Cytogenetics, Ploidy, and Genome Sizes of *Camellia* and Related Genera

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Abstract. *Camellia* L., the most speciose member of the diverse tea family Theaceae, has a long and complex horticultural history. Extensive cultivation and hybridization have produced thousands of varieties of *Camellia*, including commercially important crops such as cultivated tea, oilseed, and iconic flowering shrubs. Cytogenetics of *Camellia* and related genera is complicated; chromosome number and ploidy can vary widely between species, and interspecific and interploid hybridization occurs. However, specific information regarding cytogenetics of many species, cultivars, and modern hybrids is lacking. The objectives of this study were to compile a consolidated literature review of the cytogenetics of *Camellia* and related genera and to determine chromosome numbers, ploidy, and genome sizes of specific accessions of selected species, cultivars, and interspecific and interploid hybrids. A review of the existing literature regarding Theaceae cytogenetics is presented as a consolidated reference comprising 362 taxa. Genome sizes were determined with flow cytometry using propidium iodide as a fluorochrome and *Pisum sativum* 'Ctirad' and *Magnolia virginiana* 'Jim Wilson' as internal standards. Chromosome numbers of selected taxa were determined using traditional cytology and were used to calibrate genome sizes with ploidy level. Our results confirmed a base chromosome number of $x = 15$ for Theeae including *Camellia*, $x = 17$ for Stewartiae, and $x = 18$ for Gordoniae. Surveyed camellias ranged from $2n = 2x = 30$ to $2n = 8x = 120$, including diploids, triploids, tetraploids, pentaploids, hexaploids, and octoploids. Previously uncharacterized taxa such as *Camellia azalea*, *C. amplexicaulis*, *C. chrysanthoides*, *C. cordifolia*, *C. cucphuongensis*, *C. flava*, *C. nanyongensis*, and *C. trichoclada* were found to be diploid. Ploidy was also newly determined for *Schima argentea*, *S. khasiana*, *S. remotiserrata*, and *S. sinensis* (all diploids). Both diploid and triploid *Stewartia ovata* were found, and a ploidy series was discovered for *Polyspora* that ranged from diploid to octoploid. Ploidy determinations were used to confirm or challenge the validity of putative interploid hybrids. Monoploid genome sizes varied among subfamily and genera, with 1Cx values ranging from 0.80 pg for *Franklinia* to a mean of 3.13 pg for *Camellia*, demonstrating differential rates of genome expansion independent of ploidy. Within *Camellia,* monoploid genome sizes varied among subgenera, sections, and some species (range, 2.70–3.55 pg). This study provides a consolidated and expanded knowledgebase of ploidy, genome sizes, hybridity, and reproductive pathways for specific accessions of *Camellia* and related genera that will enhance opportunities and strategies for future breeding and improvement within Theaceae.

Theaceae (Mirb. ex Ker Gawl.), the tea family, is a small family of trees and shrubs with a disjunct eastern Asian–eastern North American and northern South American distribution (Stevens, 2001 onwards). *Camellia* L. is the largest and most commercially significant genus of Theaceae, with species found throughout southeastern and eastern Asia (Chang and Bartholomew, 1984; Luna Vega and Contreras-Medina, 2000). Approx-imately 90% of all *Camellia* species, includ-ing those of greatest commercial importance, are native to China and Japan (Bartholomew, 1986). The ornamental varieties are prized for their glossy evergreen foliage and abundant showy flowers that can bloom from autumn to early spring, when many other plants in the landscape are dormant. More than 1000 years before their western intro-duction, ornamental camellias were grown for garden use in China (Xin et al., 2015). Although tea (*C. sinensis*) arrived in Europe during approximately the middle of the 17th century, the first living *Camellia* plant was not reported until nearly one century later, in Lord Petre Thorndon's hothouses in England. Since then, ornamental camellias have be-come widely cultivated throughout Europe, North America, Australia, and New Zealand (Ackerman, 2007; Darfler, 2014; Trehane, 2007). Their popularity and phenotypic var-iability have led to tens of thousands of cultivars and hybrids (International Camellia Society, 2015). However, there are many polyploid camellias, and many species and complex hybrids have not been analyzed for ploidy or genome size. Improved knowledge of chromosome numbers and ploidy levels of key species and cultivars would be a valuable resource for further breeding and improve-ment of *Camellia*. Analyses of other closely related genera would provide a broader un-derstanding of ploidy within Theaceae and help contextualize evolutionary relationships in this family.

Taxonomy/Systematics

The genus *Camellia* has undergone sev-eral taxonomic revisions (Prince, 2007). Sealy (1958) published a revision of the genus *Camellia* that included 12 sections and 82 species with an additional group of 24 doubtful species. Chang and Bartholomew (1984) and Chang (1998) completed several taxonomic revisions of *Camellia* and reor-ganized the 238 species native to China in 18 sections and 4 subgenera. More recently, Ming (2000) published his monograph of the genus *Camellia*; in that work, he reduced the number of subgenera to 2, the sections to 14, and the species to 119, which was less than half of Chang's final tally of ≈280 species. The systems of both Ming (2000) and Chang (1998) are widely used by bota-nists today (Gao et al., 2005). In the work by Ming and Bartholomew (2007), the number of species is ≈120, and 97 of these are native to China.

Several changes to the accepted taxo-nomic status of *Camellia* have occurred since its original classification by Linnaeus. At different times, *Camellia* has been placed with the Guttiferales, Theales, and even within Ternstroemiaceae (Luna and Ochoter-ena, 2004). Theaceae is now considered a distinct family within Ericales (Stevens, 2001 onwards). Luna and Ochoterena (2004) found that Theaceae is closely related to Ternstroemiaceae; both belong to the same clade. Within Theaceae, there are three tribes: Theeae, Gordoniae, and Stewartiae. Theeae is the most diverse of these tribes and contains *Camellia*, *Polyspora*, *Pyrenaria*, *Apterosperma*, and *Laplacea*. A recent mo-lecular phylogenetic analysis of Theeae in-dicated that *Camellia* and *Pyrenaria* form a paraphyletic group; these two occur and hybridize naturally with each other (Zhang et al., 2014). Gordoniae and Stewartiae be-long to the sister clade of Theeae. Gordoniae

is composed of the North American *Frank-linia* and *Gordonia*, as well as the Asian *Schima*. Intergeneric hybrids between these species as well as between *Camellia* and *Franklinia* have been reported (Ackerman and Williams, 1982; Orton, 1977; Ranney et al., 2003; Ranney and Fantz, 2006). Stewartiae includes the disjunct North American and Asian *Stewartia* (including evergreen species sometimes classified as *Hartia*) (Prince and Parks, 2001).

Ploidy and Cytogenetics

There is some variation in the base chromosome number among members of Theaceae. Many genera including *Camellia*, *Polyspora*, and *Pyrenaria* exhibit base chromosome numbers consistently reported as $1n = 1x = 15$ (Kondo, 1977; Yang et al., 2000, 2004). Other genera, however, have inconsistent reports, such as *Stewartia* with $1n = 1x = 15$ or 17 and *Franklinia*, *Gordonia*, and *Schima* with $1n = 1x = 15$ or 18 (Bostick, 1965; Horiuchi and Oginuma, 2001; Oginuma et al., 1994; Santamour, 1963). For *Camellia*, there is also considerable variability in ploidy, both among and within species. For example, *Camellia japonica* is most commonly found to be diploid (Ackerman, 1971; Kondo, 1977), although triploids, tetraploids, pentaploids, and aneuploids have been reported (Fukushima et al., 1966; Kondo, 1977). Although *Camellia sasanqua* is often reported to be hexaploid (Ackerman, 1971; Kondo, 1977), pentaploids, heptaploids, octoploids, decaploids, and aneuploids have been noted (Ito et al., 1957; Kondo, 1977).

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Ploidy series are seen in other *Camellia* species as well, including (but not limited to) *C. hiemalis*, *C. oleifera*, *C. reticulata*, and *C. sinensis* (Ackerman, 1971; Bezbaruah, 1971; Huang et al., 2013; Kondo, 1977). The variation and confusion regarding ploidy levels are further complicated by and may be partly the result of interspecific and interploid hybridization. For example, advanced hybrids of *C. ×vernalis* (*C. sasanqua ×japonica*) can be triploid, tetraploid, pentaploid, or hexaploid (Tateishi et al., 2007). Additionally, camellias can produce both unreduced gametes (Wendel, 1984) and, in some instances, aneuploid gametes (Kondo, 1977), resulting in additional possible variations within ploidy.

Ploidy and genome size can influence reproductive compatibility, fertility, and heritability of traits. Relative ploidy levels among related taxa can reflect and help elucidate biodiversity, genomic evolution, and taxonomic relationships (Laport and Ng, 2017; Ranney et al., 2018; Soltis et al., 2015). For example, seed development from interploid crosses can be limited by the failure of endosperm formation, leading to the production of nonviable seeds (Ramsey and Schemske, 1998). Anisoploid plants, whose chromosome numbers are in odd multiples of their basic number (e.g., triploid, pentaploid, etc.), can be sterile or have greatly reduced fertility, thereby limiting their potential as breeding lines. With increasing ploidy, allelic segregation becomes more complicated, thus leading to complex patterns of heritability, especially in autopolyploids (Zielinski and Scheid, 2012). Information regarding ploidy and genome size can also be used to confirm interploid hybridity, and genome size data can be used to estimate ploidy among related taxa when calibrated with known cytological standards.

The objectives of this study were to 1) conduct an extensive literature review and compile a consolidated reference regarding the cytogenetics of *Camellia* and related genera, and 2) to augment prior research with original data regarding ploidy and genome sizes of specific accessions of selected species, cultivars, and interspecific and interploid hybrids.

Materials and Methods

Plant material. Tissue samples of species, hybrids, and cultivars of *Camellia* and closely related genera were collected from nurseries, private collections, and botanic gardens. Several species not previously reported were surveyed, and putative interploidy and interspecific hybrids were verified or challenged. Taxa with variable reported genome sizes were analyzed to determine the ploidy of specific clones. Cultivars with previously determined chromosome numbers were included to calibrate genome size with ploidy.

Genome size/Ploidy determination. Flow cytometry was used to determine genome sizes following the methods of Huang et al.

(2013). Approximately 40 to 50 mg of leaves were used for each sample preparation. A modified woody plant buffer (WPB) isolation buffer composed of 0.2 mM Tris-HCl, 4 mM MgCl₂-6 H₂O, 2.0 mM EDTA Na₂-H₂O, 86.0 mM NaCl, 2.0 mM dithiothreitol, 1% (w/v) PVP-10, and 1% (v/v) Triton X-100 1 mL with a pH of 7.5 was prepared. Ice-cold nuclei suspensions were prepared by chopping tissue in the WPB with a razor blade. The WPB buffer was used to reduce the effects of phenolic compounds, preserve chromatin integrity in the DNA, and help produce low cv values (Huang et al., 2013). The suspensions were filtered through a 50-µm nylon filter. The nuclei were subsequently treated with 50 µg·mL⁻¹ RNase and stained with propidium iodide (PI) (Huang et al., 2013). *Pisum sativum* 'Ctirad' (2C = 8.75 pg) and *Magnolia virginiana* 'Jim Wilson' (2C = 3.92 pg) were used as internal standards. Samples were analyzed using a Partec PA II flow cytometer (Partec, Görlitz, Germany) to determine genome size. Holoploid, somatic, sporophytic, unreduced 2C genome size was calculated as the DNA content of the standard (pg) × (mean fluorescence value of the sample / mean fluorescence value of the standard). Plants were sampled randomly, with two subsamples measured per plant. Monoploid 1Cx genome size (i.e., the DNA content of one complete set of chromosomes) was calculated as 2C genome size / ploidy.

Chromosome counts were completed for selected taxa to confirm ploidy and further calibrate the flow cytometry results following the methods of Lattier et al. (2014). Root squashes were prepared for selected plants by collecting actively growing root tips and placing them in a prefixative solution of 2.0 mM 8-hydroxyquinoline plus 70 mg·L⁻¹ cyclohexamide in the dark at room temperature for 3 h. The roots were then placed in the dark at 4 °C for another 3 h. After washing with dH₂O, the roots were transferred to a fixative solution of 1:3 propionic acid to 95% EtOH at room temperature overnight. The following morning, roots were transferred to a solution of 70% EtOH for long-term storage.

To prepare fixed samples for counting, the roots were moved to a hydrolysis solution of 1:3 12 M HCl to 95% EtOH for 60 to 90 s before being moved to a clean slide. Root tips were excised and moved to a final clean slide, and a drop of modified carbol fuschin stain was applied to the root tip (Carr and Walker, 1961; Kao, 1975). A coverslip was placed on the root tip and gently pressed with a pencil eraser to squash the tissue. A light microscope was used to count chromosomes in actively dividing cells and confirm ploidy (Lattier et al., 2014).

