ABSTRACT

HEMBREE, WILLIAM GARDNER. Cytogenetics of *Camellia* and Related Genera and Identification, Genome Sizes, and Ploidy of *Deutzia* (Under the direction of Dr. Thomas G. Ranney and Dr. Brian E. Jackson).

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 and *Camellia* oilseed, as well as iconic ornamentals. Cytogenetics of *Camellia* and related genera is complicated: chromosome number and ploidy can vary widely between species and interspecific and interploidy hybridization occurs. However, specific information on cytogenetics of many species, cultivars, and modern hybrids is lacking. The objectives of this study were to compile a consolidated literature review on 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 on Theaceae cytogenetics is presented as a consolidated reference covering 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 $x = 15$ in the Theeae including *Camellia*, $x = 17$ in the Stewartiae, and $x = 18$ in the Gordoniae. Surveyed camellias ranged from $2n = 2x = 30$ to $2n = 8x = 120$, including diploids, triploids, tetraploids, pentaploids, hexaploids, and octoploids. Previously uncharacterized taxa including *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 in *Polyspora* that ranged from diploid to octoploid. Ploidy determinations were used to confirm or challenge validity of putative interploid hybrids. Monoploid genome sizes varied among subfamily and genera with 1C*x* values ranging from 0.81 pg for *Franklinia* to a mean of 3.14 pg for *Camellia* demonstrating differential rates of genome expansion, independent of ploidy. Within *Camellia,* monoploid genome sizes varied among subgenera, sections, and some species (ranging from 2.70 to 3.57 pg). This study provides a consolidated and expanded knowledgebase on 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.

The genus *Deutzia* in the Hydrangeaceae includes about sixty species that range in ploidy from diploid (2*x*) to tetradecaploid (14*x*). Although there have been numerous studies into the cytogenetics of some species of *Deutzia*, the ploidy level of many species remains unknown and there is little cytogenetic data available for *Deutzia* hybrids and cultivars. The purpose of this study was to validate identification and determine the genome sizes and ploidy levels of a diverse collection of *Deutzia* using cytology and flow cytometry. Accessions were identified using the most current taxonomic key and voucher specimens were deposited for each at the North Carolina State University herbarium. Corrected and updated species names are provided for all cultivars and accessions studied. Traditional cytology was performed on roots of representative taxa to calibrate genome size with ploidy level. Genome size and estimated ploidy was determined for 46 accessions using flow cytometry. Ploidy levels were reported for the first time for three species of *Deutzia*. Base, monoploid genome size (1C*x*) was relatively conserved and ranged from 1.20 to 2.05 pg for these species. Ploidy of all interspecific hybrid taxa was consistent with the ploidy of the reported parents except for *D.* ×*myriantha* 2014-116, which was found to be an octoploid while the purported parental species were most likely diploid. No interploid hybrids were documented suggesting the presence of an interploid block. The information produced from this study should benefit future curation, research, development and improvement of this genus with corrected nomenclature and clone-specific data on cytogenetics.

Cytogenetics of *Camellia* and Related Genera and Identification, Genome Sizes, and Ploidy Levels of *Deutzia*

by
William Gardner Hembree

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APPROVED BY:

_____	_____
Dr. Thomas G. Ranney	Dr. Brian E. Jackson
Co-Chair of Advisory Committee	Co-Chair of Advisory Committee

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Dr. Julia L. Kornegay

DEDICATION

To the all the people who love nature

To those of us who revel in its endless beauty

And to those who choose to protect it for posterity

BIOGRAPHY

William Gardner Hembree was the third and final son born to James and Diane Hembree in Winston, Georgia. He came into this world silent and wide-eyed, ready to take in all that he could see. His early years were spent most memorably in the gardens of his parents and grandparents, picking tomatoes with Dada and making them into sandwiches with Dadee and riding old Ford tractors with Granddaddy and digging rutabagas with Mamaw. His parents took him to botanical gardens when other kids were going to the beach. His childhood predisposed him to comfort, familiarity, and longing for green spaces that would persist throughout his life.

His love of nature and the outdoors was formed during the frequent camping and backpacking trips with his dad and older brothers from the time he could walk. Though at the time he felt no interest in the plants that were making up the landscape he was enjoying, he would in time come to obsess over each individual tree that wove into the next to form this vivid environment. His involvement in the Cub Scouts and Boy Scouts programs allowed him to continue to develop his intense entrancement with nature throughout his childhood, and unbeknownst to him would kindle his desire to pursue the plant sciences later in life.

Will's first real introduction to the wide world of horticulture came during his first international trip when his family traveled to the United Kingdom on a garden tour modeled after one his parents had taken with Drs. Dirr and Armitage during their college years. Here he experienced his first resonant plant encounter when he saw an ancient Cedar of Lebanon at Leeds Castle in Kent. The soaring branches seemed to touch the very sky from his diminutive perspective. Touring other gardens in the UK including the Chelsea Flower Show, Kew, Bodnant, and Sissinghurst planted a seed deep in Will's soul that would remain dormant for many years before germinating into the passion for plants that he has today.

At the University of Georgia Will was able to explore and pursue many of the interests that had fascinated him growing up. Here, his passion for plants finally blossomed and he finally realized that he was destined to follow in his parents' footsteps of being a horticulturist. After his first plant identification courses, Will fell in love with ornamental plants. This love affair has guided virtually all his pursuits since then. Through many travels with the Horticulture Club, Will gained an intense appreciation for and interest in public horticulture and botanical gardens. These experiences led him to intern at the Niagara Parks Commission Botanical Garden and School of Horticulture in Ontario, where his career goals solidified. Here, he realized that the garden was where he felt most alive and decided that he would pursue a career in public horticulture.

As an intern at the Mountain Crop Improvement Lab in Mills River, Will discovered the exciting world of ornamental plant breeding, and here solidified his path to graduate school at North Carolina State University. Working with in the beautiful mountains of western North Carolina also gave Will very important and early exposure to the expansive plant diversity of the southern Appalachians.

