taken from the Parks' collection, North Carolina Botanical Garden, The University of North Carolina, Chapel Hill, N.C., and others were collected from five additional sources: (1) Ackerman's collection, Plant Science Research Division, Agricultural Research Service, United States Department of Agriculture, Glenn Dale, Maryland; (2) Descanso Gardens, La Cañada, California; (3) Huntington Botanical Garden, San Marino, California; (4) Los Angeles State and County Arboretum, Arcadia, California; and (5) Nuccio's Nurseries, Altadena, California. All of the clones used in this study are in cultivation in the above collections, and are the strains used as Ackerman's and Parks' research materials.

Flower buds were fixed in regular Carnoy's solution (95% ethanol : chloroform : glacial acetic acid in a ratio of 6:3:1). Before fixing flower buds were dissected to speed fixation and to determine if anthers were at the right stage for the meiotic study. White anthers were collected and yellow-colored mature anthers were rejected. Smear preparations of anthers were made in aceto-carmin for meiotic chromosome observations. Unless otherwise stated, the meiotic data for the species and cultivars were based on examination of a minimum of ten pollen mother-cells from each clone, and the figures on chromosome pairing were based on an analysis of thirty complete nuclei at the first metaphase of meiosis for each hybrid. Chiasma frequency, expressed as the average number per cell

Table 1. Clone identification and collection site for each diploid species and hybrid included in this study¹⁾