Data for monoploid genome sizes (1Cx) were subjected to a one-way analysis of variance (ANOVA) as a function of subfamily, genus, and species; *Camellia* was subjected to a one-way ANOVA as a function of subfamily, genus, species, subgenus, and section. Means were separated using Fisher's least significant difference test

Table 1. Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[Z]	Chromosomes	References
C. acutiserrata	$2n = 2x = 30$	Gu and Sun, 1997
C. anlungensis	$2n = 2x = 30$	Zhang and Min, 1999
C. anlungensis var. *acutiperulata*	$2n = 2x = 30$	Zhang and Min, 1999
C. albovillosa	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Kondo et al., 1986, 1988; Xiao et al., 1993
C. assamica	$2n = 2x = 30$	Chen et al., 2003; Cherian and Stephan, 1981; Li et al., 1989;
	$2n = 3x = 45$	Omman and Stephen, 1994
C. assamica var. *kucha*	$2n = 2x = 30$	Kondo, 1977; Li et al., 1989
C. assimilis	$2n = 2x = 30$	Fukushima et al., 1966; Kondo, 1977
C. brevistyla	$2n = 2x = 30$	Zhang and Min, 1999
C. caudata	$2n = 2x = 30$	Bezbaruah, 1971; Zhuang and Dong, 1984
	$2n = 4x = 60$	Gu et al., 1988b, 1989b; Gu and Sun, 1997
C. changii	$2n = 6x = 90$	Huang et al., 2013
C. chekiangoleosa	$2n = 2x = 30$	Gu et al., 1988a, 1988b, 1989a, 1989b; Huang et al., 2013;
		Huang and Hsu, 1987; Huang and Zhao, 1981;
		Zhang and Ming, 1998; Zhuang and Dong, 1984
C. chrysantha	$2n = 2x = 30$	Cao and Li 1986; Chen et al., 2003; Gu et al., 1988b; 1989b;
		Huang and Zou, 1982; Kondo et al., 1991; Kondo and Andoh, 1980;
		Kondo and Andoh, 1983; Liang, 1990; Liao, et al., 1991;
		Xiao, et al., 1991; Xiao, et al., 1993; Zhuang and Dong, 1984
C. chrysantha var. *microcarpa*	$2n = 2x = 30$	Liang, 1990; Kondo et al., 1991
C. compressa	$2n = 8x = 120$	Gu et al., 1988a, 1988b, 1989a, 1989b
C. concina	$2n = 6x = 90$	Huang et al., 2013
C. costata	$2n = 2x = 30$	Huang et al., 2013
C. costei	$2n = 2x = 30$	Gu and Sun, 1997
	$2n = 6x = 90$	Huang et al., 2013
C. crapnelliana	$2n = 2x = 30$	Huang et al., 2013; Huang and Hsu, 1987; Kondo, 1972; Kondo, 1977
	$2n = 6x = 90$	Zhuang and Dong, 1984
C. crassicolumna	$2n = 2x = 30$	Xiao et al., 1991
C. crassipes	$2n = 8x = 120$	Huang et al., 2013
C. cryptoneua	$2n = 6x = 90$	Gu et al., 1988b, 1989b; Kondo et al., 1991
C. cuspidata	$2n = 2x = 30$	Janaki-Ammal, 1952, 1955; Kondo, 1977; Patterson et al., 1950;
		Zhuang and Dong, 1984
C. dehungensis	$2n = 2x = 30$	Li et al., 1989
C. drupifera	$2n = 3x = 45$	Longley and Tourje, 1959
C. edithae	$2n = 2x = 30$	Gu et al., 1990b; Huang et al., 2013; Xiao et al., 1991
C. euphlebia	$2n = 2x = 30$	Gu and Sun 1997; Gu et al., 1988b, 1989b; Liang, 1990;
		Liao et al., 1991; Lu et al., 1993; Zhang and Ming, 1995
C. fangchengensis	$2n = 2x = 30$	Huang et al., 2013
C. fasicularis	$2n = 2x = 30$	Zhang and Ming, 1995
C. flavida	$2n = 2x = 30$	Liang, 1990; Qin and Liang, 1991; Zhang and Ming, 1995
C. forrestii	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Kondo and Andoh, 1980; 1983; Xiao et al., 1991
	$2n = 4x = 60$	Gu et al., 1988b, 1989b; Kondo et al., 1991; Xiao et al., 1991
	$2n = 6x = 90$	Gu et al., 1988b, 1989b; Xiao et al., 1991
C. fraterna	$2n = 6x = 90$	Ackerman, 1971; Huang et al., 2013; Kondo, 1977; Longley, 1958
C. funinensis	$2n = 2x = 30$	Gu et al., 1988b, 1989b
C. furfuracea	$2n = 2x = 30$	Zhang and Min, 1999
C. fusuiensis	$2n = 2x = 30$	Liang, 1990
C. gauchowensis	$2n = 2x = 30$	Gu et al., 1988a, 1989a; Gu and Sun, 1997
C. gigantocarpa	$2n = 2x = 30$	Huang and Zhao, 1981; Zhuang and Dong, 1984
C. glabispetala	$2n = 6x = 90$	Huang et al., 2013
C. grandibracteata	$2n = 2x = 30$	Huang et al., 2013; Li et al., 1989
C. granthamiana	$2n = 4x = 60$	Ackerman, 1971; Fukushima et al., 1966; Kondo, 1977;
		Kondo and Parks, 1979; Longley and Tourje, 1959
C. grijsii	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Huang et al., 2013; Lu et al., 1993; Xiao et al., 1991
	$2n = 4x = 60$	Huang and Hsu, 1987; Kondo et al., 1991
	$2n = 5x = 75$	Huang and Hsu, 1987
	$2n = 6x = 90$	Huang and Hsu, 1987; Xiao et al., 1991
C. gymnogyna	$2n = 2x = 30$	Chen et al., 2003; Huang et al., 2013; Liang et al., 1994a; Xiao et al., 1991
C. gymnogynoides	$2n = 2x = 30$	Chen et al., 2003
C. henryana	$2n = 2x = 30$	Zhang and Min, 1999
C. hiemalis	$2n = 6x = 90$	Fukushima et al., 1966; Ito et al., 1955; Longley and Tourje 1959; 1960
'Bill Wylam'	$2n = 6x = 90$	Ackerman, 1971; Kondo, 1977
'Kanjiro'	$2n = 6x = 90$	Kondo, 1977
'Milandy'	$2n = 7x = 102$	Kondo, 1977
'Shishi-Gashira'	$2n = 4x = 60$	Patterson et al., 1950
	$2n = 6x = 90$	Ackerman, 1971; Kondo, 1977; Longley, 1956; Longley and Tourje, 1959
C. hongkongensis	$2n = 2x = 30$	Ackerman, 1971; Huang et al., 2013; Janaki-Ammal, 1952; 1955; Kondo, 1977
C. huana	$2n = 2x = 30$	Huang et al., 2013; Zhang and Ming, 1995
C. hunanica	$2n = 2x = 30$	Gu et al., 1992
C. icana	$2n = 2x = 30$	Huang et al., 2013
C. impressinervis	$2n = 2x = 30$	Cao and Li, 1986; Gu et al., 1988b, 1989b; Huang et al., 2013;
		Kondo et al., 1991; Liang, 1990; Liao et al., 1991; Xiao et al., 1991, 1993
C. irrawadiensis	$2n = 2x = 30$	Bezbaruah, 1968b; 1971; Kondo, 1977
	$2n = 3x = 45$	Kondo, 1977

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Table 1. (*Continued*) Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[Z]	Chromosomes	References
C. japonica	$2n = 2x = 30$	Ackerman, 1971; Bezbaruah, 1971; Cao and Li, 1986; Chen et al., 2003; Fukushima et al., 1966; Gu et al., 1990a, 1990b, 1991; Ito et al., 1955; Kondo, 1977; Kondo and Parks, 1979; Longley and Tourje, 1960; Morinaga and Fukushima, 1931; Patterson et al., 1950; Tanaka, 1974; Tanaka et al., 2005; Terasaka and Tanaka, 1974; Uemoto et al., 1980
	$2n = 3x = 45$	Bezbaruah, 1971; Fukushima et al., 1966; Ito et al., 1955; Janaki-Ammal, 1952, 1955; Longley, 1958; Longley and Tourje 1960; Patterson et al., 1950; Uemoto et al., 1980
	$2n = 4x = 60$	Gu, et al., 1990a, 1991
'Adolpha Audusson'	$2n = 2x = 30$	Kondo, 1977
'Akashi-Gata'	$2n = 3x = 45$	Longley and Tourje, 1960; Ito et al., 1955
'Akazu-Nishiki'	$2n = 2x = 30$	Ito et al., 1955
'Akebono'	$2n = 3x = 45$	Ito et al., 1955
'Aki-No-Yama'	$2n = 2x = 30$	Ito et al., 1955
'Ara-Jishi'	$2n = 2x = 30$	Ito et al., 1955
'Arrabella' — Open pollinated seedling	$2n = \approx 2x = 32$	Kondo, 1977
'Bella Romana'	$2n = 2x = 30$	Kondo, 1977
'Beni-Botan'	$2n = 2x = 30$	Ackerman, 1971
'Beni-Karako'	$2n = 2x = 30$	Ito et al., 1955
'Benten-Tsubaki'	$2n = 2x = 30$	Ito et al., 1955
'Berenice Boddy'	$2n = 2x = 30$	Kondo, 1977; Patterson et al., 1950
'Bokuhan'	$2n = 2x = 30$	Ito et al., 1955
'Bon-Shirotama'	$2n = 2x = 30$	Ackerman, 1971
'California'	$2n = 3x = 45$	Kondo, 1977
'Chiri-Tsubaki'	$2n = 2x = 30$	Ito et al., 1955
'Conrad Hilton'	$2n = 2x = 30$	Kondo, 1977
'Coral Pink Lotus'	$2n = 3x = 45$	Kondo, 1977
'Daikagura'	$2n = 2x = 30$	Patterson et al., 1950
'Donckelarii'	$2n = 2x = 30$	Kondo, 1977
'Drama Girl'	$2n = 3x = 45$	Kondo, 1977
'Elegans'	$2n = 2x = 30$	Kondo, 1977
'Elegans Chandler'	$2n = 2x = 30$	Kondo, 1977
'Elena Noble'	$2n = 2x = 30$	Kondo, 1977
'Emmet Barnes'	$2n = 3x = 45$	Kondo, 1977
'Eureka'	$2n = 2x = 30$	Kondo, 1977
'Fimbriata'	$2n = 2x = 30$	Kondo, 1977
'Firebrand'	$2n = 2x = 30$	Kondo, 1977
'Fragrant Frill'	$2n = 2x = 30$	Kondo, 1977
'Frank Gibson'	$2n = 3x = 45$	Janaki-Ammal, 1952
'Furin-Tsubaki'	$2n = 2x = 30$	Ito et al., 1955
'Geisha Girl'	$2n = 2x = 30$	Kondo, 1977
'Genji-Karako'	$2n = 2x = 30$	Ito et al., 1955
'Gigantea'	$2n = 3x = 45$	Kondo, 1977
'Glenn Allan'	$2n = 2x = 30$	Kondo, 1977
'Grandiflora'	$2n = 3x = 45$	Janaki-Ammal, 1955
'Hagoromo'	$2n = 3x = 45$	Kondo, 1977
'Hakugan'	$2n = 2x = 30$	Ito et al., 1955
'Hana-Guruma'	$2n = 2x = 30$	Ito et al., 1955
'Hasumi-Shiro'	$2n = 2x = 30$	Ackerman, 1971
'Hayaoi'	$2n = 2x = 30$	Kondo, 1977
'High Hat'	$2n = 2x = 30$	Kondo, 1977
'Higurashi'	$2n = 2x = 30$	Ito et al., 1955
'Honpoji-Atsu-Ba'	$2n = 5x = 75$	Fukushima et al., 1966
'Iwane'	$2n = 2x = 30$	Patterson et al., 1950
'Iwane-Shibori'	$2n = 2x = 30$	Ito et al., 1955
'Jenny Jones'	$2n = 2x = 30$	Patterson et al., 1950
'Jitsu-Getsu'	$2n = 2x = 30$	Ito et al., 1955
'Joshua E. Youtz'	$2n = 2x = 34$	Kondo, 1977
'Judge Solomon'	$2n = 2x = 30$	Kondo, 1977
'Kanyo-Tai'	$2n = 2x = 30$	Ackerman, 1971
'Kauha-Shiratama'	$2n = 2x = 30$	Longley and Tourje, 1960
'Kifukurin-Beni-Karako'	$2n = 2x = 30$	Ito et al., 1955
'Kingyo-Ba'	$2n = 2x = 30$	Ito et al., 1955
'Kingyo-Tsubaki'	$2n = 2x = 30$	Longley and Tourje, 1960; Kondo, 1977
'Ko-Kirin'	$2n = 2x = 30$	Ito et al., 1955
'Kominato'	$2n = 2x = 30$	Kondo, 1977
'Komyo'	$2n = 3x = 45$	Ito et al., 1955
'Komyo-Tai'	$2n = 2x = 30$	Ackerman, 1971
'Konron-Koku'	$2n = 2x = 30$	Longley and Tourje, 1960
'Ko-Otome'	$2n = 2x = 30$	Ito et al., 1955
'Kumasaka'	$2n = 2x = 30$	Ito et al., 1955