After the completion of his undergraduate degree, Will traveled to the United Kingdom for 10 months as the Royal Horticultural Society / Garden Club of America Interchange Fellow for 2015/2016. Here he worked and studied at numerous botanical gardens around the UK including RHS Wisley, RBG Kew, The Sir Harold Hillier Gardens, and RBG Edinburgh, among others. In the UK Will found his passion for plant conservation through his work at the Royal Botanic Gardens.

At NC State he took this newfound passion and fed it through coursework on rare plants, systematics, and nomenclature, while also preparing to enter the nonprofit world of plant conservation. His experiences as a student, teaching assistant, and researcher in Raleigh only continued to fan his passion for the world of botany and horticulture. After graduation Will plans to enter the field of botanical garden-based plant conservation.

ACKNOWLEDGMENTS

The tremendous support I have received throughout my life and especially at NC State have played a crucial role not only in my success as a student but in my growth as a person and as a professional in horticulture. Surely without the guidance of my parents, my professors, and my peers none of this would have possible.

I know now that I can blame my plant affliction on my loving parents, and I couldn't be more grateful to them for allowing me to discover it on my own. They always provided me every opportunity that they could and have allowed me to experience life in an extraordinary way. I can never thank them enough for their endless love and kindness which I try so hard to emulate every day. Mom and Dad, you are and have always been my biggest role models and I count my lucky stars that I got to have you both as parents. Thank you.

To my advisors, thank you for allowing my interests to flourish into an unquenchable passion for plants and horticulture. Dr. Ranney, your guidance and support changed my life from day one of my internship, when you suggested I look into something called the McLaren fellowship, and has continued every day throughout my master's program. Your mentorship has impressed upon me the virtues of imagination, which has allowed me to pursue other extra-horticultural interests. For unrelenting patience and kindness, I can never thank you enough. Dr. Jackson, your smiling face and precise wisdom helped me to feel comfortable as a student in a new role at a new university. I will never forget your lessons on plant identification on campus and at the JC Raulston Arboretum. To my committee members Mark Weathington and Julia Kornegay, your guidance in the preparation of my thesis have been as invaluable as the advice on my future career in public horticulture. Thank you.

To all my professors and other horticulture graduate and undergraduate colleagues surely too numerous to name, I am eternally grateful for each your roles in turning my time at NC State into some of the best years of my life. To Nate and Lauren, my lab mates, I thank you for lending me your ears to listen and your shoulders to cry on. You and your families treated me like family from the beginning, which was more helpful to me than you will ever know.

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CHAPTER 1: Cytogenetics of *Camellia* and Related Genera

William G. Hembree[1] and Thomas G. Ranney[2,5]

Mountain Crop Improvement Laboratory, Department of Horticultural Science, Mountain Horticultural Crops Research and Extension Center, North Carolina State University, 455 Research Drive, Mills River, NC 28759

Brian E. Jackson[3]

Department of Horticultural Science, North Carolina State University, Campus Box 7609, Raleigh, NC, 27695-7609

Mark Weathington[4]

JC Raulston Arboretum, North Carolina State University, Campus Box 7522, Raleigh, NC 27695-7522

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[1]Graduate Research Assistant.

[2]JC Raulston Distinguished Professor, corresponding author. E-mail: tom_ranney@ncsu.edu

[3]Associate Professor.

[4]Director, JC Raulston Arboretum

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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 and *Camellia* oilseed, as well as iconic ornamentals. 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 on cytogenetics of many species, cultivars, and modern hybrids is lacking. The objectives of this study were to compile a consolidated literature review on 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 on Theaceae cytogenetics is presented as a consolidated reference covering 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 $x = 15$ in the Theeae including *Camellia*, $x = 17$ in the Stewartiae, and $x = 18$ in the Gordoniae. Surveyed camellias ranged from $2n = 2x = 30$ to $2n = 8x = 120$, including diploids, triploids, tetraploids, pentaploids, hexaploids, and octoploids. Previously uncharacterized taxa including *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 in *Polyspora* that ranged from diploid to octoploid. Ploidy determinations were used to confirm or challenge validity of putative interploid hybrids. Monoploid genome sizes varied among subfamily**

and genera with 1C*x* values ranging from 0.81 pg for *Franklinia* to a mean of 3.14 pg for *Camellia* demonstrating differential rates of genome expansion, independent of ploidy. Within *Camellia,* monoploid genome sizes varied among subgenera, sections, and some species (ranging from 2.70 to 3.57 pg). This study provides a consolidated and expanded knowledgebase on 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 in Theaceae with species found throughout southeastern and eastern Asia (Chang and Bartholomew, 1984; Luna Vega and Contreras-Medina, 2000). About 90% of all *Camellia* species, including those of the greatest commercial importance, are native to China (Bartholomew, 1986). The ornamental varieties are prized for their glossy evergreen foliage and abundant, showy flowers which can bloom from Autumn to Spring, when many other plants in the landscape are dormant. Over a thousand years before western introduction, ornamental camellias were being grown for garden use in China (Xin et al., 2015). Though tea (*C. sinensis*) arrived in Europe around the middle of the 17th century, the first living *Camellia* plant was not reported until nearly a century later in Lord Petre Thorndon's hothouses in England. Since then, ornamental camellias have become widely cultivated throughout Europe, North America, Australia, and New Zealand (Trehane, 2007). Their popularity and phenotypic variability have given rise to tens of thousands of cultivars and hybrids (ICS, 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 improvement of *Camellia*. Analysis of other closely related genera would provide a broader understanding of ploidy within Theaceae and help contextualize evolutionary relationships in this family.

Taxonomy/Systematics. The genus *Camellia* has undergone several 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 (1984; 1998) completed several taxonomic revisions of *Camellia* culminating with Chang (1998) where he reorganized the 238 species native to China in 18 sections and 4 subgenera. More

recently, Ming (2000) published his Monograph of the Genus *Camellia* in which he reduced the number of subgenera to 2, the sections to 14, and the species to 119, less than half of Chang's final tally of about 280 species. Both Ming (2000) and Chang (1998) systems are still widely used by botanists today (Gao et al., 2005). In the Flora of China, Ming and Bartholomew (2007) list the number of species at approximately 120, 97 of which are native to China.