Taxon : Clone Number and (Source ²⁾)
<p>SECT. THEOPSIS COHEN-STUART</p> <p><i>C. cuspidata</i> (Kochs) Wright : Kono 1134, 1245, 1252 (DG) ; 15474 B or Kondo 1223 (HBG). <i>C. maliflora</i> Lindley : 14373 B (HBG) ; Kondo 1274 (DG). <i>C. lutchuensis</i> Ito : Kondo 1243, 1244 (DG). <i>C. nokoensis</i> Hayata : P. I. 324955 (USDA).</p> <p>SECT. CAMELLIOPSIS (PIERRE) SEALY</p> <p><i>C. salicifolia</i> Champion ex Benthham : 15476 E or Kondo 1187 (HBG). <i>C. assimilis</i> Champion ex Benthham : Kondo 1270 (DG).</p> <p>SECT. THEA (L.) DYER</p> <p><i>C. sinensis</i> (L.) O. Kuntze, var. <i>sinensis</i> Sealy : 631 (LASCA). <i>C. irrawadiensis</i> P. K. Barua : Kondo 1297 (DG) ; 15488 B (HBG).</p> <p>SECT. CAMELLIA (L.) DYER</p> <p><i>C. hongkongensis</i> Seemann : 26910, 12945 B (HBG) ; 5-12 (USDA). <i>C. japonica</i> L. : 100 (LASCA) ; P. I. 275387 (USDA) ; 11211 A (HBG) ; Kondo 1214 (DG) ; Kondo 1216 (DG) ; 12117 A (HBG) ; 11789 (HBG) ; 11797 (HBG) ; Kondo 1249 (DG) ; Kondo 1302 (DG) ; 12563 B (HBG) ; Kondo 1236 (DG) ; Kondo 1292 (DG) ; Kondo 1311 (DG) ; Kondo 1269 (DG). <i>C. japonica</i> L., subsp. <i>rusticana</i> (Honda) Kitamura : 11421 G or Kondo 1178 (HBG). <i>C. saluenensis</i> Stapf ex Bean : Kondo 1227 or 12851 H (HBG) ; Kondo 1238, 1240, and 1241 (DG). <i>C. saluenensis</i> Stapf ex Bean, cultivar 'Tourje-form' : Kondo 1228, 1251, 1258, and 1265 (DG).</p> <p>SECT. PARACAMELLIA SEALY</p> <p><i>C. kissi</i> Wallich : 15474 E or Kondo 1206 (HBG) ; Kondo 1256 (DG).</p> <p>DUBIAE</p> <p><i>C. wabisuke</i> (Makino) Kitamura, cultivar 'Sukiya' : Kondo 1303 (DG).</p> <p>HYBRIDS</p> <p>Intraspecific hybrids of <i>C. japonica</i> : 1-4 (PC) ; 2 A-15 and 2 A-19 (PC) ; 4 B-5 (PC) ; 14 G-66 (PC) ; 18 F-21 (PC) ; 43 A-23 (PC) ; 45 D-17 (PC) ; 60 W-1 (PC) ; 63 Q-5 (PC) ; 63 Z-4 (PC) ; 102 R-1 (PC) ; 102 U-7 (PC) ; 103 N-9 and 103 N-11 (PC) ; 113 G-19 (PC) ; 114 D-1 (PC) ; 149 F (PC). <i>C. japonica</i> × <i>C. japonica</i> subsp. <i>rusticana</i> : 5-25 (USDA). <i>C. saluenensis</i> × <i>C. saluenensis</i> : S 2-4 (PC).</p> <p>Intrasectional hybrids in Sect. <i>Camellia</i> :</p> <p><i>C. japonica</i> × <i>C. hongkongensis</i> : 5-18 (USDA). <i>C. saluenensis</i> × <i>C. japonica</i> : 44 I-41, 44 I-42, 44 I-70, 44 I-71, and 44 I-74 (PC). <i>C. saluenensis</i> cv. 'Tourje-form' × <i>C. japonica</i> : 49 B-2 and 49 B-5 (PC).</p> <p>Intersectional hybrids between Sect. <i>Theopsis</i> and Sect. <i>Camellia</i> :</p> <p><i>C. cuspidata</i> × <i>C. japonica</i> : Griffiths 4125 or Kondo 1246 (DG). <i>C. cuspidata</i> × <i>C. saluenensis</i> : Griffiths 4842 or Kondo 1136 (DG) ; Kondo 1353 (Nuccio's Nurseries). <i>C. saluenensis</i> × <i>C. cuspidata</i> : 12851 J or Kondo 1200 and 1220 (HBG). <i>C. japonica</i> × <i>C. lutchuensis</i> : 3-24, 3-28 and 4-55 (USDA) ; 18 E-4 (PC) ; 43 M-1 (PC) ; 69-2 (PC). <i>C. japonica</i> subsp. <i>rusticana</i> × <i>C. lutchuensis</i> : 2-10 and 2-11 (USDA) ; 315106 (USDA). <i>C. saluenensis</i> × <i>C. lutchuensis</i> : 44 C-6 and 44 C-13 (PC).</p> <p>Intersectional hybrids between Sect. <i>Thea</i> and Sect. <i>Camellia</i></p> <p><i>C. japonica</i> × <i>C. taliensis</i> : B-58442 (USDA) ; 103 L-11 (PC) ; 113 T-13 (PC). <i>C. sinensis</i> × <i>C. japonica</i> : 171 P-1 and 171 P-2 (PC). <i>C. japonica</i> × <i>C. irrawadiensis</i> : Kondo 1185 (Nuccio's Nurseries).</p> <p>Intersectional hybrid between Sect. <i>Thea</i> and Sect. <i>Paracamellia</i></p> <p><i>C. sinensis</i> × <i>C. kissi</i> : 9-597 (USDA).</p>

- 1) The names are those listed by SEALY (1958) and WOODROOF (1974), and those named in personal communications with Parks and other collectors. Since some materials from collections at Descanso Gardens, used in this study, do not bear accession numbers, voucher specimens from these are deposited in the Herbarium, The University of North Carolina, Chapel Hill (NCU).
- 2) The sources from which the author has obtained these collections are indicated by the following abbreviations : DG=Descanso Gardens ; HBG=Huntington Botanical Garden ; USDA=Ackerman's Collection ; LASCA=Los Angeles State and County Arboretum ; PC=Parks' Collection.

and per bivalent chromosome for the cells, was scored.

Results and Discussion

Meiosis in the pollen mother-cells of diploid *Camellia* taxa was studied in detail with reference to the pairing behavior of chromosomes at metaphase I.

Pairing between the homologous chromosomes in most of the cultivated species and cultivars of diploid *Camellia* studied was found to be complete and normal at metaphase I (Table 2).

In diploid species the comparative study of meiosis did not reveal any particular, marked difference in chromosome pairing. The diploid species studied showed 15 bivalent chromosomes at diakinesis and metaphase I of meiosis in PMC's. Each of their forms was mostly ring-shaped, strongly conjugated at both equal ends.

The data concerning chromosome associations and the number of chiasmata at metaphase I in PMC's of hybrids between diploid species or cultivars of *Camellia* are given in Table 3.