Table 1. (*Continued*) Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[z]	Chromosomes	References
'Kuro-Tsubaki'	$2n = 2x = 30$	Ackerman, 1971; Kondo, 1977
'Latifolia Variegata'	$2n = 3x = 45$	Kondo, 1977
'Lauren Bacall'	$2n = 2x = 30$	Patterson et al., 1950
'Le Lys'	$2n = 2x = 30$	Ackerman, 1971
'Leviathan'	$2n = 2x = 30$ (plus fragment)	Kondo, 1977
'Lotus'	$2n = 2x = 30$	Patterson et al., 1950
'Magnoliaeflora'	$2n = 2x = 30$	Kondo, 1977
'Margaret Ratcliffe'	$2n = 2x = 30$	Kondo, 1977
'Mathotiana'	$2n = 3x = 45$	Patterson et al., 1950
'Miken-Jaku'	$2n = 3x = 45$	Ito et al., 1955
'Miura-Otome'	$2n = 2x = 30$	Fukushima and Iwasa, 1968
'Miyuki-Nishiki'	$2n = 2x = 30$	Ito et al., 1955
'Montelanc'	$2n = 2x = 30$	Kondo, 1977
'Moshio'	$2n = 2x = 30$	Ackerman, 1971
'Mrs. Howard Asper'	$2n = 2x = 30$	Patterson et al., 1950
'Mrs. John Laing'	$2n = 2x = 30$	Patterson et al., 1950
'Nagasaki'	$2n = 3x = 45$	Patterson et al., 1950
'Nochise-Yama'	$2n = 2x = 30$	Fukushima and Iwasa, 1968; Ito et al., 1955
'Oki-No-Ishi'	$2n = 2x = 30$	Ito et al., 1955
'Ooshiratama'	$2n = 2x = 30$	Ito et al., 1955
'Otome'	$2n = 2x = 30$	Ito et al., 1955
'Paige #592'	$2n = 2x = 30$	Kondo, 1977
'Pink Clouds'	$2n = 2x = 30$	Kondo, 1977
'Pink Perfection'	$2n = 2x = 30$	Patterson et al., 1950
'Professor Sargent'	$2n = 2x = 30$	Patterson et al., 1950
'Purpurea'	$2n = 2x = 30$	Kondo, 1977
'Rainy Sun'	$2n = 2x = 30$	Patterson et al., 1950
'Ro-Getsu'	$2n = 2x = 30$	Ito et al., 1955
'S. Peter Nyce'	$2n = 3x = 45$	Kondo, 1977
'Sakuzuki-Ba'	$2n = {\approx}3x = 44$	Fukushima et al., 1966
'Saotome'	$2n = 2x = 30$	Ito et al., 1955
'Saudade de Martins Blanco'	$2n = 2x = 30$	Ackerman, 1971
'Seiobo'	$2n = 2x = 30$	Fukushima et al., 1966
'Shibori-Karako'	$2n = 2x = 30$	Ito et al., 1955
'Shibori-Otome'	$2n = 2x = 30$	Ito et al., 1955
'Shiranui'	$2n = 2x = 30$	Ito et al., 1955
'Shiratama'	$2n = 2x = 30$	Patterson et al., 1950
'Shishi-Gashira'	$2n = 2x = 30$	Ito et al., 1955
'Some-Kawa'	$2n = 2x = 30$	Fukushima and Iwasa, 1968; Ito et al., 1955
'Soshi-Arai'	$2n = 2x = 30$	Ito et al., 1955
'Sunset Glory'	$2n = 2x = 30$	Kondo, 1977
'Tafuku-Benten'	$2n = 2x = 30$	Ito et al., 1955
'Tomorrow's Dawn'	$2n = 2x = 30$	Kondo, 1977
'Tori-No-Ko'	$2n = 2x = 30$	Ito et al., 1955
'Tsubaki'	$2n = 2x = 30$	Ackerman, 1971
'Utamakura'	$2n = 2x = 30$	Ackerman, 1971
'Victory Queen'	$2n = 2x = 30$	Kondo, 1977
'Ville de Nantes'	$2n = 2x = 30$	Kondo, 1977; Patterson et al., 1950
	$2n = {\approx}2x = 29$	Kondo, 1977
'White Nun'	$2n = 2x = 30$	Kondo, 1977
	$2n = 3x = 45$	Kondo, 1977
'Yamato-Nishiki'	$2n = 2x = 30$	Ito et al., 1955
'Yanagi-Ba'	$2n = 2x = 30$	Fukushima and Iwasa, 1968
'Yuki-Botan'	$2n = 2x = 30$	Ackerman, 1971
'Yukimi-Guruma'	$2n = 2x = 30$	Ito et al., 1955
C. japonica ssp. *rusticana*	$2n = 2x = 30$	Fukushima et al., 1966; Janaki-Ammal, 1952
'B White Plena'	$2n = 2x = 30$	Ackerman, 1971
'Hatano'	$2n = 2x = 30$	Ackerman, 1971
'Koshiji'	$2n = 2x = 30$	Ackerman, 1971
'Yoshida'	$2n = 2x = 30$	Ackerman, 1971
C. japonica syn. *C. hozanensis* (Hayata) Hayata	$2n = 2x = 30$	Kondo, 1977
C. japonica syn. *C. japonica* var. *spontanea* (Makino) Makino	$2n = 2x = 30$	Kato and Simura, 1970
C. jingdonensis	$2n = 6x = 90$	Gu et al., 1988b, 1989b
C. jiuyishanica	$2n = 2x = 30$	Gu et al., 1992
C. jungkiangensis	$2n = 2x = 30$	Liang et al., 1994a
C. kissii	$2n = 2x = 30$	Ackerman, 1971; Bezbaruah, 1971; Gu et al., 1992; Huang and Hsu, 1985, 1987; Kondo, 1977
	$2n = 4x = 60$ $2n = 5x = 75$	Huang and Hsu, 1987; Huang and Hsu, 1987
C. kwangnanica	$2n = 2x = 30$	Li et al., 1989
C. kwangsiensis	$2n = 2x = 30$	Huang et al., 2013
C. kweichowensis	$2n = 6x = 90$	Gu et al., 1988a, 1989a; Gu and Sun, 1997

Table 1. (*Continued*) Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[Z]	Chromosomes	References
C. lanceolata	$2n = 2x = 30$	Janaki-Ammal, 1952, 1955
C. lapidea	$2n = 4x = 60$	Gu et al., 1992
C. lawii	$2n = 2x = 30$	Huang et al., 2013
C. leptophylla	$2n = 2x = 30$	Huang et al., 2013; Zhang and Min, 1999
C. limonia	$2n = 2x = 30$	Liang, 1990; Qin and Liang, 1991
C. limonia f. obovata	$2n = 2x = 30$	Liao et al., 1988
C. longgangensis	$2n = 2x = 30$	Liao et al., 1988
C. longipedicellata	$2n = 2x = 30$	Huang et al., 2013
C. longissima	$2n = 2x = 30$	Huang et al., 2013
C. longruiensis	$2n = 2x = 30$	Liang, 1990
C. longzhouensis	$2n = 2x = 30$	Liang, 1990
C. lutchuensis	$2n = 2x = 30$	Ackerman, 1971; Kondo, 1977; Kondo and Parks, 1979
C. luteoflora	$2n = 2x = 30$	Gu et al., 1988a, 1989a; Gu and Sun, 1997; Huang et al., 2013
C. magniflora	$2n = 6x = 90$	Gu et al., 1992
C. mairei	$2n = 2x = 30$	Huang et al., 2013
	$2n = 6x = 90$	Kondo et al., 1988
C. mairei var. *velutina*	$2n = 2x = 30$	Gu et al., 1988a, 1989b
	$2n = 6x = 90$	Gu et al., 1988b, 1989b; Kondo et al., 1986
C. makuanica	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Gu and Sun, 1997
C. maliflora	$2n = 2x = 30$	Janaki-Ammal, 1952, 1955; Kondo, 1977; Patterson et al., 1950
C. manglaensis	$2n = 2x = 30$	Li et al., 1989
C. meiocarpa	$2n = 4x = 60$	Huang and Zhao, 1981; Kondo et al., 1991; Zhuang and Dong, 1984
C. micrantha	$2n = 2x = 30$	Liang, 1990; Liao et al., 1988
C. microcarpa	$2n = 2x = 30$	Liao et al., 1988, 1991
C. mingyueshanensis	$2n = 2x = 30$	Huang and Zhao, 1981
C. nanchuanica	$2n = 2x = 30$	Chen et al., 2003
C. nanyoungensis	$2n = 2x = 30$	Huang and Zhao, 1981; Zhuang and Dong, 1984
	$2n = 4x = 60$	Huang and Zhao, 1981
	$2n = 5x = 75$	Huang and Zhao, 1983
C. neriifolia	$2n = 2x = 30$	Gu and Sun, 1997
C. nitidissima	$2n = 2x = 30$	Huang et al., 2013; Qin et al., 1992;
C. nitidissima var. *phaeopubisperma*	$2n = 2x = 30$	Qin et al., 1992
C. nokoensis	$2n = 2x = 30$	Ackerman, 1971; Kondo, 1977
C. oblata	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Kondo et al., 1991
C. octopetala	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Gu and Sun, 1997; Huang and Hsu, 1987; Huang and Zhao, 1983; Patterson et al., 1950
	$2n = 4x = 60$	Zhuang and Dong, 1984
C. oleifera	$2n = 4x = 60$	Patterson et al., 1960
	$2n = 6x = 90$	Ackerman, 1971; Huang and Hsu, 1987; Janaki-Ammal, 1952, 1955; Kondo, 1977; Kondo et al., 1991; Longley, 1958; Longley and Tourje, 1959; Patterson et al., 1950; Zhuang and Dong, 1984
	$2n = 8x = 120$	Huang et al., 2013
C. oleifera syn. *C. drupiefera* Loureiro	$2n = 2x = 30$	Arora, 1961
	$2n = 6x = 90$	Kondo, 1977; Longley and Tourje, 1959
C. oleifera syn. *C. oleosa* (Lour.) Wu	$2n = 6x = 90$	Longley and Tourje, 1959
C. parvicuspidata	$2n = 2x = 30$	Huang and Hsu, 1987
C. parvipetala	$2n = 2x = 30$	Zhang and Ming, 1995
C. petelotii	$2n = 2x = 30$	Huang et al., 2013; Li et al., 1994
C. pingguoensis	$2n = 2x = 30$	Cao and Li, 1986; Chen et al., 1988; Liang, 1990; Liao et al., 1988; Zhang and Ming, 1995
C. pingguoensis var. *terminalis*	$2n = 2x = 30$	Zhang and Ming, 1995
C. pitardii	$2n = 2x = 30$	Gu, 1997; Janaki-Ammal, 1952; Zhang and Min, 1999; Zhang and Ming, 1998
C. pitardii var. *pitardii*	$2n = 2x = 30$	Ackerman, 1971; Gu, 1996; Gu et al., 1988b, 1989b, 1990b; Janaki-Ammal, 1955; Kondo et al., 1986, 1988; Longley and Tourje, 1959; Xiao et al., 1993
	$2n = 6x = 90$	Kondo, 1977
C. pitardii var. *yunnanica*	$2n = 6x = 90$	Gu et al., 1988b, 1989b; Janaki-Ammal, 1952, 1955; Kondo, 1977; Kondo et al., 1986, 1988; Longley and Tourje, 1960; Xiao et al., 1993
C. polyodonta	$2n = 2x = 30$	Cao and Li, 1986; Gu et al., 1988a, 1988b, 1989a, 1989b; Huang and Hsu, 1987; Zhuang and Dong, 1984
C. ptilophylla	$2n = 2x = 30$	Huang et al., 2013; Li and Yan, 1985
C. ptilosperma	$2n = 2x = 30$	Cao and Li, 1986
C. pubicosta	$2n = 2x = 30$	Huang et al., 2013
C. pubifurfuracea	$2n = 2x = 30$	Huang et al., 2013
C. pubipetala	$2n = 2x = 30$	Cao and Li, 1986; Liang, 1990; Zhang and Ming, 1995
C. purpurea	$2n = 2x = 30$	Gu and Sun, 1997; Gu et al., 1988b, 1989b; Lu et al., 1993
C. pyxidiacea	$2n = 2x = 30$	Zhang and Min, 1999
C. pyxidiacea var. *rubituberculata*	$2n = 2x = 30$	Zhang and Min, 1999
C. quinquelocularis	$2n = 2x = 30$	Liang et al., 1994a
C. reticulata	$2n = 2x = 30$	Gu, 1996, 1997; Xia et al., 1994
	$2n = 4x = 60$	Gu, 1996, 1997

(*Continued on next page*)