Several changes to the accepted taxonomic status of *Camellia* have occurred since its original classification by Linnaeus. At different times *Camellia* has been placed in the Guttiferales, Theales, and even included within Ternstroemiaceae (Luna and Ochoterena, 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 belonging 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.* Recent molecular phylogenetic analysis of the Theeae indicate that *Camellia* and *Pyrenaria* form a paraphyletic group which occur and hybridize naturally with each other (Zhang, 2014). Gordoniae and Stewartiae belong to the sister clade of Theeae. Gordoniae is composed of the North American *Franklinia* and *Gordonia*, as well as the Asian *Schima*. Intergeneric hybrids between these genera as well as between *Camellia* and *Franklinia* have been reported (Orton, 1977; Ackerman and Williams, 1982; Ranney et al., 2003; Ranney et al., 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 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 generated inconsistent reports such as *Stewartia* with $1n = 1x = 15$ or 17 and *Franklinia, Gordonia,* and *Schima* having $1n = 1x = 15$ or 18 (Bostick, 1965; Horiuchi and Oginuma, 2001; Oginuma et al., 1994; Santamour, 1963). Within *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), though triploids, tetraploids, pentaploids, and aneuploids have been reported (Kondo, 1977; Fukushima et al., 1966). Though *Camellia sasanqua* is often reported to be hexaploid (Ackerman, 1971; Kondo, 1977), pentaploids, heptaploids, octoploids, decaploids, and aneuploids have been noted (Kondo, 1977; Ito et al., 1957). 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; Kondo, 1977; Huang et al., 2013). The variation and confusion regarding ploidy levels is further complicated by, and may be, in part, 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 (Wendell, 1984) and, in some instances, aneuploid gametes (Kondo, 1977) resulting in additional possible variation 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 non-viable 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 limiting their potential as breeding lines. With increasing ploidy, allelic segregation becomes more complicated, leading to complex patterns of heritability especially in autopolyploids (Zielinski & Scheid, 2012). Information on 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 on cytogenetics of *Camellia* and related genera and 2) to augment prior research with original data on 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 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 40-50 mg of leaves were used for each sample preparation. Using a

modified WPB Isolation Buffer, composed of 0.2 mM Tris.HCl, 4 mM $MgCl_2.6H_2O$, 2.0 mM EDTA $Na_2.H_2O$, 86.0 mM NaCl, 2.0 mM dithiothreitol, 1% (w/v) PVP-10, and 1 % (v/v) Triton X-100, pH 7.5. 1 mL, with a pH of 7.5, ice-cold nuclei suspensions were prepared by chopping tissue in the WPB with a sharp 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 to determine genome size. Holoploid, somatic, sporophytic, unreduced, 2C genome size was calculated as DNA content of the standard (pg) x (mean fluorescence value of the sample / mean fluorescence value of the standard). Plants were sampled randomly with two subsamples measured per plant. Monoploid, 1C*x*, genome size (i.e., DNA content of one complete set of chromosomes) was calculated as 2C genome size / ploidy.

Chromosome counts were completed on selected taxa to confirm ploidy and further calibrate with 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 pre-fixative solution of 2.0 mM 8-hydroxyquinoline + 70 $mg.L^{-1}$ cyclohexamide in the dark at room temperature for 3 hours. The roots were then placed in the dark at 4°C for another 3 hours. After washing with dH_2O, 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 seconds 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 (1C*x*) were subjected to one-way analysis of variance as a function of subfamily, genus, and species, and within *Camellia* also as a function of subgenus and section. Means were separated using Fisher's LSD test (Proc GLM; SAS Version 9.4; SAS Inst., Cary, NC).

Results and Discussion

Our compilation of literature on cytogenetics in Theaceae spans nearly a century of research and includes published results on 7 genera, 160 species and 202 cultivars (Table 1). Because cytological studies in *Camellia* cover a broad range of time, many of these referenced studies utilized different taxonomic treatments, dependent upon conventions of naming at the time of publication. Without vouchered specimens, it is essentially impossible to verify exactly which species, according to modern taxonomic treatments, were used in these previous studies. For this reason, the names in Table 1 have been left as they were reported in the original publications. Therefore, 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; Yang et al., 2003; Yang et al., 2004). Additional work in Stewartiae including *Stewartia* indicates a base chromosome number of $1n = 1x = 17$ (Horiuchi and Oginuma, 2001) while the Gordoniae including *Franklinia, Gordonia,* and *Schima* have $1n = 1x = 18$ (Bostick, 1965; Oginuma et al., 1994). Numerous *Camellia* species have isoploid 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 are 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 non-recurrent apomixis (Ozias-Akins and van Dijk, 2007). The prior research summarized in Table 1 emphasizes the cytogenetic diversity within the Theaceae and aids in the understanding of relationships between members of Theaceae. This previous cytogenetic and cytometric data serves as an accessible reference for plant breeders, taxonomists, and others studying Theaceae.

Cytology was completed on 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 base

chromosome numbers for these genera and provide additional, direct standards to further calibrate ploidy with genome size.

Flow cytometry was completed on a broad range of taxa in the Theaceae providing data on 2C holoploid genome size, 1C*x* monoploid genome size, and estimated ploidy for 123 non-hybrid accessions (Table 2). Our study represents new data on 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, though there were many exceptions (Table 1). The accession of *C. assimilis* CGBG2 was found to be diploid, consistent with Fukushima et al. (1966) and Kondo (1977). In Ming and Bartholomew's treatment of *Camellia* (2007), *C. assimlis* is synonymous with *C. caudata* which has been reported both as a 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, though 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, though *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, in agreement with prior 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', 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, has been estimated by Huang et al. (2013) to be hexaploid, though the accession of this species surveyed in this study was

confirmed to be diploid through flow cytometry and cytology. This result is further supported by the diploidy of *C.* 'Wendzalea', a hybrid between *C. azalea* and a diploid *C. japonica*. Confusion and complexity of *Camellia* nomenclature and variation in ploidy within species emphasize the need to collect and reference data on individual clones and accessions.