The intervarietal hybrid of *Camellia saluenensis* gave the data of perfect chromosome association and the mean chiasma frequency of 30 (Table 3). Each of the bivalents was

Table 2. Chromosome pairing and number of chiasmata at metaphase I in PMC's of diploid species and cultivars of *Camellia*

Taxon and clone identification	Pairing	Mean no. of chiasmata per PMC	Mean no. of chiasmata per bivalent	No. of PMC's	Taxon and clone identification	Pairing	Mean no. of chiasmata per PMC	Mean no. of chiasmata per bivalent	No. of PMC's
<i>C. cuspidata</i> : Kondo 1134	15 _{II}	30	2.0	10	Kondo 1249	15 _{II}	30	2.0	10
Kondo 1245	15 _{II}	30	2.0	10	Kondo 1302	15 _{II}	29.3	2.0	10
Kondo 1252	15 _{II}	30	2.0	10	12563 B	15 _{II}	30	2.0	10
15474 B	15 _{II}	30	2.0	10	Kondo 1236	15 _{II}	29.9	2.0	10
<i>C. maliflora</i> : 14373 B	15 _{II}	30	2.0	10	Kondo 1292	15 _{II}	30	2.0	10
<i>C. lutchuensis</i> : Kondo 1243	15 _{II}	30	2.0	10	Kondo 1311	15 _{II}	27.5	1.8	10
Kondo 1244	15 _{II}	30	2.0	10	Kondo 1269	15 _{II}	30	2.0	10
<i>C. nokoensis</i> : P. I. 324955	15 _{II}	29.7	2.0	30	<i>C. japonica</i> subsp.	15 _{II}	30	2.0	10
<i>C. salicifolia</i> : 15476 E	15 _{II}	29.8	2.0	10	<i>rusticana</i> : 11421 G				
<i>C. assimilis</i> : Kondo 1270	15 _{II}	30	2.0	10	<i>C. saluenensis</i> : 12851 H	15 _{II}	30	2.0	10
<i>C. sinensis</i> : 631	15 _{II}	29.6	2.0	10	Kondo 1227	15 _{II}	30	2.0	10
<i>C. irrawadiensis</i> : Kondo 1297	15 _{II}	29.7	2.0	10	Kondo 1238	15 _{II}	30	2.0	10
15488 B	15 _{II}	29.8	2.0	10	Kondo 1241	15 _{II}	30	2.0	10
<i>C. hongkongensis</i> : 5-12	15 _{II}	29.3	2.0	10	Kondo 1250	15 _{II}	30	2.0	10
<i>C. japonica</i> : 100	15 _{II}	30	2.0	10	<i>C. saluenensis</i> cv.	15 _{II}	28.5	1.9	30
P. I. 275387	15 _{II}	30	2.0	10	'Tourje-form' : Kondo 1228				
11211 A	15 _{II}	30	2.0	10	Kondo 1251	15 _{II}	29.0	1.9	30
Kondo 1214	15 _{II}	30	2.0	10	Kondo 1258	15 _{II}	28.7	1.9	30
Kondo 1216	15 _{II}	30	2.0	10	Kondo 1265	15 _{II}	29.4	2.0	10
12117 A	15 _{II}	30	2.0	10	<i>C. kissi</i> : 15474 E	15 _{II}	30	2.0	10
11789	15 _{II}	30	2.0	10	Kondo 1256	15 _{II}	30	2.0	10
12081	15 _{II}	30	2.0	10	<i>C. wabisuke</i> cv. 'Sukiya' :	15 _{II}	29.7	2.0	10
11797	15 _{II}	30	2.0	10	Kondo 1303				

Table 3. Chromosome configurations and number of chiasmata at metaphase I in PMC's of hybrids between diploid species of *Camellia*