Table 1. (*Continued*) Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[z]	Chromosomes	References
	$2n = 6x = 90$	Gu, 1996, 1997; Gu et al., 1988b, 1989b; Huang and Hsu, 1987; Ito et al., 1955; Kondo, 1977; Kondo et al., 1986; 1988; Janaki-Ammal 1952; 1955; Patterson et al., 1950; Xia et al., 1994; Xiao et al., 1993; Zhuang and Dong, 1984
'Butterfly Wings'	$2n = 6x = 90$	Longley, 1956; Kondo, 1977
'Butterfly Wings Reticulate'	$2n = 6x = 90$	Longley, 1956
'Captain Rawes'	$2n = 3x = 45$	Patterson et al., 1950
'Chang's Temple'	$2n = 6x = 90$	Longley, 1956
'Chrysanthemum Petal'	$2n = 6x = 90$	Longley, 1956
'Cornelian'	$2n = 6x = 90$	Longley, 1956
'Crimson Robe'	$2n = 6x = 90$	Longley, 1956
'Lion Head'	$2n = 6x = 90$	Longley, 1956
'Moutancha'	$2n = 6x = 90$	Longley, 1956
'Noble Pearl'	$2n = 6x = 90$	Kondo, 1977; Longley, 1956;
'Ootani-To-Tsubaki'	$2n = \approx 6x = 91$	Fukushima et al., 1966
'Osmanthus Leaf'	$2n = 6x = 90$	Kondo, 1977
'Pagoda'	$2n = 6x = 90$	Longley, 1956
'Professor Tsai'	$2n = 6x = 90$	Longley, 1956
'Purple Gown'	$2n = 6x = 90$	Longley, 1956
'Shot Silk'	$2n = 6x = 90$	Longley, 1956
'Shot Silk Reticulate'	$2n = 6x = 90$	Longley, 1956
'Tali Queen'	$2n = 6x = 90$	Kondo, 1977
'Tuchsia Rose'	$2n = 6x = 90$	Kondo, 1977
'William Hertrich'	$2n = 6x = 90$	Kondo, 1977
'Willow Wand'	$2n = 6x = 90$	Kondo, 1977; Longley, 1956
C. reticulata f. *simplex*	$2n = 6x = 90$	Kondo, 1977
C. rhytidocarpa	$2n = 2x = 30$	Huang et al., 2013
C. rosaeflora	$2n = 3x = 45$	Bezbaruah, 1971; Kondo, 1977
	$2n = 6x = 90$	Ackerman, 1971
C. rosthorniana	$2n = 2x = 30$	Huang et al., 2013
C. rubituberculata	$2n = 2x = 30$	Gu and Sun, 1997; Gu et al., 1989b; Huang et al., 2013
	$2n = 4x = 60$	Gu et al., 1988b
C. salicifolia	$2n = 2x = 30$	Fukushima et al., 1966; Janaki-Ammal, 1952, 1955; Kondo, 1977; Longley and Tourje, 1959
	$2n = 4x = 60$	Huang et al., 2013
C. saluenensis	$2n = 2x = 30$	Ackerman, 1971; Fukushima et al., 1966; Gu, 1996, 1997; Gu et al., 1990b; Kondo, 1977; Kondo et al., 1986; Janaki-Ammal 1952, 1955; Longley and Tourje, 1960; Patterson et al., 1950; Xiao et al., 1993
'Tourje Form'	$2n = 2x = 30$	Kondo, 1977
C. sasanqua	$2n = 5x = 75$	Ito et al., 1957
	$2n = \approx 5x = 80$	Kondo, 1977
	$2n = 6x = 90$	Ackerman, 1971; Bezbaruah, 1971; Gu et al., 1988b, 1989b; Janaki-Ammal, 1955; Kondo, 1977; Tanaka et al., 2005; Uemoto et al., 1980; Zhuang and Dong, 1984
	$2n = 7x = 105$	Ito et al., 1957
	$2n = 8x = 120$	Huang et al., 2013; Ito et al., 1957; Kondo, 1977
'Apple Blossom'	$2n = 6x = 90$	Kondo, 1977
'Asahi-No-Umi'	$2n = 6x = 90$	Kondo, 1977
'Asahi-Zuru'	$2n = 3x = 45$	Ito et al., 1957
'Azuma-Nishiki'	$2n = 6x = 90$	Janaki-Ammal, 1952
'Bodnant'	$2n = 6x = 90$	Janaki-Ammal, 1952
'Bonanza'	$2n = 6x = 90$	Kondo, 1977
'Candy Reiter'	$2n = 8x = 120$	Kondo, 1977
'Charmer'	$2n = 10x = 150$	Kondo, 1977
'Cleopatra's Bush'	$2n = 6x = 90$	Kondo, 1977
'Crimson Bride'	$2n = 6x = 90$	Kondo, 1977
'Crinkley Flowers'	$2n = 6x = 90$	Patterson et al., 1950
'Fuki-No-Mine'	$2n = 6x = 90$	Janaki-Ammal, 1952
'Fukuzutsumi'	$2n = 8x = 120$	Kondo, 1977
'Gossamer Wings'	$2n = 6x = 90$	Kondo, 1977
'Hana-Jiman'	$2n = 6x = 90$	Kondo, 1977
'Hinode-Gumo'	$2n = 6x = 90$	Kondo, 1977
'Hinode-No-Umi'	$2n = 6x = 90$	Kondo, 1977
'Hiodoshi'	$2n = 6x = 90$	Kondo, 1977
'Jean May'	$2n = 6x = 90$	Kondo, 1977
'Kenkyo'	$2n = 8x = 120$	Kondo, 1977
'Kokinran'	$2n = 6x = 90$	Ackerman, 1971
'Lavender Queen'	$2n = 6x = 90$	Kondo, 1977
'Mavajo'	$2n = 6x = 90$	Kondo, 1977
'Memere'	$2n = 10x = 150$	Kondo, 1977
'Mine-No-Yuki'	$2n = 6x = 90$	Kondo, 1977; Patterson et al., 1950
'Minina'	$2n = 6x = 90$	Kondo, 1977
'Momosono-Nishiki'	$2n = 6x = 90$	Kondo, 1977

Table 1. (*Continued*) Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[Z]	Chromosomes	References
'Moon Moth'	$2n = 6x = 90$	Kondo, 1977
'Narumi-Gata'	$2n = 5x = 75$	Ackerman, 1971; Kondo, 1977
	$2n = \approx 7x = 106$	Kondo, 1977
	$2n = 8x = 120$	Kondo, 1977
'Ocean Spring'	$2n = 8x = 120$	Kondo, 1977
'Okina-Goromo'	$2n = 6x = 90$	Kondo, 1977
'Onishiki'	$2n = 6x = 90$	Ackerman, 1971
'Pale Moon Light'	$2n = 6x = 90$	Kondo, 1977
'Papaver'	$2n = 6x = 90$	Kondo, 1977
'Pink Snow'	$2n = 6x = 90$	Kondo, 1977
'Rainbow'	$2n = 8x = 120$	Kondo, 1977
'Sazanka'	$2n = 6x = 90$	Ackerman, 1971
'Setsugekka'	$2n = 6x = 90$	Kondo, 1977
'Shichi-Hoden'	$2n = 6x = 90$	Kondo, 1977
'Shining Star'	$2n = 6x = 90$	Kondo, 1977
'Shinonome'	$2n = 10x = 150$	Kondo, 1977
'Small White'	$2n = 6x = 90$	Patterson et al., 1950
'Snowflake'	$2n = 6x = 90$	Kondo, 1977
'Stain Pink'	$2n = 6x = 90$	Kondo, 1977
'Tagoto-No-Tsuki'	$2n = 7x = 105$	Fukushima et al., 1966
'Taimei-Nishiki'	$2n = 6x = 90$	Kondo, 1977
'Vel Vety'	$2n = 8x = 120$	Kondo, 1977
'White Doves'	$2n = 6x = 90$	Patterson et al., 1950
'Willow Leaf'	$2n = 6x = 90$	Kondo, 1977
'Winsome'	$2n = 6x = 90$	Kondo, 1977
'Wisley'	$2n = 6x = 90$	Janaki-Ammal, 1952
C. sasanqua syn. *C. miyagii* (Koidz.) Makino and Nemoto	$2n = 6x = 90$	Ackerman, 1971; Kondo, 1977
C. semiserrata	$2n = 2x = 30$	Cao and Li, 1986; Gu and Sun, 1997; Gu et al., 1988a, 1988b, 1989a, 1989b; Huang et al., 2013; Huang and Hsu, 1987; Kondo and Andoh, 1980, 1983; Zhuang and Dong, 1984
C. semiserrata var. *albiflora*	$2n = 2x = 30$	Huang and Hsu, 1987
C. semiserrata var. *magnocarpa*	$2n = 2x = 30$	Zhang and Ming, 1998
C. septempetala	$2n = 2x = 30$	Gu et al., 1992
C. septempetala var. *rubra*	$2n = 2x = 30$	Gu et al., 1992
C. sinensis	$2n = 2x = 30$	Chen et al., 2003; Cherian and Stephan, 1981; Datta and Agarwal, 1992; Janaki-Ammal, 1955; Kato and Simura, 1970; Kondo, 1977; Li et al., 1986, 1989, 1999; Liang, 1994; Liang and Liu 1990; Liang et al., 1992, 1994a, 1994b; Morinaga et al., 1929; Simura, 1935; Xu et al., 2003; Zhou et al., 1991, 1992; Zhuang et al., 1992; Zou et al., 1992
	$2n = 3x = 45$	Ackerman, 1971; Zhuang et al., 1992
	$2n = 4x = 60$	Ackerman, 1971
'Benji-Fuji'	$2n = 2x = 30$	Ackerman, 1971
'Beni-Homare'	$2n = 2x = 30$	Ackerman, 1971
'Makinowara-Wase'	$2n = 2x = 30$	Ackerman, 1971
'Tama-Midori'	$2n = 2x = 30$	Ackerman, 1971
'Yamato-Midori'	$2n = 2x = 30$	Ackerman, 1971
C. sinensis var. *assamica*	$2n = 2x = 30$	Bezbaruah, 1968a; Janaki-Ammal, 1952, 1955; Li and Yan, 1985
C. sinensis var. *bohea*	$2n = 2x = 30$	Li and Yan, 1985
C. sinensis var. *sinensis* f. *macrophylla*	$2n = 2x = 30$	Cao and Li, 1986; Li and Yan, 1985; Liang et al., 1990
	$2n = 3x = 45$	Bezbaruah, 1971; Janaki-Ammal, 1952, 1955; Karasawa, 1932, 1935; Simura, 1935
	$2n = \approx 3x = 44$	Simura and Inaba, 1953
	$2n = 4x = 60$	Simura, 1935
C. sinensis var. *sinensis* f. *parvifolia*	$2n = 2x = 30$	Bezbaruah, 1971
C. sinensis var. *rubella*	$2n = 2x = 30$	Liang et al., 1994a
C. sinensis var. *shan*	$2n = 2x = 30$	Li and Yan, 1985
C. subintegra	$2n = 2x = 30$	Huang et al., 2013; Huang and Hsu, 1987
C. tachangensis	$2n = 2x = 30$	Huang et al., 2013
C. taliensis	$2n = 2x = 30$	Gu and Sun, 1997; Gu et al., 1988b, 1989b; Huang et al., 2013; Janaki-Ammal, 1952, 1955; Li et al., 1989; Liang et al., 1994a; Longley and Tourje, 1959
C. tenuiflora	$2n = 2x = 30$	Longley and Tourje, 1959
C. tetracocca	$2n = 2x = 30$	Gu and Sun, 1997; Gu et al., 1988b, 1989b; Liang et al., 1994a
C. tonkinensis	$2n = 2x = 30$	Zhang and Ming, 1995
C. transarisanensis	$2n = 2x = 30$	Huang et al., 2013
C. transnokoensis	$2n = 6x = 90$	Kondo, 1977
C. trichosperma	$2n = 2x = 30$	Huang et al., 2013; Xiao et al., 1991
C. tsaii	$2n = 4x = 60$	Kondo et al., 1991
	$2n = 6x = 90$	Huang et al., 2013
C. tsingpienensis	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Kondo et al., 1991
C. tsingpienensis var. *pubisepala*	$2n = 2x = 30$	Gu et al., 1988b, 1989b

Table 1. (*Continued*) Previous cytological and cytometric reports of chromosome numbers for *Camellia* and related taxa.

Taxa[z]	Chromosomes	References
C. tuberculata	$2n = 4x = 60$	Huang et al., 2013
C. tunganica	$2n = 2x = 30$	Gu et al., 1992
C. tunghinensis	$2n = 2x = 30$	Cao and Li, 1986; Liang, 1990; Qin and Liang, 1991
C. uraku	$2n = 2x = 30$	Huang et al., 2013; Longley and Tourje, 1959; 1960
C. ×vernalis	$2n = 3x = 45$	Tanaka et al., 1986, 2005
	$2n = 4x = 60$	Tanaka et al., 1986, 2005; Uemoto et al., 1980
	$2n = 5x = 75$	Tanaka et al., 1986, 2005
'Dawn'	$2n = 3x = 45$	Longley and Tourje, 1960
'Egao'	$2n = 4x = 60$	Tateishi et al., 2007
'Ginryu'	$2n = 3x = 45$	Ito et al., 1955; Tanaka et al., 2005
'Hiryu'	$2n = 3x = 45$	Longley and Tourje, 1960; Kondo, 1977
	$2n = 6x = 90$	Longley, 1956
'Gaisen'	$2n = 4x = 60$	Tanaka et al., 2005
'Gaisen' (OP)	$2n = 5x = 75$	Tateishi et al., 2007
'Omi-goromo'	$2n = 4x = 60$	Tateishi et al., 2007
'Star-Above-Star'	$2n = 6x = 90$	Kondo, 1977
'Takarazuka'	$2n = 4x = 60$	Tateishi et al., 2007
'Tamuke-yama'	$2n = 4x = 60$	Tateishi et al., 2007
'Ume-ga-ka'	$2n = 4x = 60$	Tateishi et al., 2007
'Ume-ga-ka' (OP)	$2n = 6x = 90$	Tateishi et al., 2007
C. vietnamensis	$2n = 7x = 105$	Xiao et al., 1991
	$2n = 8x = 120$	Huang and Hsu, 1987; Xiao et al., 1991; Zhuang and Dong, 1984
C. wabisuke	$2n = 2x = 30$	Ito et al., 1955; Janaki-Ammal, 1952; Kato and Simura, 1970; Kitamura, 1970; Longley and Tourje, 1960
C. wabisuke f. *rosea*	$2n = 2x = 30$	Ito et al., 1955
'Sukiya'	$2n = 2x = 30$	Kondo, 1977
C. weiningensis	$2n = 2x = 30$	Zhuang and Dong, 1984
C. wenshanensis	$2n = 2x = 30$	Gu and Sun, 1997; Gu et al., 1988b, 1989b; Lu et al., 1993
C. wumingensis	$2n = 2x = 30$	Liang, 1990
C. xiashiensis	$2n = 2x = 30$	Liang, 1990; Liao et al., 1988
C. xylocarpa	$2n = 4x = 60$	Gu and Sun, 1997; Gu et al., 1988b, 1989b
C. yuhsienensis	$2n = 4x = 60$	Zhuang and Dong, 1984
	$2n = 5x = 75$	Zhuang and Dong, 1984
	$2n = 6x = 90$	Huang et al., 2013; Xiao et al., 1993; Zhuang and Dong, 1984
C. yungkiangensis	$2n = 2x = 30$	Chen et al., 2003; Kondo et al., 1991; Li et al., 1989
	$2n = 6x = 90$	Gu et al., 1988b, 1989b
C. yunnanensis	$2n = 2x = 30$	Gu et al., 1988b, 1989b; Huang et al., 2013; Kondo and Andoh, 1980, 1983; Kondo et al., 1991; Lu et al., 1993; Zhang and Min, 1999
Related species		
Apterosperma oblata	$2n = 2x = 30$	Wang et al., 2006
Franklinia alatamaha	$2n = 2x = 36$	Santamour, 1963
Gordonia lasianthus	$2n = 2x = 36$	Bostick, 1965
	$2n = 2x = 30$	Santamour, 1963
Polyspora chrysandra	$2n = 2x = 30$	Yang et al., 2004
P. excelsa	$2n = 2x = 30$	Mehra and Sareen, 1973
P. hainanensis	$2n = 2x = 30$	Yang et al., 2004
P. longicarpa	$2n = 2x = 30$	Yang et al., 2004
P. axillaris	$2n = 2x = 30$	Mehra and Sareen, 1973
Pyrenaria diospyricarpa	$2n = 2x = 30$	Yang et al., 2000
P. oblongicarpa	$2n = 2x = 30$	Yang et al., 2000
P. turbinata	$2n = 2x = 30$	Yang et al., 2000
Schima mertensiana	$2n = 2x = 36$	Ono, 1975, 1977; Goldblatt 1981
S. superba	$2n = 2x = 36$	Ming and Bartholomew, 2007
S. wallichii	$2n = 2x = 30$	Malla et al., 1977
	$2n = 2x = 36$	Oginuma et al., 1994
Stewartia malacodendron	$2n = 2x = 30$	Santamour, 1963
S. monadelpha	$2n = 2x = 30$	Santamour, 1963
	$2n = 2x = 34$	Horiuchi and Oginuma, 2001
S. ovata	$2n = 2x = 30$	Santamour, 1963
S. pseudocamellia	$2n = 2x = 30$	Santamour, 1963
	$2n = 2x = 34$	Horiuchi and Oginuma, 2001
S. serrata	$2n = 2x = 30$	Santamour, 1963
	$2n = 2x = 34$	Horiuchi and Oginuma, 2001
S. sinensis	$2n = 2x = 30$	Santamour, 1963
Tutcheria greeniae	$2n = 2x = 30$	Yang et al., 2000
T. hirta	$2n = 2x = 30$	Yang et al., 2000
T. microcarpa	$2n = 2x = 30$	Yang et al., 2000
T. pingpienensis	$2n = 2x = 30$	Yang et al., 2000
T. spectabilis	$2n = 2x = 30$	Ackerman, 1971; Yang et al., 2000
T. subsessililflora	$2n = 2x = 30$	Yang et al., 2003
T. symplocifolia	$2n = 2x = 30$	Yang et al., 2000
T. virgata	$2n = 2x = 30$	Ackerman, 1971
T. wuana	$2n = 2x = 30$	Yang et al., 2000