The other genera in the Theaceae included in this study are much less commonly cultivated and have been less studied compared to *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* are reported for the first time as diploids. A triploid accession of *Stewartia ovata* included in this study represented the first polyploid report of this genus, possibly the result of an unreduced gamete.

Monoploid genome sizes (1C*x*) varied considerably by subfamily (Table 3) with the Gordoniae having a mean of 0.84 pg while the Stewartiae and Theeae had substantially larger values of 2.50 and 3.01 pg, respectively. The much larger 1C*x* values of the Stewartiae and Theeae indicate 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 impacts of genome size variation are still being elucidated, but 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 3.14 pg compared with 1.75 pg for *Polyspora* and 1.39 pg for *Pyrenaria*, showing differential rates of genome expansion among these groups. Even within *Camellia*, there were significant differences in 1C*x* values among subgenera, sections, and some species (ranging from 2.70 to 3.57 pg) showing that chromosome and genome size evolution has been particularly dynamic compared to sister lineages.

Genome size was also used to estimate ploidy of interspecific hybrids and was particularly useful to validate interploid and intergeneric hybrids (Table 4). All non-interploid, 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* x *F. alatamaha* (USNA 79387; Ackerman and Williams, 1982) was inconsistent with the reported parentage. Genome sizes are considerably different in these two parents (2C = 5.78- 6.62 pg in *C.*

japonica and 2C = 1.62 pg in *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 do not have intermediate genome sizes consistent with interploid hybridization, suggesting they are the result of pollen contamination or mis-labeling. Other interploid hybrids including 'Scarlet Temptations' and 'Starry Pillar' are putative hybrids between hexaploid and diploid taxa, but were pentaploid, suggesting they are the result of an unreduced gamete from the diploid parent as has been documented in *Camellia* (Wendell, 1984).

Camellia ×*vernalis* has been documented to be a group of interspecific hybrids between *C. sasanqua* and *japonica,* originally represented by F_1 'Gaisen' type tetraploids found on Hirado Island, Japan originating 400 years ago (Uemoto et al., 1980; Tanaka et al., 1986; Tanaka 1988a; 1988b; Tanaka et al., 2005). These hybrids are fertile and can produce progeny that may be 3x, 4x, 5x, 6x, or aneuploid depending on the ploidy of the other parent, occurrence of unreduced gametes, or other meiotic irregularities (Tateishi et al., 2007). 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 a triploid seedling (GrN 08-070) that may have resulted from apomixis.

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 which 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 is considered by some to be synonymous with *C. sasanqua* (Jiang et al., 2012). Another name, 'Hiryu' has been associated with *C. japonica*, *C. sasanqua*, and the hybrid of those two species, *C.* ×*vernalis*. This confusion is further complicated by having incomplete knowledge of parentage and ploidy, coupled with the potential for pollen contamination, mis-

labeling, and variable reproductive pathways (e.g., unreduced gametes, apomixis, etc.). These challenges underscore the need for clone-specific data for individual accessions and breeding lines.

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

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Table 1.1. Previous cytological and cytometric reports of chromosome numbers in *Camellia* and related taxa.

Taxa[z]	Chromosome No.	References
C. acutiserrata	2*n* = 2*x* = 30	Gu and Sun, 1997
C. anlungensis	2*n* = 2*x* = 30	Zhang and Min, 1999
C. anlungensis var. *acutiperulata*	2*n* = 2*x* = 30	Zhang and Min, 1999
C. albovillosa	2*n* = 2*x* = 30	Gu et al., 1988b; 1989b; Kondo et al., 1986; 1988; Xiao et al., 1993
C. assamica	2*n* = 2*x* = 30	Chen et al., 2003; Cherian and Stephan, 1981; Li et al., 1989;
	2*n* = 3*x* = 45	Omman and Stephen, 1994
C. assamica var. *kucha*	2*n* = 2*x* = 30	Kondo, 1977; Li et al., 1989
C. assimilis	2*n* = 2*x* = 30	Fukushima et al., 1966; Kondo, 1977
C. brevistyla	2*n* = 2*x* = 30	Zhang and Min, 1999
C. caudata	2*n* = 2*x* = 30	Bezbaruah, 1971; Zhuang and Dong, 1984
	2*n* = 4*x* = 60	Gu et al., 1988b; 1989b; Gu and Sun, 1997
C. changii	2*n* = 6*x* = 90	Huang et al., 2013
C. chekiangoleosa	2*n* = 2*x* = 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	2*n* = 2*x* = 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*	2*n* = 2*x* = 30	Liang, 1990; Kondo et al., 1991
C. compressa	2*n* = 8*x* = 120	Gu et al., 1988a; 1988b; 1989a; 1989b

Table 1.1 (continued).

C. concina	2*n* = 6*x* = 90	Huang et al., 2013
C. costata	2*n* = 2*x* = 30	Huang et al., 2013
C. costei	2*n* = 2*x* = 30	Gu and Sun, 1997
	2*n* = 6*x* = 90	Huang et al., 2013
C. crapnelliana	2*n* = 2*x* = 30	Huang et al., 2013; Huang and Hsu, 1987; Kondo, 1972; Kondo, 1977
	2*n* = 6*x* = 90	Zhuang and Dong, 1984
C. crassicolumna	2*n* = 2*x* = 30	Xiao et al., 1991
C. crassipes	2*n* = 8*x* = 120	Huang et al., 2013
C. cryptoneura	2*n* = 6*x* = 90	Gu et al., 1988b; 1989b; Kondo et al., 1991
C. cuspidata	2*n* = 2*x* = 30	Janaki-Ammal, 1952; 1955; Kondo, 1977; Patterson et al., 1950; Zhuang and Dong, 1984
C. dehungensis	2*n* = 2*x* = 30	Li et al., 1989
C. drupifera	2*n* = 3*x* = 45	Longley and Tourje, 1959
C. edithae	2*n* = 2*x* = 30	Gu et al., 1990b; Huang et al., 2013; Xiao et al., 1991
C. euphlebia	2*n* = 2*x* = 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	2*n* = 2*x* = 30	Huang et al., 2013
C. fasicularis	2*n* = 2*x* = 30	Zhang and Ming, 1995
C. flavida	2*n* = 2x = 30	Liang, 1990; Qin and Liang, 1991; Zhang and Ming, 1995
C. forrestii	2*n* = 2x = 30	Gu et al., 1988b; 1989b; Kondo and Andoh, 1980; 1983; Xiao et al., 1991
	2*n* = 4*x* = 60	Gu et al., 1988b; 1989b; Kondo et al., 1991; Xiao et al., 1991
	2*n* = 6*x* = 90	Gu et al., 1988b; 1989b; Xiao et al., 1991
C. fraterna	2*n* = 6*x* = 90	Ackerman, 1971; Huang et al., 2013; Kondo, 1977; Longley, 1958