Taxon and clone identification	Configurations		No. of cells	Xta range	Mean no. of Xta per PMC	Mean no. of Xta per bivalent	Total no. of PMC's
	I	II					
Intraspecific hybrids of <i>C. japonica</i> (intercultivarietal hybrids) :							
1-4		15	10	30	30	2.0	10
2 A-15		15	10	30	30	2.0	10
2 A-19	2	14 15	1 9	28~30	29.8	2.0	10
4 B-5		15	10	30	30	2.0	10
14 G-66		15	10	30	30	2.0	10
18 F-21		15	10	30	30	2.0	10
43 A-23	2	14 15	1 9	28~30	29.8	2.0	10
45 D-17		15	10	30	30	2.0	10
60 W-1	2	14 15	1 9	28~30	29.8	2.0	10
63 Q-5	2	14 15	1 9	28~30	29.8	2.0	10
63 Z-4		15	10	30	30	2.0	10
102 R-1		15	10	29~30	29.9	2.0	10
102 U-7		15	10	30	30	2.0	10
103 N-9	2	14 15	1 9	27~30	29.7	2.0	10
103 N-11		15	10	30	30	2.0	10
113 G-19		15	10	30	30	2.0	10
114 D-1		15	10	30	30	2.0	10
149 F		15	10	30	30	2.0	10
Intervarietal hybrid of <i>C. japonica</i> × <i>C. japonica</i> subsp. <i>rusticana</i> :							
5-25		15	10	30	30	2.0	10
Intervarietal hybrid of <i>C. saluenensis</i> :							
S 2-4		15	10	30	30	2.0	10
<i>C. japonica</i> × <i>C. hongkongensis</i> :							
5-18	2	14 15	2 28	24~30	27.0	1.8	30
<i>C. saluenensis</i> × <i>C. hongkongensis</i> :							
158 A-4		15	30	28~30	29.4	2.0	30
<i>C. saluenensis</i> × <i>C. japonica</i> :							
44 I-41		15	30	29~30	29.8	2.0	30
44 I-42		15	30	29~30	30.0	2.0	30
44 I-70		15	30	30	30	2.0	30
44 I-71		15	30	28~30	29.9	2.0	30
44 I-74		15	30	28~30	29.8	2.0	30
44 I-78		15	30	28~30	29.7	2.0	30
<i>C. saluenensis</i> cv. 'Tourje-form'× <i>C. japonica</i> :							
49 B-2		15	30	27~30	28.1	1.9	30
49 B-5		15	30	27~30	28.3	1.9	30
<i>C. cuspidata</i> × <i>C. japonica</i> :							
Kondo 1246		15	30	27~30	29.6	2.0	30
<i>C. cuspidata</i> × <i>C. saluenensis</i> :							
Kondo 1136		15	30	27~30	28.8	1.9	30
Kondo 1353		15	30	27~30	29.0	1.9	30

Taxon and clone identification	Configurations		No. of cells	Xta range	Mean no. of Xta per PMC	Mean no. of Xta per bivalent	Total no. of PMC's
	I	II					
<i>C. saluenensis</i> × <i>C. cuspidata</i> :							
12851 J	4 2	13 14 15	1 6 3	26~29	27.5	1.8	10
<i>C. japonica</i> × <i>C. lutchuensis</i> :							
3-24		15	30	27~30	29.3	2.0	30
3-28		15	30	28~30	29.6	2.0	30
4-55		15	30	29~30	29.9	2.0	30
18 E-4		15	10	29~30	29.7	2.0	10
43 M-1		15	10	29~30	29.7	2.0	10
69-2		15	10	29~30	29.9	2.0	10
<i>C. japonica</i> subsp. <i>rusticana</i> × <i>C. lutchuensis</i> :							
2-10		15	10	30	30	2.0	10
2-11		15	10	30	30	2.0	10
315106		15	10	30	30	2.0	10
<i>C. saluenensis</i> × <i>C. lutchuensis</i> :							
44 C-6		15	30	27~29	28.7	1.9	30
44 C-13		15	10	30	30	2.0	10
<i>C. japonica</i> × <i>C. taliensis</i> :							
B-58442		15	30	25~30	28.7	1.9	30
103 L-11		15	30	27~29	28.0	1.9	30
<i>C. sinensis</i> × <i>C. japonica</i> :							
171 P-1		15	30	27~30	29.4	2.0	30
171 P-2		15	10	30	30	2.0	10
<i>C. japonica</i> × <i>C. irrawadiensis</i> :							
Kondo 1185		15	30	24~29	26.2	1.7	30
145 A-17		15	30	29~30	29.6	2.0	30
<i>C. sinensis</i> × <i>C. kissi</i> :							
9-597		15	30	26~29	28.2	1.9	30