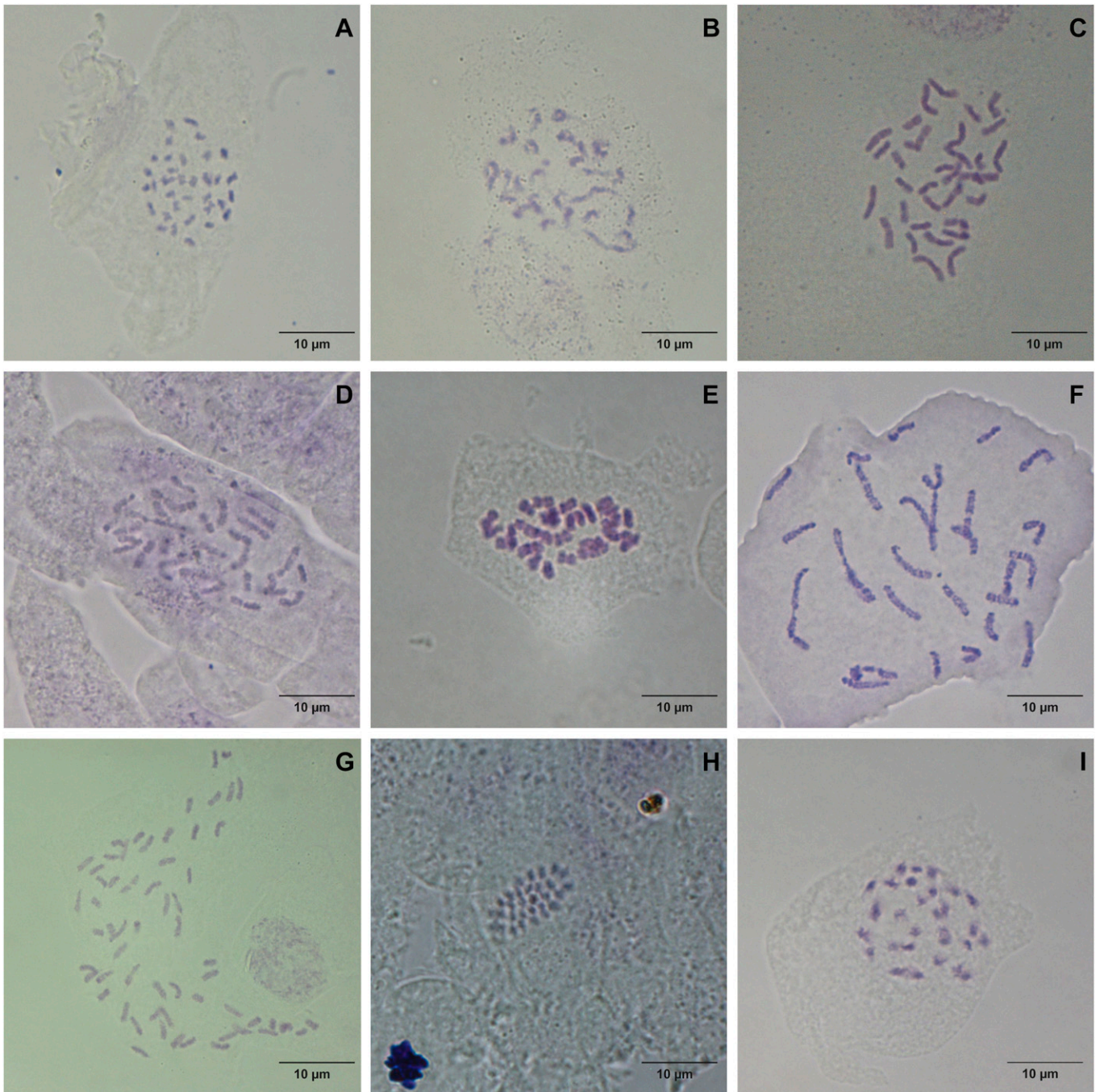[z]Nomenclature and species names are listed per the original publications.

Fig. 1. Photomicrographs of condensed stained chromosomes of Theaceae. (**A**) *Gordonia lasianthus* 2006-220, $2n \ 2x = 36$. (**B**) *Schima superba* 2018-009, $2n = 2x = 36$. (**C**) *Stewartia pseudocamellia* 2018-111, $2n = 2x = 34$. (**D**) *Camellia japonica* 'Dr. JC Raulston' 2017-060, $2n = 2x = 30$. (**E**) *Camellia sinensis* 'Red Leaf' 2017-111, $2n = 2x = 30$. (**F**) *Camellia azalea* 2018-063, $2n = 2x = 30$. (**G**) *Camellia ×vernalis* 'Egao Corkscrew' 2017-062, $2n = 4x = 60$. (**H**) *Polyspora chrysandra* 2015-114, $2n = 2x = 30$. (**I**) *Pyrenaria spectabilis* 2018-008 $2n = 2x = 30$.

(Proc GLM; SAS version 9.4; SAS Institute, Cary, NC).

Results and Discussion

Our compilation of literature regarding the cytogenetics of Theaceae spans nearly one century of research and includes published results for 7 genera, 160 species, and 202 cultivars (Table 1). Because cytological studies of *Camellia* span a broad range of time, many of these referenced studies used different taxonomic treatments dependent on the naming conventions at the time of publication. Without vouchered specimens, it is essentially impossible to verify exactly which species, according to modern taxonomic treatments, were used during these previous studies. Therefore, the names in Table 1 remain as they were reported in the original publications. As a result, there are numerous taxa represented here by duplicate names, such as *C. assamica*, which is now treated as a variety of *C. sinensis* in the *Flora of China* (Ming and Bartholomew, 2007). Discrepancies regarding base chromosome numbers continue to be resolved over time, with more recent studies supporting that Theeae, including *Apterosperma*, *Camellia*, *Polyspora*, and *Pyrenaria* (*Tutcheria*), has $1n = 1x = 15$ (Kondo et al., 1991; Yang et al., 2000, 2003, 2004). Additional work regarding Stewartiae, including *Stewartia*, indicated a base chromosome number of $1n = 1x = 17$ (Horiuchi and Oginuma, 2001), whereas Gordoniae, including *Franklinia*, *Gordonia*, and *Schima*, had $1n = 1x = 18$ (Bostick, 1965; Oginuma et al., 1994). Numerous *Camellia* species have isoploid

Table 2. Genome sizes and estimated ploidy levels of cultivated *Camellia* and related taxa.

Taxa[z]	Cultivar/selection	Source/accession[y]	2C genome size[x] (pg)	1Cx genome size (pg)[w]	Estimated ploidy (x)
Subfamily *Gordoniae*					
Genus *Franklinia*					
F. alatamaha		NCSU 1998-450	1.62 ± 0.19	0.81	2
Genus *Gordonia*					
G. lasianthus		NCSU 2006-220	1.67 ± 0.14	0.84	2[v]
Genus *Schima*					
S. argentea		NCSU 1999-098	1.70 ± 0.15	0.85	2
S. khasiana		NCSU 2002-084	1.66 ± 0.29	0.83	2
S. remotiserrata		CF	1.76 ± 0.13	0.88	2
		(SM) HJM 15095	1.87 ± 0.22	0.94	2
S. sinensis		(SM) 91-339	1.65 ± 0.21	0.83	2
S. superba		NCSU 2018-009	1.53 ± 0.20	0.77 0.82	2[v]
		GrN	1.64 ± 0.13		
S. wallichii		NCSU 2002-082	1.71 ± 0.17	0.86	2
Subfamily *Stewartiae*					
Genus *Stewartia*					
S. ovata		NCSU 2018-110	4.69 ± 0.49	2.35	2
		JJ	7.04 ± 0.54	3.52	3
S. pseudocamellia		NCSU 2018-111	5.42 ± 0.43	2.71	2[v]
S. sp. = *Hartia* sp.		(SM) 20161960	5.22 ± 0.57	2.61	2
Subfamily *Theeae*					
Genus *Camellia*					
Subgenus *Camellia*					
Section *Camellia*					
C. azalea = changii		*CGBG*	5.41 ± 0.34	2.71	2[v]
C. chekiangoleosa		NCSU 2017-085	6.11 ± 0.37	3.06	2
C. chekiangoleosa		UF 20010380	5.74 ± 0.28	2.87	2
C. edithae		CF	6.21 ± 0.44	3.11	2
C. hongkongensis		GN	5.85 ± 0.32	2.93	2
C. japonica	'Anacostia'	NCSU 2015-057	6.34 ± 0.41	3.17	2
C. japonica	'April Dawn'	NCSU 2014-164	5.78 ± 0.58	2.89	2
C. japonica	'April Kiss'	NCSU 2016-093	6.54 ± 0.39	3.27	2
C. japonica	'April Pink'	NCSU 2014-075	6.36 ± 0.42	3.18	2
C. japonica	'April Remembered'	NCSU 2014-170	6.14 ± 0.53	3.07	2
C. japonica	'April Rose'	NCSU 2014-165	5.94 ± 0.57	2.97	2
C. japonica	'April Snow'	NCSU 2014-179	6.34 ± 0.37	3.17	2
C. japonica	'Autumn Mist'	NCSU 2016-109	6.51 ± 0.38	3.26	2
C. japonica	'Black Magic'	NCSU 2015-004	6.13 ± 0.44	3.07	2
C. japonica	'Curly Lady'	JCRA 130976	6.25 ± 0.47	3.13	2
C. japonica	'Daikagura'	NCSU 2015-074	6.13 ± 0.44	3.07	2
C. japonica	'Dr. J.C. Raulston'	JCRA 080238	6.13 ± 0.47	3.07	2[v]
C. japonica	'Early Autumn'	NCSU 2016-069	6.21 ± 0.42	3.10	2
C. japonica	'Frost Queen'	NCSU 2014 181	5.85 ± 0.63	2.93	2
C. japonica	'Francis Eugene Phillips'	GN	6.44 ± 0.40	3.22	2
C. japonica	'Francis Eugene Phillips' (sport)	GN	6.48 ± 0.34	3.24	2
C. japonica	'Governor Mouton'	NCSU 2016-005	6.47 ± 0.39	3.24	2
C. japonica	'Kramer's Supreme'	GN	6.16 ± 0.52	3.08	2
C. japonica	Korean Source	NCSU 1998-142	6.27 ± 0.42	3.14	2
C. japonica	'Korean Fire'	NCSU 2014-168	6.33 ± 0.44	3.17	2
C. japonica	'Korean Snow'	NCSU 2014-028	6.21 ± 048	3.11	2
C. japonica	'Kotsuya Nomura'	GrN	6.10 ± 0.56	3.05	2
C. japonica	'Kuro Delight'	NCSU 2014-178	5.84 ± 0.62	2.92	2
C. japonica	'Irrational Exuberance'	GN	6.33 ± 0.41	3.17	2
		GrN	6.31 ± 0.49	3.16	2
C. japonica	'Lady Vansittart'	NCSU 2016-107	6.62 ± 0.37	3.31	2
C. japonica	'Longwood Valentine'	NCSU 2014-176	6.22 ± 0.47	3.11	2
C. japonica	'Meadowbrook'	NCSU 2014-141	6.09 ± 0.47	3.05	2
C. japonica	'Morris Mercury'	NCSU 2014-167	6.25 ± 0.47	3.12	2
C. japonica	'Night Rider'	NCSU 2016-101	6.38 ± 0.40	3.19	2
C. japonica	'October Affair'	NCSU 2015-075	5.91 ± 0.53	2.96	2
C. japonica	'Portuensis'	GN	6.35 ± 0.44	3.18	2
C. japonica	'Professor Sargent'	JCRA xx0503	5.98 ± 0.47	2.99	2
C. japonica	'Quercifolia'	JCRA 940448	6.53 ± 0.32	3.27	2
C. japonica	'Red Jade'	NCSU 2014-180	6.07 ± 0.55	3.04	2
C. japonica	'Royal Velvet'	NCSU 2017-003	6.56 ± 0.38	3.28	2
C. japonica	'Sadaharu Oh'	GrN	6.33 ± 0.48	3.17	2
C. japonica	'Sakuraba Tsubaki'	GN	6.37 ± 0.45	3.19	2
C. japonica	'Tama No Ura'	NCSU 2017-002	6.33 ± 0.43	3.17	2
C. japonica 'Tama No Ura' OP	(Formal White unnamed selection)	GrN	6.16 ± 0.52	3.08	2
C. japonica	'Tama Electra'	NCSU 2017-001	6.39 ± 0.41	3.20	2
C. japonica	'Tiny Tot'	NCSU 2014-172	6.19 ± 0.45	3.10	2
C. japonica	'White By The Gate'	JCRA xx0504	6.42 ± 0.46	3.21	2

Table 2. (*Continued*) Genome sizes and estimated ploidy levels of cultivated *Camellia* and related taxa.