Table 1.1 (continued).

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., 1988; 1989; 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., 1994; 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’	$2n \sim 7x = 102$	Kondo, 1977
‘Shishi-Gashira’	$2n = 4x = 60$	Patterson et al., 1950
	$2n = 6x = 90$	Ackerman, 1971; Kondo, 1977; Longley, 1956; Longley and Tourje, 1959

Table 1.1 (continued).

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, 1968; 1971; Kondo, 1977
	$2n = 3x = 45$	Kondo, 1977
C. japonica	$2n = 2x = 30$	Ackerman, 1971; Arizuma, 1950; 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., 1968
'Akazu-Nishiki'	$2n = 2x = 30$	Ito et al., 1968
'Akebono'	$2n = 3x = 45$	Ito et al., 1968
'Aki-No-Yama'	$2n = 2x = 30$	Ito et al., 1968
'Ara-Jishi'	$2n = 2x = 30$	Ito et al., 1968

Table 1.1 (continued).

‘Arrabella’ – Open pollinated seedling	$2n \sim 2x = 32$	Kondo, 1977
‘Bella Romana’	$2n = 2x = 30$	Kondo, 1977
‘Beni-Botan’	$2n = 2x = 30$	Ackerman, 1971
‘Beni-Karako’	$2n = 2x = 30$	Ito et al., 1968
‘Benten-Tsubaki’	$2n = 2x = 30$	Ito et al., 1968
‘Berenice Boddy’	$2n = 2x = 30$	Kondo, 1977; Patterson et al., 1950
‘Bokuhan’	$2n = 2x = 30$	Ito et al., 1968
‘Bon-Shirotama’	$2n = 2x = 30$	Ackerman, 1971
‘California’	$2n = 3x = 45$	Kondo, 1977
‘Chiri-Tsubaki’	$2n = 2x = 30$	Ito et al., 1968
‘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., 1968
‘Geisha Girl’	$2n = 2x = 30$	Kondo, 1977

Table 1.1 (continued).

‘Genji-Karako’	$2n = 2x = 30$	Ito et al., 1968
‘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., 1968
‘Hana-Guruma’	$2n = 2x = 30$	Ito et al., 1968
‘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., 1968
‘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., 1968
‘Jenny Jones’	$2n = 2x = 30$	Patterson et al., 1950
‘Jitsu-Getsu’	$2n = 2x = 30$	Ito et al., 1968
‘Joshua E. Youtz’	$2n \sim 2x = 34$	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., 1968
‘Kingyo-Ba’	$2n = 2x = 30$	Ito et al., 1968
‘Kingyo-Tsubaki’	$2n = 2x = 30$	Longley and Tourje, 1960; Kondo, 1977
‘Ko-Kirin’	$2n = 2x = 30$	Ito et al., 1968
‘Kominato’	$2n = 2x = 30$	Kondo, 1977
‘Komyo’	$2n = 3x = 45$	Ito et al., 1968
‘Komyo-Tai’	$2n = 2x = 30$	Ackerman, 1971

Table 1.1 (continued).

‘Konron-Koku’	$2n = 2x = 30$	Longley and Tourje, 1960
‘Ko-Otome’	$2n = 2x = 30$	Ito et al., 1968
‘Kumasaka’	$2n = 2x = 30$	Ito et al., 1968
‘Kuro-Tsubaki’	$2n = 2x = 30$	Ackerman, 1972; 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., 1968
‘Miura-Otome’	$2n = 2x = 30$	Fukushima et al., 1968
‘Miyuki-Nishiki’	$2n = 2x = 30$	Ito et al., 1968
‘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 et al., 1968; Ito et al., 1968
‘Oki-No-Ishi’	$2n = 2x = 30$	Ito et al., 1968
‘Ooshiratama’	$2n = 2x = 30$	Ito et al., 1968
‘Otome’	$2n = 2x = 30$	Ito et al., 1968
‘Paige #592’	$2n = 2x = 30$	Kondo, 1977
‘Pink Clouds’	$2n = 2x = 30$	Kondo, 1977

Table 1.1 (continued).

‘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., 1968
‘S. Peter Nyce’	$2n = 3x = 45$	Kondo, 1977
‘Sakuzuki-Ba’	$2n \sim 3x = 44$	Fukushima et al., 1966
‘Saotome’	$2n = 2x = 30$	Ito et al., 1968
‘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., 1968
‘Shibori-Otome’	$2n = 2x = 30$	Ito et al., 1968
‘Shiranui’	$2n = 2x = 30$	Ito et al., 1968
‘Shiratama’	$2n = 2x = 30$	Patterson et al., 1950
‘Shishi-Gashira’	$2n = 2x = 30$	Ito et al., 1968
‘Some-Kawa’	$2n = 2x = 30$	Fukushima et al., 1968; Ito et al., 1968
‘Soshi-Arai’	$2n = 2x = 30$	Ito et al., 1968
‘Sunset Glory’	$2n = 2x = 30$	Kondo, 1977
‘Tafuku-Benten’	$2n = 2x = 30$	Ito et al., 1968
‘Tomorrow’s Dawn’	$2n = 2x = 30$	Kondo, 1977
‘Tori-No-Ko’	$2n = 2x = 30$	Ito et al., 1968
‘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
	$2n \sim 2x = 29$	Kondo, 1977

Table 1.1 (continued).