"Xta" = chiasmata

Configurations identified : I = univalent ; II = bivalent

mostly ring-shaped, strongly conjugated at both equal ends. In this hybrid, chromosome pairing and chiasma frequency did not deviate significantly from those of its parents (comparison in the mean number of chiasmata : $F_1 = P_1 = P_2$; $F_1 = F_1$ hybrid, P_1 = maternal parent, and P_2 = paternal parent). All other diploid hybrid combinations listed in Table 3 did not deviate significantly from their parents in chromosome pairing and chiasma frequency. Comparison in mean chiasma frequency are as follows :

$F_1 = P_1 = P_2$: *C. japonica* subsp. *rusticana* × *C. lutchuensis*

$F_1 \leq P_1 = P_2$: *C. saluenensis* × *C. japonica* ;

C. saluenensis × *C. lutchuensis*

$F_1 \leq P_1 < P_2$: *C. saluenensis* cv. 'Tourje-form' × *C. japonica* ;

C. sinensis × *C. japonica*

$F_1 < P_1 = P_2$: *C. cuspidata* × *C. japonica* ;

C. cuspidata × *C. saluenensis* ;

C. saluenensis × *C. cuspidata* ;

C. japonica × *C. lutchuensis*

$F_1 < P_1 < P_2$: *C. sinensis* × *C. kissi*

$F_1 < P_2 < P_1$: *C. japonica* × *C. hongkongensis* ;

C. saluenensis × *C. hongkongensis* ;

C. japonica × *C. irrawadiensis*

$F_1 < P_1 ? P_2$: *C. japonica* × *C. taliensis*

Other hybrid combinations which were not listed above did not supply any data of meiotic chromosomes during the course of investigation. It is due to either no available hybrid-clone in Ackerman's and Parks' collections or deeply associated petaloidy of available hybrid-clones.

The above interspecific hybrids show normal chromosome pairing (e. g., Fig. 1). The data of pollen viability in the materials used in this paper have been reported by ACKERMAN (1969, 1971) and KONDO (1975). Varying degree of pollen viability is found in these

Fig. 1. ($\times 1180$) Meiotic chromosomes in PMC's of diploid *Camellia* hybrids. a. *C. saluenensis* × *C. japonica* (44I-41), 15_{II} ; b. *C. cuspidata* × *C. japonica* (Kondo 1246), 15_{II} ; c. *C. sinensis* × *C. japonica* (171P-2), 15_{II} ; and d. *C. sinensis* × *C. kissi* (9-597), 15_{II} .

hybrids and it is often very low or sometimes close to zero.

Normal chromosome pairing and the reduction of chiasma frequency at metaphase I in meiosis and low pollen viability are indirect evidences which might be results of cryptic structural differences between paired chromosomes (STEBBINS 1945).

Among the diploid hybrid combinations, the combination of *Camellia saluenensis* × *C. japonica* shows quite high interfertility (PARKS and GRIFFITHS 1963; ACKERMAN 1969, 1971, 1973). Since they are highly ornamental, and crossings of this hybrid combination have been attempted more than those of other combinations, F₁ hybrid clones of this combination are the most common among the hybrid collections of *Camellia* (WOODROOF 1974). Many of the F₁ hybrids of this combination retain high fertility (PARKS and GRIFFITHS 1963). The similarity of leaf-scleroid patterns suggests a close relationship between the two species (PARKS and GRIFFITHS 1963). Crossability of the other interspecific hybrid combinations which appeared in this paper was completely analyzed by PARKS and GRIFFITHS (1963), ACKERMAN (1969, 1971), and PARKS (unpublished data). According to HILSMAN (1966) and SAVIGE (1967) the most successful interspecific crosses will be found within a section, particularly in species of *Camellia* with the same ploidy level. The study of the cross compatibility in *Camellia* made by ACKERMAN (1969, 1971) noted that hybridizing results generally substantiate the assumption of Hilsman and Savige that certain sections are more closely related than others.