Taxa[z]	Cultivar/selection	Source/accession[y]	2C genome size[x] (pg)	1C*x* genome size (pg)[w]	Estimated ploidy (*x*)
Subfamily *Gordoniae*					
Genus *Franklinia*					
C. japonica	Unnamed selection ('Royal Velvet' × 'Francis Eugene Phillips')	GN	6.49 ± 0.41	3.25	2
C. japonica var. decumbens	'Madoka'	JCRA 100395	6.18 ± 0.45	3.09	2
C. pitardii var. compressa = magniflora		CF	20.72 ± 1.49	3.45	6
C. polyodonta		CGBG12	5.42 ± 0.37	2.71	2
		DZ068-14	6.96 ± 0.34	3.48	2
C. reticulata	'Captain Rawes'	CGBG22	16.67 ± 1.05	2.78	6
C. reticulata	'Purple Gown'	CF	17.17 ± 1.11	2.86	6
C. semiserrata		UF 20010410	6.04 ± 0.49	3.02	2
Section *Heterogenea*					
C. crapnelliana = giganticarpa		CGBG13	6.41 ± 0.46	3.21	2
C. crapnelliana = octopetala		CF	6.76 ± 0.42	3.38	2
Section *Paracamellia*					
C. brevistyla var. brevistyla = puniceiflora		CGBG14	12.35 ± 0.50	3.09	4
C. grijsii		CF	5.65 ± 0.51	2.83	2
C. grijsii var. grijsii = odorata		CF	16.33 ± 0.81	2.72	6
C. hiemalis	'Rose of Autumn'	JCRA 070075	21.11 ± 1.59	3.52	6
C. oleifera		NCSU 2015-099	19.67 ± 1.50	3.16	6
C. oleifera		SM14227	17.43 ± 1.68	2.91	6
C. oleifera	'Lu Shan Snow'	CF	18.96 ± 1.70	3.11	6
C. oleifera	'Plain Jane'	CF	18.66 ± 1.31	3.18	6
C. sasanqua	'Autumn Moon'	NCSU 2016-112	22.44 ± 1.25	3.74	6
C. sasanqua	'Autumn Rocket'	NCSU 2015-071	20.39 ± 0.82	3.40	6
C. sasanqua	'Autumn Sentinel'	NCSU 2016-108	20.64 ± 1.36	3.44	6
C. sasanqua	'Dwarf Shishi'	NCSU 2016-116	17.19 ± 1.51	2.87	6
C. sasanqua	(Gold Leaf)	JCRA 070618	24.2 ± 1.07	3.03	8
C. sasanqua	'Green 94-035'	JCRA 110770	16.59 ± 1.45	2.77	6
C. sasanqua	'Green 99-031'	NCSU 2015-005	22.11 ± 1.44	3.69	6
C. sasanqua	'Green's Blues'	NCSU 2015-065	17.69 ± 1.62	2.95	6
C. sasanqua	'Hiryu'	JCRA xx0501	18.97 ± 1.43	3.16	6
C. sasanqua	'Narumigata'	GrN	22.04 ± 0.72	3.67	6
C. sasanqua	'Reverend Ida'	GN	18.92 ± 0.72	3.15	6
C. sasanqua	'Rosy Pillar'	NCSU 2016-105	15.37 ± 1.04	2.56	6
C. sasanqua	'Sarrel'	CF	19.76 ± 1.63	3.29	6
C. sasanqua	'Seventh Desire'	JCRA 050109	22.11 ± 1.62	3.69	6
C. sasanqua	'Silver Dollar'	CF	19.82 ± 1.15	3.30	6
C. sasanqua	'Yuletide'	CF	18.38 ± 2.29	3.06	6
C. drupifera = vietnamensis		GrN	23.00 ± 1.50	2.88	8
C. drupifera = vietnamensis		CGBG11	22.87 ± 1.22	2.86	8
C. grijsii var. grijsii = yuhsienensis		CF	16.25 ± 1.45	2.71	6
C. grijsii var. grijsii = yuhsienensis		CGBG25	17.19 ± 1.05	2.87	6
Subgenus *Thea*					
Section *Archecamellia*					
C. chrysanthoides		GN	5.53 ± 0.37	2.77	2
C. euphlebia		GN	5.70 ± 0.39	2.85	2
C. petelotii var. microcarpa = microcarpa		DZ039-13	6.11 ± 0.47	3.06	2
C. petelotii var. petelotii = nitidissima		DZ047	5.41 ± 0.47	2.21	2
Section *Camelliopsis*					
C. caudata var. caudata = assimilis		CGBG2	6.71 ± 0.37	3.36	2
C. cordifolia		CGBG27	6.38 ± 0.43	3.19	2
Section *Thea*					
C. sinensis	'Black Sea'	NCSU 2016-103	6.69 ± 0.39	3.35	2
C. sinensis	'Charles Town Tea'	GN	13.48 ± 0.67	3.37	4
C. sinensis	'Korean Tea'	NCSU 2018-131	6.46 ± 0.43	3.23	2
C. sinensis	'Large Leaf Form'	CF	12.97 ± 0.75	3.24	4
C. sinensis	'Rosea'	NCSU 2018-108	5.98 ± 0.62	2.99	2
C. sinensis	'Red Leaf'	NCSU 2017-111	6.22 ± 0.49	3.11	2[v]
C. sinensis	'Small Leaf Tea'	NCSU 2016-106	6.82 ± 0.36	3.41	2
C. sinensis	'Sochi'	NCSU 2016-099	6.95 ± 0.35	3.48	2
Section *Theopsis*					
C. rosthorniana = buxifolia		CGBG24	7.29 ± 0.33	3.65	2
C. fraterna		JCRA 110895	18.19 ± 1.06	3.03	6
C. rosthorniana = handellii		UF 20110290	6.86 ± 0.53	3.43	2
C. rosthorniana = handellii	'Mark'	GN	7.27 ± 0.37	3.64	2
C. lutchuensis		CGBG9	6.31 ± 0.45	3.16	2
C. lutchuensis var. lutchuensis = transnokoensis		GN	6.52 ± 0.41	3.26	2
C. trichoclada		CGBG3	6.58 ± 0.46	3.29	2
C. tsaii var. syaptica	'Elina Cascade'	CF	7.11 ± 0.32	3.56	2
Genus *Polyspora*					
P. axillaris		GrN	11.32 ± 0.54	1.89	6

(*Continued on next page*)

Table 2. (*Continued*) Genome sizes and estimated ploidy levels of cultivated *Camellia* and related taxa.

Taxa[z] Subfamily *Gordoniae* Genus *Franklinia*	Cultivar/selection	Source/accession[y]	2C genome size[x] (pg)	1Cx genome size (pg)[w]	Estimated ploidy (x)
P. axillaris		UF 20171030	3.27 ± 0.34	1.63	2
P. axillaris		UF 20030900	9.27 ± 0.84	1.55	6
P. chrysandra		NCSU 2015-114	3.66 ± 0.32	1.88	2[v]
P. chrysandra		USNA 81628	3.58 ± 0.32	1.79	2
P. sp.		JCRA 131041	13.61 ± 0.75	1.70	8
P. sp.		UF 20111400	15.69 ± 0.97	1.96	8
Genus *Pyrenaria*					
P. microcarpa		JCRA 140655	2.31 ± 0.20	1.16	2
P. microcarpa		GrN	3.34 ± 0.33	1.67	2
P. spectabilis = Tutcheria spectabilis		GrN	2.66 ± 0.13	1.33	2[v]
***Unplaced in Ming & Bartholmew (2007) Genus *Camellia*					
C. amplexicaulis		GN	4.40 ± 0.36	2.20	2
C. flava		GN	5.28 ± 0.31	2.64	2
C. cucphuongensis		GN	5.11 ± 0.40	2.55	2
C. nanyongensis		CF	6.34 ± 0.46	3.17	2
C. meiocarpa		CGBG5	12.44 ± 0.77	3.11	4

[z]Taxonomy according to Ming and Bartholomew (2007). Synonyms if applicable, are given.
[y]CGBG = Coastal Georgia Botanical Garden, Savannah, GA; CF = Camellia Forest Nursery (Clifford and David Parks), Chapel Hill, NC; DZ = Donglin Zhang, University of Georgia, Athens, GA; GN = Gene's Nursery (Gene Phillips), Savannah, GA; GrN = Green Nurseries, Fairhope, AL; JCRA = JC Raulston Arboretum, Raleigh, NC; NCSU = North Carolina State University Mountain Horticultural Crops Research and Extension Center, Mills River, NC; SM = Scott McMahan, Atlanta Botanical Garden, Atlanta, GA; UF 2 = North Florida Research and Education Center, Quincy, FL; USNA = United States National Arboretum, Washington, DC.
[x]Holoploid genome sizes were determined using propidium iodide as the fluorochrome stain. Values are x ± SEM, n = 2–3.
[w]1Cx values were calculated as 2C value/ploidy level.
[v]Ploidy levels were confirmed by cytology.

series, including *C. caudata, costeri, crapnelliana, forrestii, grijsii, hiemalis, japonica, kissii, mairei, nanyoungensis, octopetala, oleifera, pitardii, reticulata, rubituberculata, salicifolia, saluenensis, sasanqua, sinensis, tsaii, yuhsienensis,* and *yungkiangensis.* There have been occasional reports of anisoploids in *C. assamica, irrawadiensis, japonica, rosaeflora, sasanqua, sinensis, vietnamensis,* and some cultivars of the interspecific hybrid *C. ×vernalis* that may have resulted from unreduced gametes, interploid hybridization, or nonrecurrent apomixis (Ozias-Akins and van Dijk, 2007). Previous research summarized in Table 1 has emphasized the cytogenetic diversity within Theaceae and has aided in the understanding of relationships between members of Theaceae. The previous cytogenetic and cytometric data serve as an accessible reference for plant breeders, taxonomists, and others studying Theaceae.

Cytology was completed for representative Theaceae, including species of *Camellia, Gordonia, Polyspora, Pyrenaria, Schima,* and *Stewartia* (Fig. 1). Results documented *Camellia azalea* (2018-063) as $2n = 2x = 30$, *Camellia japonica* 'Dr. JC Raulston' as $2n = 2x = 30$, *Camellia sinensis* (2017-111) as $2n = 2x = 30$, *Camellia ×vernalis* 'Egao Corkscrew' as $2n = 4x = 60$, *Gordonia lasianthus* (2006-220) as $2n = 2x = 36$, *Polyspora chrysandra* (2015-114) as $2n = 2x = 30$, *Schima superba* (2018-009) as $2n = 2x = 36$, *Stewartia pseudocamellia* (2018-111) as $2n = 2x = 34$, and *Pyrenaria spectabilis* (2018-008) as $2n = 2x = 30$. These results further substantiate the base chromosome numbers for these genera and provide additional direct standards to further calibrate ploidy with genome size.

Flow cytometry was completed for a broad range of taxa for Theaceae, providing data regarding 2C holoploid genome size, 1Cx monoploid genome size, and estimated ploidy for 123 nonhybrid accessions (Table 2). Our study represents new data for many cultivars of *C. japonica, C. sasanqua, C. sinensis, C. oleifera, C. rosthorniana,* and *C. hiemalis.* Furthermore, the ploidy level of seven previously unreported species of *Camellia,* including *C. amplexicaulis, C. chrysanthoides, C. cordifolia, C. cucphuongensis, C. flava, C. nanyongensis,* and *C. trichoclada,* was found to be diploid. The majority of tested *Camellia* species exhibited 2C genome sizes consistent with previously reported ploidy, although there were many exceptions (Table 1). The accession of *C. assimilis* CGBG2 was found to be diploid, consistent with the results of Fukushima et al. (1966) and Kondo (1977). Regarding *Camellia* (Ming and Bartholomew, 2007), *C. assimilis* is synonymous with *C. caudata,* which has been reported both as diploid (Bezbaruah, 1971; Zhuang and Dong, 1984) and tetraploid (Gu et al., 1988b; 1989b; Gu and Sun, 1997), indicating the existence of a possible ploidy series. *Camellia brevistyla,* reported by Zhang and Min (1999) as diploid, was found to be tetraploid in this study, although the tested accession was received as *C. puniceiflora,* which, according to Ming and Bartholomew (2007), is synonymous with *C. brevistyla* var. *brevistyla. Camellia grijsii* has a reported ploidy series including diploids (Gu et al., 1988b; 1989b; Huang et al., 2013; Lu et al., 1993; Xiao et al., 1991), tetraploids (Huang and Hsu, 1987; Kondo et al., 1991), pentaploids (Huang and Hsu, 1987), and hexaploids (Huang and Hsu, 1987; Xiao

et al., 1991). The surveyed accession of *C. grijsii* was diploid, and the accession of *C. odorata* syn. *C. grijsii* var. *grijsii* (Ming and Bartholomew, 2007) was hexaploid. Both accessions of *C. yuhsienensis,* which is also synonymous with *C. grijsii* var. *grijsii,* were hexaploid, although *C. yuhsienensis* has been reported as tetraploid (Zhuang and Dong, 1984), pentaploid (Zhuang and Dong, 1984), and hexaploid (Huang et al., 2013; Xiao et al., 1993; Zhuang and Dong, 1984). Both accessions of *C. lutchuensis* were diploid, which was in agreement with previous reports (Ackerman, 1971; Kondo, 1977; Kondo and Parks, 1979). However, one of the accessions of *C. lutchuensis* was received as *C. transnokoensis,* which is synonymous with *C. lutchuensis* var. *lutchuensis* (Ming and Bartholomew, 2007). Kondo (1977) reported *C. transnokoensis* as hexaploid. The surveyed accession of *C. reticulata* 'Captain Rawes', which was reported to be triploid by Patterson et al. (1950), was found to be hexaploid. *Camellia azalea* (=*C. changii*), a relatively newly discovered species with considerable breeding potential, was estimated by Huang et al. (2013) to be hexaploid, although the accession of this species surveyed in this study was confirmed to be diploid through flow cytometry and cytology. This result was further supported by the diploidy of *C.* 'Wendzalea', a hybrid of *C. azalea* and *C. japonica* (diploid). The confusion and complexity of *Camellia* nomenclature and variations in ploidy within species emphasize the need to collect and reference data regarding individual clones and accessions.