‘White Nun’	2*n* = 2*x* = 30	Kondo, 1977
	2*n* = 3*x* = 45	Kondo, 1977
‘Yamato-Nishiki’	2*n* = 2*x* = 30	Ito et al., 1968
‘Yanagi-Ba’	2*n* = 2*x* = 30	Fukushima et al., 1968
‘Yuki-Botan’	2*n* = 2*x* = 30	Ackerman, 1971
‘Yukimi-Guruma’	2*n* = 2*x* = 30	Ito et al., 1968
C. japonica ssp. rusticana	2*n* = 2*x* = 30	Fukushima et al., 1966; Janaki-Ammal, 1952; Kobayashi and Kirino, 1960
‘B White Plena’	2*n* = 2*x* = 30	Ackerman, 1971
‘Hatano’	2*n* = 2*x* = 30	Ackerman, 1971
‘Koshiji’	2*n* = 2*x* = 30	Ackerman, 1971
‘Yoshida’	2*n* = 2*x* = 30	Ackerman, 1971
C. japonica syn. *C. hozanensis* (Hayata) Hayata	2*n* = 2*x* = 30	Kondo, 1977
C. japonica syn. *C. japonica* var. *spontanea* (Makino) Makino	2*n* = 2*x* = 30	Kato and Simura, 1970
C. jingdonensis	2*n* = 6*x* = 90	Gu et al., 1988b; 1989b
C. jiuyishanica	2*n* = 2*x* = 30	Gu et al., 1992
C. jungkiangensis	2*n* = 2*x* = 30	Liang et al., 1994
C. kissii	2*n* = 2*x* = 30	Ackerman, 1971; Bezbaruah, 1971; Gu et al., 1992; Huang and Hsu, 1985; 1987; Kondo, 1977
	2*n* = 4*x* = 60	Huang and Hsu, 1987
	2*n* = 5*x* = 75	Huang and Hsu, 1987
C. kwangnanica	2*n* = 2*x* = 30	Li et al., 1989
C. kwangsiensis	2*n* = 2*x* = 30	Huang et al., 2013
C. kweichowensis	2*n* = 6*x* = 90	Gu et al., 1988; 1989; Gu and Sun, 1997

Table 1.1 (continued).

C. lanceolata	2*n* = 2*x* = 30	Janaki-Ammal, 1952; 1955
C. lapidea	2*n* = 4*x* = 60	Gu et al., 1992
C. lawii	2*n* = 2*x* = 30	Huang et al., 2013
C. leptophylla	2*n* = 2*x* = 30	Huang et al., 2013; Zhang and Min, 1999
C. limonia	2*n* = 2*x* = 30	Liang, 1990; Qin and Liang, 1991
C. limonia f. obovata	2*n* = 2*x* = 30	Liao et al., 1988
C. longgangensis	2*n* = 2*x* = 30	Liao et al., 1988
C. longipedicellata	2*n* = 2*x* = 30	Huang et al., 2013
C. longissima	2*n* = 2*x* = 30	Huang et al., 2013
C. longruiensis	2*n* = 2*x* = 30	Liang, 1990
C. longzhouensis	2*n* = 2*x* = 30	Liang, 1990
C. lutchuensis	2*n* = 2*x* = 30	Ackerman, 1971; Kondo, 1977; Kondo and Parks, 1979
C. luteoflora	2*n* = 2*x* = 30	Gu et al., 1988; 1989; Gu and Sun, 1997; Huang et al., 2013
C. magniflora	2*n* = 6*x* = 90	Gu et al., 1992
C. mairei	2*n* = 2*x* = 30	Huang et al., 2013
	2*n* = 6*x* = 90	Kondo et al., 1988
C. mairei var. *velutina*	2*n* = 2*x* = 30	Gu et al., 1988a; 1989b
	2*n* = 6*x* = 90	Gu et al., 1988b; 1989b; Kondo et al., 1986
C. makuanica	2*n* = 2*x* = 30	Gu et al., 1988b; 1989b; Gu and Sun, 1997
C. maliflora	2*n* = 2*x* = 30	Janaki-Ammal, 1952; 1955; Kondo, 1977; Patterson et al., 1950
C. manglaensis	2*n* = 2*x* = 30	Li et al., 1989
C. meiocarpa	2*n* = 4*x* = 60	Huang and Zhao, 1981; Kondo et al., 1991; Zhuang and Dong, 1984
C. micrantha	2*n* = 2*x* = 30	Liang, 1990; Liao et al., 1988
C. microcarpa	2*n* = 2*x* = 30	Liao et al., 1988; 1991

Table 1.1 (continued).

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

Table 1.1 (continued).

C. petelotii	2*n* = 2*x* = 30	Huang et al., 2013; Li et al., 1994
C. pingguoensis	2*n* = 2*x* = 30	Cao and Li, 1986; Chen et al., 1988; Liang, 1990; Liao et al., 1988; Zhang and Ming, 1995
C. pingguoensis var. *terminalis*	2*n* = 2*x* = 30	Zhang and Ming, 1995
C. pitardii	2*n* = 2*x* = 30	Gu, 1997; Janaki-Ammal, 1952; Zhang and Min, 1999; Zhang and Ming, 1998
C. pitardii var. pitardii	2*n* = 2*x* = 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
	2*n* = 6*x* = 90	Kondo, 1977
C. pitardii var. *yunnanica*	2*n* = 6*x* = 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	2*n* = 2*x* = 30	Cao and Li, 1986; Gu et al., 1988a; 1988b; 1989a; 1989b; Huang and Hsu, 1987; Zhuang and Dong, 1984
C. ptilophylla	2*n* = 2*x* = 30	Huang et al., 2013; Li and Yan, 1985
C. ptilosperma	2*n* = 2*x* = 30	Cao and Li, 1986
C. pubicosta	2*n* = 2*x* = 30	Huang et al., 2013
C. pubifurfuracea	2*n* = 2*x* = 30	Huang et al., 2013
C. pubipetala	2*n* = 2*x* = 30	Cao and Li, 1986; Liang, 1990; Zhang and Ming, 1995
C. purpurea	2*n* = 2*x* = 30	Gu and sun, 1997; Gu et al., 1988b; 1989b; Lu et al., 1993
C. pyxidiacea	2*n* = 2*x* = 30	Zhang and Min, 1999
C. pyxidiacea var. *rubituberculata*	2*n* = 2*x* = 30	Zhang and Min, 1999
C. quinquelocularis	2*n* = 2*x* = 30	Liang et al., 1994