During the course of investigations on meiotic behavior of chromosomes in pollen mother-cells indiploid *Camellia* taxa and their hybrids, among three clones of diploid *Camellia* taxa listed in Table 2, only one clone showed cytomixis, micronuclei, and multinuclei. In contrast, among nine clones of diploid interspecific F₁ hybrids (intrasectional) in Sect. *Camellia*, five clones showed cytomixis, three clones showed micronuclei, two clones showed multinuclei, and three clones showed multipolarity (mostly tripolar division). Among 20 clones of diploid intervarietal F₁ hybrids in Sect. *Camellia*, four clones showed cytomixis, one clone showed multinuclei, and three clones showed multipolarity. Among sixteen clones of diploid intersectional F₁ hybrids between diploid species of Sect. *Theopsis* and of Sect. *Camellia*, four clones showed cytomixis, one clone showed multinuclei, and two clones showed multipolarity. In six clones of a diploid intersectional F₁ hybrid between diploid species of Sect. *Thea* and of Sect. *Camellia*, only one clone showed cytomixis.

All the above meiotic irregularities with hybrid heterozygosity as the major cause of genetic unbalance are probably responsible for some portion of the production of abortive pollen in *Camellia*. A portion of the meiotic irregularities might have resulted from certain inherent physiological properties of the plant working in co-ordination with environmental fluctuations, and it has been speculated that most pollen irregularities result from cryptic structural differences between homologous chromosome segments. These factors interact with each other, and thus it is difficult to determine exactly how much aborted pollen is caused by each factor.

The high degree of pairing coupled with only a slight decrease in chiasma frequency in

F₁ hybrids involving these species has led me to suspect that there are no major karyological differences between these species ; and consequently, they are, on this basis, closely related.

Concluding remarks

Camellia cultivation has a long history from earlier than approximately 500 B.C. During this long period of cultivation, interspecific hybrids and intraspecific (or intervarietal) hybrids have been made naturally and artificially. These hybrids produce heterozygous chromosome complexes which have been being analyzed in our research series.

Among the cultivated *Camellia* taxa studied, the majority (70.8%) is diploid ($2n=30$; KONDO, in press). The dominant formation of bivalents and the high chiasma frequency per bivalent at metaphase I in meiosis were shown in the population of diploid clones of cultivated *Camellia* taxa. The presence of partial pollen sterility shown in many cultivated species, cultivars, and F₁ hybrids of diploid *Camellia* studied is not correlated with chromosome configurations at metaphase I in PMC's. The sterility and partial sterility shown in diploid species and their hybrids of cultivated *Camellia* might be due to either genetic differences or cryptic structural differences. Petaloidy also causes sterility in cultivated *Camellia* taxa. Since cultivated *Camellia* is longeval tree or shrub and is artificially selected for economic purposes, all the genetical and cytogenetical factors discussed have been accumulated and incorporated into the genus without regard to reproductive fitness.

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ツバキ属栽培種における細胞学的研究

I. 二倍体種とそれらの雑種¹⁾

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この研究は米国農務省 W. L. ACKERMAN とノースカロライナ大学 C. R. PARKS の研究シリーズの一部としておこなわれている。米国ツバキ協会に記録され、栽培されているツバキ属中、二倍体種 ($2n=30$) 11 種と、それらの種間および品種間雑種中花粉母細胞が得られた 15 組合せ 52 個体を供試し、減数分裂における染色体を調査した。他の雑種組合せは幼苗であるか、または弁化が進んで雄ずいのみられないもので、今回供試できなかった。

二倍体種 11 種において、減数分裂第一中期で検鏡したすべての花粉母細胞に 15 個の二価染色体がみられた。それぞれの二価染色体で、キアズマはほとんど常に 2 個ずつみられた。減数分裂は全体に安定していた。

52 雑種においてもまたすべての個体で 15 個の二価染色体が減数分裂第一中期で観察された。減数分裂は全体に安定していた。雑種とそれらの両親となった栽培種の減数分裂第一中期で比較できうる点は、雑種においてキアズマの頻度がほんの少々落ちる程度である。

ACKERMAN (1969, 1971, 1973) と PARKS (未発表) により、同じ材料を使った交雑能力テストでは、SEALY (1958) に従ったツバキ属分類学上の各節内種間の方がより交雑が可能であり、さらにその中でも同数の染色体をもったものとの組合せがより高い交雑能力をもっている。しかし今回の減数分裂第一中期の染色体観察からは上記の結果を裏付ける傾向はまったくみられない。ACKERMAN (1969, 1971) のおこなった花粉稔性テストにも何ら相関関係を示さない。減数分裂第一中期染色体の対合状態に限っていえば、節内節外に関係なく互いにそれぞれの二倍体種は近縁であるといえよう。