The other genera of Theaceae included in this study are muc h less commonly cultivated and have been less studied compared

Table 3. Monoploid genome sizes (1Cx), determined by flow cytometry, for *Camellia* and related taxa grouped by subfamily, section, genus, species within the Theaceae.

Subfamily	1Cx (pg)[z]	Genus	1Cx (pg)[z]	Subgenus	1Cx (pg)	Section	1Cx (pg)[z]	Species	1Cx (pg)[z]
Gordoniae	0.84 C	*Franklinia*	0.81 D					*F. alatamaha*	0.81 O
		Gordonia	0.84 D					*G. lasianthus*	0.84 O
		Schima	0.84 D					*S. argentea*	0.85 O
								S. khasiana	0.83 O
								S. remotiserrata	0.91 NO
								S. sinensis	0.82 O
								S. superba	0.79 O
								S. wallichii	0.86 O
Stewartiae	2.50 B	*Stewartia*	2.50 B					*S. ovata*	2.34 JK
								S. pseudocamellia	2.71 HIJ
								S. sp. (*Hartia* sp.)	2.61 IJ
Theeae	3.00 A	*Camellia*	3.13 A	*Camellia*	3.11 B	*Camellia*	3.10 AB	*C. azalea*	2.70 HIJ
								C. chekiangoleosa	2.96 DEFGHI
								C. edithae	3.11 BCDEFGH
								C. hongkongensis	2.93 DEFGHI
								C. japonica	3.13 ABCDEFGH
								C. pitardii	3.45 ABC
								C. polyodonta	3.10 BCDEFGH
								C. reticulata	2.82 GHI
								C. semiserrata	3.02 CDEFGHI
						Heterogenea	3.29 A	*C. crapnelliana*	3.29 ABCDEF
						Paracamellia	3.11 AB	*C. brevistyla*	3.09 BCDEFGH
								C. drupifera	2.87 FGHI
								C. grijsii	2.78 GHIJ
								C. oleifera	3.11 BCDEFGH
								C. sasanqua	3.21 ABCDEF
				Thea	3.25 A	*Archecamellia*	2.84 B	*C. chrysanthoides*	2.76 GHIJ
								C. euphlebia	2.85 FGHI
								C. petelotii	2.88 EFGHI
						Eriandria	3.27 A	*C. caudata*	3.36 ABCD
								C. cordifolia	3.19 ABCDEFG
						Thea	3.32 A	*C. sinensis*	3.32 ABCD
						Theopsis	3.38 A	*C. fraterna*	3.03 CDEFGHI
								C. lutchuensis	3.21 ABCDEF
								C. rosthorniana	3.57 A
								C. trichoclada	3.29 ABCDE
								C. tsaii	3.56 A
		Polyspora	1.75 C					*P. axillaris*	1.69 LM
								P. chrysandra	1.75 LM
								P. sp. (UF20111400)	1.96 LK
								P. sp. (JCRA) 131041)	1.70 LM
		Pyrenaria	1.39 C					*P. microcarpa*	1.41 M
								P. spectabilis	1.33 MN

Values followed by different letters within a column are significantly different according to Fisher's least significant difference test, $P \leq 0.05$.

with *Camellia*. Ploidy levels of 24 accessions of six other genera were determined, including *Franklinia*, *Gordonia*, *Schima*, *Stewartia*, *Polyspora*, and *Pyrenaria*. The genus *Polyspora* (many species of which were previously included in *Gordonia*) (Yang et al. 2004) was found to have a ploidy series ranging from $2n = 2x = 30$ to $2n = 8x = 120$. The ploidy levels of four species of *Schima*, including *S. argentea*, *S. khasiana*, *S. remotiserrata*, and *S. sinensis*, have been reported as diploid for the first time. A triploid accession of *Stewartia ovata* included in this study represented the first polyploid report of this genus; however, this was possibly the result of an unreduced gamete.

Monoploid genome sizes (1Cx) varied considerably by subfamily (Table 3), with the Gordoniae having a mean of 0.84 pg, and the Stewartiae and Theeae having substantially larger values of 2.50 and 3.00 pg, respectively. The much larger 1Cx values of the Stewartiae and Theeae indicated that they underwent considerable genome expansion

independent of increased ploidy levels as these lineages diverged. Genome expansion such as this can occur through amplification of noncoding repetitive DNA including retrotransposons (Leitch and Leitch, 2013). The biological impact of genome size variation is still being elucidated, but the speciation rate has been shown to be correlated with the rate of genomic evolution and genome size (Bromham et al. 2015; Puttick et al., 2015). Within the subfamily Theeae, *Camellia* also had a significantly higher mean genome size of 3.13 pg compared with 1.75 pg for *Polyspora* and 1.39 pg for *Pyrenaria*, indicating differential rates of genome expansion among these groups. Even within *Camellia*, there were significant differences in 1Cx values among subgenera, sections, and some species (range, 2.70–3.57 pg), indicating that the evolution of chromosomes and genome size has been particularly dynamic compared with sister lineages.

Genome size has been used to estimate ploidy of interspecific hybrids, and it has been particularly useful for validating inter-

ploid and intergeneric hybrids (Table 4). All noninterploid, interspecific *Camellia* hybrids had estimated ploidy levels that were consistent with their reported parentage. However, the genome size of one putative intergeneric hybrid, *C. japonica* × *F. alatamaha* (USNA 79387) (Ackerman and Williams, 1982), was inconsistent with the reported parentage. Genome sizes are considerably different for these two parents (2C = 5.78–7.11 pg for *C. japonica* and 2C = 1.62 pg for *F. alatamaha*), yet the putative hybrid was 2C = 5.94, effectively discounting hybridity. Many putative interspecific interploid hybrids also had genome sizes and estimated ploidy levels that were inconsistent with their reported parentage. For example, 'Arctic Dawn', 'Fire 'N' Ice', 'Ice Follies', 'Pink Icicle', 'Red Fellow', 'Spring Cardinal', and 'Spring Circus' are all putative hybrids between hexaploid and diploid taxa, yet they have genome sizes consistent with diploids, suggesting they are the result of pollen contamination, mislabeling, or apomixis. Similarly, 'Spring Frill' is a putative hybrid between a

Table 4. Genome sizes and estimated ploidy levels of interspecific *Camellia* hybrids.

Purported parentage	Cultivar/selection	Source/accession[z] Intraploid hybrids	2C genome size [mean ± SEM (pg)][y]	Weighted 1Cx genome size (pg)[x]	Purported parental ploidy levels (x)	Estimated ploidy (x)[w]
C. japonica ssp. *rusticana* ×*lutchuensis*	'Fragrant Joy'	NCSU 2016-096	6.52 ± 0.36	3.17	2 × 2	2
C. ×*williamsii*	'Freedom Bell'	CF	6.35 ± 0.41	2.96	2 × 2	2
C. japonica ×*C. edithae*	'Heimodan'	CF	6.35 ± 0.45	3.12	2 × 2	2
C. ×*williamsii*	'Mary Christian'	JCRA xx0193	5.84 ± 0.48	2.96	2 × 2	2
C. pitardii × *C. japonica*	'Nicky Crisp'	NCSU 2015-134	5.85 ± 0.58	3.29	2 × 2	2
C. flava × *C. japonica*	'Optical Illusion'	CF	5.71 ± 0.46	2.89	2 × 2	2
C. japonica × *C. lutchuensis*	'Quintessence'	UF 20071130	6.11 ± 0.49	3.17	2 × 2	2
C. japonica × *C. sinensis*	'Robiraki'	CF	5.91 ± 0.53	3.20	2 × 2	2
C. ×*williamsii*	'Taylor's Perfection'	CGBG1	6.35 ± 0.41	2.96	2 × 2	2
C. japonica 'Wendy' × *C. azalea*	'Wendzalea'	GN	6.17 ± 0.39	2.92	2 × 2	2
C. flava × *C. japonica* 'Snowman'	Unnamed selection	GN	5.91 ± 0.33	2.89	2 × 2	2
C. japonica × *C. flava*	Unnamed selection	GN	5.93 ± 0.36	2.89	2 × 2	2
C. amplexicaulis × *C. japonica* 'Royal Velvet'	Unnamed selection	GN	5.45 ± 0.33	2.67	2 × 2	2
C. amplexicaulis × *C. japonica* 'Kramer's Supreme'	Unnamed selection	GN	5.56 ± 0.31	2.67	2 × 2	2
Camellia japonica × *Franklinia alatamaha*	Unnamed selection	USNA 79387	5.94 ± 0.51[x]	1.97	2 × 2	2[v]
C. sasanqua 'Shikishima' × *C. oleifera* 'Plain Jane'	'Ashton's Ballet'	NCSU 2015-071	20.44 ± 0.82	3.09	6 × 6	6
C. sasanqua 'Shikishima' × *C. oleifera* 'Plain Jane'	'Ashton's Ballet'	USNA 82775	21.24 ± 0.99	3.09	6 × 6	6
C. oleifera 'Plain Jane' × *C. sasanqua* 'Santō-zaki'	'Ashton's Pride'	CF	18.67 ± 1.47	3.12	6 × 6	6
(*C. sasanqua* 'Bill Wylam' × *C. oleifera* 'Plain Jane') × (*C. sasanqua* 'Narumi-gata' × *C. oleifera* 'Plain Jane')	'Ashton's Supreme'	NCSU 2016-098	20.14 ± 0.93	3.16	6 × 6	6
(*C. sasanqua* 'Bill Wylam' × *C. oleifera* 'Plain Jane') × (*C. sasanqua* 'Narumi-gata' × *C. oleifera* 'Plain Jane')	'Ashton's Supreme'	USNA 79392	20.77 ± 0.93	3.16	6 × 6	6
C. oleifera × *C. sasanqua*	'Carolina Moonmist'	NCSU 2014-166	20.98 ± 1.07	3.08	6 × 6	6
C. sasanqua 'Narumi gata' × *C. oleifera*	'CF21'	H2003-023-011	18.53 ± 1.51	3.16	6 × 6	6
(*C. reticulata* × *C. fraterna*) OP	'Crimson Candles'	JCRA	15.26 ± 0.94	2.92	6 × ?	6
C. 'Yume' OP	'Dream Quilt'	NCSU 2015-003	18.73 ± 1.67	3.15	6 × ?	6
C. hiemalis 'Bill Wylam' × *C. oleifera*	'Frost Princess'	USNA 75304	20.64 ± 0.98	3.32	6 × 6	6
C. oleifera 'Plain Jane' × *C. sasanqua*	'Londontowne Blush'	USNA 73731	21.84 ± 1.44	3.12	6 × 6	6
C. 'Yume' OP	'Marshall'	GN	17.56 ± 1.04	3.15	6 × ?	6
C. × 'Frost Princess' (*C. hiemalis* 'Bill Wylam' × *C. oleifera*) × *C. oleifera*	'Polar Ice'	CF	19.98 ± 1.94	3.22	6 × 6	6
C. oleifera 'Plain Jane' × *C.* × 'Frost Princess' (*C. hiemalis* 'Bill Wylam' × *C. oleifera* 'Plain Jane')	'Snow Flurry'	CF	20.17 ± 1.59	3.22	6 × 6	6
C. sasanqua 'Narumi-gata' × *C. oleifera*	'Survivor'	CF	22.00 ± 1.52	3.08	6 × 6	6
C. sasanqua 'Takara-wase' × *C. oleifera* 'Plain Jane'	'Winter's Charm'	CGBG17	20.40 ± 1.59	3.08	6 × 6	6
C. oleifera 'Plain Jane' × (*C. sasanqua* 'Narumi-gata' × *hiemalis* 'Shishigashira')	'Winter's Cupid'	USNA 69933	21.30 ± 1.02	3.12	6 × 6	6
C. hiemalis 'Shishigashira' × *C. oleifera* 'Lu Shan Snow'	'Winter's Darling'	USNA 75299	22.30 ± 1.08	3.32	6 × 6	6
C. hiemalis 'Bill Wylam' × (*C. hiemalis* 'Shishigashira' × *C. oleifera* 'Plain Jane')	'Winter's Fancy'	USNA 69934	19.78 ± 0.89	3.52	6 × 6	6
C. oleifera Lu Shan Snow' × *C.* 'Frost Princess'	'Winter's Hope'	CF	19.65 ± 1.27	3.22	6 × 6	6
C. oleifera 'Plain Jane' × *C.* sp. 'Pink Tea;	'Winter's Interlude'	CF	20.07 ± 2.03	3.12	6 × ?	6
(*C. sasanqua* 'Narumi-gata' × *C. hiemalis* 'Shishigashira') × *C. oleifera* 'Plain Jane'	'Winter's Joy'	CF	20.47 ± 1.69	3.16	6 × 6	6
C. oleifera 'Plain Jane' × (*C. sasanqua* 'Narumi-gata' × *C. hiemalis* 'Shishigashira')	'Winter's Peony'	CF	20.47 ± 1.69	3.16	6 × 6	6
C. hiemalis 'Shishigashira' × *C. oleifera* 'Lu Shan Snow'	'Winter's Red Rider'	CF	21.28 ± 0.99	3.16	6 × 6	6
C. oleifera 'Plain Jane' × *C. hiemalis* 'Otome'	'Winter's Rose'	CF	20.79 ± 1.37	3.32	6 × 6	6
C. oleifera × *C. hiemalis* 'Show-no-sakae'	'Winter's Star'	CGBG19	20.97 ± 1.50	3.32	6 × 6	6
C. oleifera 'Lu Shan Snow' × *C. hiemalis* 'Show-no-sakae'	'Winter's Star'	JCRA 090424	21.02 ± 1.02	3.32	6 × 6	6
Sport of 'Winter's Star'	'Winter's Star Light'	JCRA 960468	17.265 ± 1.45	3.32	6	6

Table 4. (*Continued*) Genome sizes and estimated ploidy levels of interspecific *Camellia* hybrids.