Table 1.1 (continued).

C. reticulata	$2n = 2x = 30$	Gu, 1996; 1997; Xia et al., 1994
	$2n = 4x = 60$	Gu, 1996; 1997
	$2n = 6x = 90$	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'	$2n \sim 6x = 91$	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

Table 1.1 (continued).

‘Willow Wand’	2*n* = 6*x* = 90	Kondo, 1977; Longley, 1956
C. reticulata f. *simplex*	2*n* = 6*x* = 90	Kondo, 1977
C. rhytidocarpa	2*n* = 2*x* = 30	Huang et al., 2013
C. rosaeflora	2*n* = 3*x* = 45	Bezbaruah, 1971; Kondo, 1977
	2*n* = 6*x* = 90	Ackerman, 1971
C. rosthorniana	2*n* = 2*x* = 30	Huang et al., 2013
C. rubituberculata	2*n* = 2*x* = 30	Gu and Sun, 1997; Gu et al. 1989b; Huang et al., 2013
	2*n* = 4*x* = 60	Gu et al., 1988b
C. salicifolia	2*n* = 2*x* = 30	Fukushima et al., 1966; Janaki-Ammal, 1952; 1955; Kondo, 1977; Longley and Tourje, 1959
	2*n* = 4*x* = 60	Huang et al., 2013
C. saluenensis	2*n* = 2*x* = 30	Ackerman, 1971; Fukushima et al., 1966; Gu, 1996; 1997; Gu et al., 1990; Kondo, 1977; Kondo et al., 1986; Janaki-Ammal 1952; 1955; Longley and Tourje, 1960; Patterson et al., 1950; Xiao et al., 1993
‘Tourje Form’	2*n* = 2*x* = 30	Kondo, 1977
C. sasanqua	2*n* = 5*x* = 75	Ito et al., 1957
	2*n* ~ 5*x* = 80	Kondo, 1977
	2*n* = 6*x* = 90	Ackerman, 1971; Bezbaruah, 1971; Gu et al., 1988b; 1989b; Ito et al., 1971; Janaki-Ammal, 1955; Kondo, 1977; Tanaka et al., 2005; Uemoto et al., 1980; Zhuang and Dong, 1984
	2*n* = 7*x* = 105	Ito et al., 1957
	2*n* = 8*x* = 120	Huang et al., 2013; Ito et al., 1957; Kondo, 1977
‘Apple Blossom’	2*n* = 6*x* = 90	Kondo, 1977
‘Asahi-No-Umi’	2*n* = 6*x* = 90	Kondo, 1977
‘Asahi-Zuru’	2*n* = 3*x* = 45	Ito et al., 1957

Table 1.1 (continued).

‘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
‘Moon Moth’	$2n = 6x = 90$	Kondo, 1977

Table 1.1 (continued)

‘Narumi-Gata’	$2n = 5x = 75$	Ackerman, 1971; Kondo, 1977
	$2n \sim 7x = 106$	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

Table 1.1 (continued).

C. sasanqua syn. *C. miyagii* (Koidz.) Makino and Nemoto	2*n* = 6*x* = 90	Ackerman, 1971; Kondo, 1977
C. semiserrata	2*n* = 2*x* = 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*	2*n* = 2*x* = 30	Huang and Hsu, 1987
C. semiserrata var. *magnocarpa*	2*n* = 2*x* = 30	Zhang and Ming, 1998
C. septempetala	2*n* = 2*x* = 30	Gu et al., 1992
C. septempetala var. *rubra*	2*n* = 2*x* = 30	Gu et al., 1992
C. sinensis	2*n* = 2*x* = 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
	2*n* = 3*x* = 45	Ackerman, 1971; Zhuang et al., 1992
	2*n* = 4*x* = 60	Ackerman, 1971
‘Benji-Fuji’	2*n* = 2*x* = 30	Ackerman, 1971
‘Beni-Homare’	2*n* = 2*x* = 30	Ackerman, 1971
‘Makinowara-Wase’	2*n* = 2*x* = 30	Ackerman, 1971
‘Tama-Midori’	2*n* = 2*x* = 30	Ackerman, 1971
‘Yamato-Midori’	2*n* = 2*x* = 30	Ackerman, 1971

Table 1.1 (continued).

C. sinensis syn. *C. theifera* Griffith	$2n = 2x = 30$	Cohen-Stuart, 1918
C. sinensis var. *assamica*	$2n = 2x = 30$	Bezbaruah, 1968; Janaki-Ammal, 1952; 1955; Li and Yan, 1985; Yamashita, 1935
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
	$2n \sim 3x = 44$	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., 1994
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., 1994; 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., 1994
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

Table 1.1 (continued).