Purported parentage	Cultivar/selection	Source/accession[z] Intraploid hybrids	2C genome size [mean ± SEM (pg)][y]	Weighted 1Cx genome size (pg)[x]	Purported parental ploidy levels (x)	Estimated ploidy (x)[w]
C. oleifera 'Plain Jane' × *C. sasanqua* 'Jean May'	'Winter's Toughie'	CF	15.90 ± 1.48	3.16	6 × 6	6
C. oleifera 'Plain Jane' × *C. sasanqua* 'Mine-no-yuki'	'Winter's Waterlily'	CF	20.74 ± 1.45	3.16	6 × 6	6
C. hiemalis 'Shishigashira' × *C. yushienensis*	'Yume'	CF	17.25 ± 1.51	2.93	6 × 6	6
C. 'Winter's Charm' (*C. sasanqua* 'Takara-wase' × *C. oleifera*) OP	Unnamed selection	H2003-022-002	20.96 ± 0.92	3.16	6 × ?	6
C. 'CF.21' (*C. sasanqua* 'Narumigata' × *C. oleifera*) OP	Unnamed selection	NCSU H2003-023-011	19.24 ± 1.61	3.16	6 × 6	6
C. 'Winter's Charm' (*C. sasanqua* 'Takara-wase' × *C. oleifera*) OP	Unnamed selection	H2003-024-001	18.14 ± 1.22	3.16	6 × ?	6
C. 'Winter's Charm' (*C. sasanqua* 'Takara-wase' × *C. oleifera*) OP	Unnamed selection	H2003-024-005	18.74 ± 0.70	3.16	6 × ?	6
Putative Interploid Hybrids						
C. ×*williamsii* 'November Pink' × *C. oleifera* 'Lu Shan Snow'	'Arctic Dawn'	USNA 82774	6.01 ± 0.44	3.04	2 × 6	2[v]
C. japonica × *C. oleifera*	'Fire 'N' Ice'	USNA 63544	6.05 ± 0.57	3.10	2 × 6	2[v]
C. ×*williamsii* 'November Pink' × *C. oleifera* 'Lu Shan Snow'	'Ice Follies'	CF	6.27 ± 0.42	3.10	2 × 6	2[v]
C. ×*williamsii* 'November Pink' × *C. oleifera* 'Lu Shan Snow'	'Pink Icicle'	CF	5.99 ± 0.56	3.04	2 × 6	2[v]
C. japonica 'Tricolor Red' × *C. oleifera* 'Plain Jane'	'Red Fellow'	CF	6.23 ± 0.44	3.10	2 × 6	2[v]
C. japonica 'Tricolor Red' × *C. oleifera* 'Plain Jane'	'Spring Cardinal'	CF	6.14 ± 0.51	3.10	2 × 6	2[v]
C. japonica 'Tricolor Red' × *C. oleifera* 'Plain Jane'	'Spring Circus'	USNA 73726	6.10 ± 0.52	3.10	2 × 6	2[v]
C. oleifera 'Plain Jane' × *C.* ×*vernalis* 'Egao'	'Spring Frill'	CF	6.02 ± 0.49	3.14	6 × 4	2[v]
C. ×*vernalis* 'Egao' OP	'Christmas Candy'	GrN	9.52 ± 0.69	3.17	4 × ?	3
C. ×*vernalis*	'Ginryu' ('Dawn')	GrN	8.90 ± 0.48	2.97	? × ?	3
C. ×*vernalis*	'Starman'	GrN	9.35 ± 0.64	3.17	3 × ?	≈3
C. ×*vernalis* 'Ginryu' OP	Unnamed selection	GrN 00-020	9.29 ± 0.92	3.17	4 × ?	3
C. ×*vernalis* 'Star-Above-Star' OP	Unnamed selection	GrN 05-017	9.93 ± 0.69	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-051	10.13 ± 0.72	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-052	8.45 ± 1.13*	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-053	9.85 ± 0.57	3.17	4 × ?	3
C. ×*vernalis* 'Star-Above-Star' OP	Unnamed selection	GrN 07-054	9.73 ± 0.76	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-065	9.16 ± 0.69	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-066	9.86 ± 1.04*	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 08-054	8.91 ± 0.83	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 08-056	9.27 ± 0.87	3.17	4 × ?	3
C. ×*vernalis* 'Ginryu' OP	Unnamed selection	GrN 08-070	9.78 ± 0.60	3.17	3 × ?	≈3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 08-071	9.68 ± 0.47	3.17	4 × ?	3
C. ×*vernalis* 'Egao' OP	Unnamed selection	GrN 13-007	9.92 ± 0.38	3.17	4 × ?	3
C. japonica × *C. oleifera*	'Ashton's Pink'	NCSU 2015-066	12.87 ± 0.67	3.13	2 × 6	4
C. ×*vernalis* 'Star-Above-Star' OP	'Dabney's Star'	GrN	12.84 ± 0.78	3.17	4 × ?	4
C. ×*vernalis*	'Egao'	GrN	13.08 ± 0.81	3.08	2 × 6	4
Sport of *C.* ×*vernalis* 'Egao'	'Egao Corkscrew'	JCRA	12.81 ± 0.92	3.08	2 × 6	4[u]
C. japonica 'Mrs. Bertha A. Harms' × *C. oleifera* 'Plain Jane'	'Elaine Lee'	CF	13.47 ± 0.94	3.17	2 × 6	4
C. japonica 'Frost Queen' × *C. oleifera*	'Fairweather Favorite'	USNA 73958	13.19 ± 0.91	12.2	2 × 6	4
C. ×*vernalis*	'Star Above Star'	NCSU 2017-104	12.23 ± 0.63	3.17	2 × 6	4
C. japonica 'Billie McCaskill' × *C. oleifera* 'Plain Jane'	'Winter's Beauty'	CGBG21	12.92 ± 0.61	3.17	2 × 6	4
C. japonica × *C. yushienensis*	Unnamed selection	CF	12.12 ± 0.62	2.88	2 × 6	4
C. 'Christmas Candy' (*C.* ×*vernalis* OP) OP	Unnamed selection	GrN J-081	12.52 ± 0.73	3.17	3 × ?	4
C. ×*vernalis* 'Ginryu' OP	Unnamed selection	GrN 08-080	12.90 ± 0.72	3.17	3 × ?	4
C. 'Christmas Candy' (*C.* ×*vernalis* 'Egao' OP) OP	Unnamed selection	GrN J-031	12.10 ± 0.38	3.17	3 × ?	4
C. ×*williamsii* 'William's Lavender' × *C. reticulata* 'Purple Gown'	'Scarlet Temptations'	CF	14.27 ± 0.94	2.89	2 × 6	5[v]
C. sasanqua × *C. tenuiflora*	'Starry Pillar'	NCSU 2016-102	14.94 ± 1.01	3.15	6 × 2	5[v]
C. 'Frost Prince' ×*vernalis* 'Takarazuka'	'Winter's Fire'	CGBG23	16.17 ± 1.14	3.09	6 × 4	5
C. ×*vernalis* 'Egao' OP	'Egao Spring Snowfall'	GrN	17.33 ± 1.35	3.17	4 × ?	6

(*Continued on next page*)

Table 4. (*Continued*) Genome sizes and estimated ploidy levels of interspecific *Camellia* hybrids.

Purported parentage	Cultivar/selection	Source/accession[z]	2C genome size [mean ± SEM (pg)][y]	Weighted 1Cx genome size (pg)[x]	Purported parental ploidy levels (x)	Estimated ploidy (x)[w]
Intraploid hybrids						
C. ×*vernalis* 'Ginryu' OP	'Eos'	GrN	19.43 ± 1.94	3.17	3 × ?	6
C. 'Eos' (C. ×*vernalis* 'Ginryu' OP) OP	Unnamed selection	GrN 10-005	18.74 ± 0.88	3.17	6 × ?	6
C. 'Dabney's Star' (C ×*vernalis* 'Star-Above-Star' OP) OP	Unnamed selection	GrN 12-001	18.07 ± 0.76	3.17	4 × ?	6

[z] CF = Camellia Forest Nursery (Clifford and David Parks), Chapel Hill, NC; JCRA = JC Raulston Arboretum, Raleigh, NC; GN = Gene's Nursery (Gene Phillips), Savannah, GA; CGBG = Coastal Georgia Botanical Garden, Savannah, GA; NCSU = North Carolina State University Mountain Horticultural Crops Research and Extension Center, Mills River, NC. OP = open pollinated.

[y] Holoploid genome sizes were determined using propidium iodide as the fluorochrome stain. Values are means ± SEM; n = 2–3.

[x] Weighted 1Cx values were calculated as [(1Cx of female parent × ploidy of female parent / 2) + (1Cx value of male parent × ploidy of male parent / 2)] / [ploidy of female parent × ploidy of male parent / 2]. When the 1Cx was known for the exact parent, then the average for the parental species or section was used.

[w] Estimated ploidies were calculated as 2C genome size / weighted 1Cx.

[v] Ploidy and/or genome size are inconsistent with reported parentage.

[u] Ploidy confirmed with cytology.

hexaploid and tetraploid, but the estimated ploidy is diploid, suggesting mislabeling. Other interploid hybrids such as 'Scarlet Temptations' and 'Starry Pillar' are crosses between hexaploid and diploid taxa, but they were pentaploid, suggesting they are the result of an unreduced gamete from the diploid parent, as has been documented for *Camellia* (Wendel, 1984).

Camellia ×*vernalis* has been documented as a group of interspecific hybrids between *C. sasanqua* and *japonica* that were originally represented by F₁ 'Gaisen'-type tetraploids found on Hirado Island in Japan 400 years ago (Tanaka, 1988a, 1988b; Tanaka et al., 1986, 2005; Uemoto et al., 1980). These hybrids are fertile and can produce progeny that may have three-times, four-times, five-times, or six-times the number of chromosomes, or they may be aneuploid, depending on the ploidy of the other parent, occurrence of unreduced gametes, or other meiotic irregularities (Tateishi et al., 2007). *Camellia* ×*vernalis* 'Ginryu', also known as its westernized name 'Dawn', was found to be a triploid. This cultivar most likely resulted from a 'Gaisen'-type tetraploid *C.* ×*vernalis* backcrossed to a diploid *C. japonica*. Open-pollinated seedlings derived from *C.* ×*vernalis* 'Egao' and 'Star-Above-Star' (both tetraploids) included triploids (most likely crossed with diploids), tetraploids (most likely crossed with other tetraploids), and hexaploids (most likely unreduced gametes from both the tetraploid *C.* ×*vernalis* and a diploid). Two triploid *C.* ×*vernalis*, 'Christmas Candy' and 'Ginryu', produced seedlings that were tetraploid (most likely producing unreduced gametes and crossed with diploids). Interestingly, 'Ginryu' also produced seedlings ('Starman' and GrN 08-070) that were triploid or nearly triploid and may have resulted from either apomixis or aneuploid/2x gametes.

The extensive history of *Camellia* breeding and selection has produced tens of thousands of cultivars that now serve as potential parents and breeding lines. Considerable progress has been made in resolving the taxonomy, systematics, and cytogenetics of the genus, but challenges remain. The long history of *Camellia* cultivation, global exchange of historical varieties, cultivar names that often relate to the origin of the variety or a quality of the flower, and variable translations can cause considerable confusion. One such name, 'Shishigashira', has been attributed to several species and hybrids, including *C. japonica*, *C. sasanqua*, and *C. hiemalis*, which some believe to be a form of *C. sasanqua* (Jiang et al., 2012). 'Hiryu' is another name that has been associated with *C. japonica* and *C. sasanqua*, as well as with *C.* ×*vernalis*, which is the hybrid of those two species. This confusion is further complicated by incomplete knowledge of the parentage and ploidy, along with the potential for pollen contamination, mislabeling, and variable reproductive pathways (e.g., unreduced gametes, apomixis, etc.). These challenges underscore

the need for clone-specific data regarding cytogenetics for individual accessions and breeding lines.

This study builds on an extensive body of cytogenetic research regarding *Camellia* and provides new information regarding ploidy, genome size, hybridity, and reproductive pathways for a broad range of cultivated *Camellia* and related genera. This expanding knowledgebase provides improved characterization of genetic resources for Theaceae that will aid in the development of improved hybrids and cultivars.

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