C. trichosperma	2*n* = 2*x* = 30	Huang et al., 2013; Xiao et al., 1991
C. tsaii	2*n* = 4*x* = 60	Kondo et al., 1991
	2*n* = 6*x* = 90	Huang et al., 2013
C. tsingpienensis	2*n* = 2*x* = 30	Gu et al., 1988b; 1989b; Kondo et al., 1991
C. tsingpienensis var. *pubisepala*	2*n* = 2*x* = 30	Gu et al., 1988b; 1989b
C. tuberculata	2*n* = 4*x* = 60	Huang et al., 2013
C. tunganica	2*n* = 2*x* = 30	Gu et al., 1992
C. tunghinensis	2*n* = 2*x* = 30	Cao and Li, 1986; Liang, 1990; Qin and Liang, 1991
C. uraku	2*n* = 2*x* = 30	Huang et al. 2013; Longley and Tourje, 1959; 1960
C. ×vernalis	2*n* = 3*x* = 45	Tanaka et al., 1986; 2005
	2*n* = 4*x* = 60	Tanaka et al., 1986; 2005; Uemoto et al., 1980
	2*n* = 5*x* = 75	Tanaka et al., 1986; 2005
‘Dawn’	2*n* = 3*x* = 45	Longley and Tourje, 1960
‘Egao’	2*n* = 4*x* = 60	Tateishi et al., 2007
‘Ginryu’	2*n* = 3*x* = 45	Ito et al., 1955; Tanaka et al., 2005
‘Hiryu’	2*n* = 3*x* = 45	Longley and Tourje, 1960; Kondo, 1977
	2*n* = 6*x* = 90	Longley, 1956
‘Gaisen’	2*n* = 4*x* = 60	Tanaka et al., 2005
‘Gaisen’ (OP)	2*n* = 5*x* = 75	Tateishi et al., 2007
‘Omi-goromo’	2*n* = 4*x* = 60	Tateishi et al., 2007
‘Star-Above-Star’	2*n* = 6*x* = 90	Kondo, 1977
‘Takarazuka’	2*n* = 4*x* = 60	Tateishi et al., 2007
‘Tamuke-yama’	2*n* = 4*x* = 60	Tateishi et al., 2007
‘Ume-ga-ka’	2*n* = 4*x* = 60	Tateishi et al., 2007
‘Ume-ga-ka’ (OP)	2*n* = 6*x* = 90	Tateishi et al., 2007

Table 1.1 (continued).

C. vietnamensis	2*n* = 7*x* = 105	Xiao et al., 1991
	2*n* = 8*x* = 120	Huang and Hsu, 1987; Xiao et al., 1991; Zhuang and Dong, 1984
C. wabisuke	2*n* = 2*x* = 30	Ito et al., 1955; Janaki-Ammal, 1952; Kato and Simura, 1970; Kitamura, 1970; Longley and Tourje, 1960
C. wabisuke f. *rosea*	2*n* = 2*x* = 30	Ito et al., 1955
'Sukiya'	2*n* = 2*x* = 30	Kondo, 1977
C. weiningensis	2*n* = 2*x* = 30	Zhuang and Dong, 1984
C. wenshanensis	2*n* = 2*x* = 30	Gu and Sun, 1997; Gu et al., 1988b; 1989b; Lu et al., 1993
C. wumingensis	2*n* = 2*x* = 30	Liang, 1990
C. xiashiensis	2*n* = 2*x* = 30	Liang, 1990; Liao et al., 1988
C. xylocarpa	2*n* = 4*x* = 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	2*n* = 2*x* = 30	Chen et al., 2003; Kondo et al., 1991; Li et al., 1989
	2*n* = 6*x* = 90	Gu et al., 1988b; 1989b
C. yunnanensis	2*n* = 2*x* = 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
<u>*Related species*</u>		
Apterosperma oblata	2*n* = 2*x* = 30	Wang et al., 2006
Franklinia alatamaha	2*n* = 2*x* = 36	Santamour, 1963
Gordonia lasianthus	2*n* = 2*x* = 36	Bostick, 1965
	2*n* = 2*x* = 30	Santamour, 1963
Polyspora chrysandra	2*n* = 2*x* = 30	Yang et al., 2004

Table 1.1 (continued).

P. excelsa	2*n* = 2*x* = 30	Mehra and Sareen, 1973
P. hainanensis	2*n* = 2*x* = 30	Yang et al., 2004
P. longicarpa	2*n* = 2*x* = 30	Yang et al., 2004
P. axillaris	2*n* = 2*x* = 30	Mehra and Sareen, 1973
Pyrenaria diospyricarpa	2*n* = 2*x* = 30	Yang et al., 2000
P. oblongicarpa	2*n* = 2*x* = 30	Yang et al., 2000
P. turbinata	2*n* = 2*x* = 30	Yang et al., 2000
Schima mertensiana	2*n* = 2*x* = 36	Ono, 1975; 1977 (Goldblatt 1981 IPCN)
S. superba	2*n* = 2*x* = 36	Ming and Bartholomew, 2007
S. wallichii	2*n* = 2*x* = 30	Malla et al., 1977
	2*n* = 2*x* = 36	Oginuma et al., 1994
Stewartia malacodendron	2*n* = 2*x* = 30	Santamour, 1963
S. monadelpha	2*n* = 2*x* = 30	Santamour, 1963
	2*n* = 2*x* = 34	Horiuchi and Oginuma, 2001
S. ovata	2*n* = 2*x* = 30	Santamour, 1963
S. pseudocamellia	2*n* = 2*x* = 30	Santamour, 1963
	2*n* = 2*x* = 34	Horiuchi and Oginuma, 2001
S. serrata	2*n* = 2*x* = 30	Santamour, 1963
	2*n* = 2*x* = 34	Horiuchi and Oginuma, 2001
S. sinensis	2*n* = 2*x* = 30	Santamour, 1963
Tutcheria greeniae	2*n* = 2*x* = 30	Yang et al., 2000
T. hirta	2*n* = 2*x* = 30	Yang et al., 2000
T. microcarpa	2*n* = 2*x* = 30	Yang et al., 2000
T. pingpienensis	2*n* = 2*x* = 30	Yang et al., 2000
T. spectabilis	2*n* = 2*x* = 30	Ackerman, 1971; Yang et al., 2000
T. subsessililflora	2*n* = 2*x* = 30	Yang et al., 2003
T. symplocifolia	2*n* = 2*x* = 30	Yang et al., 2000

Table 1.1 (continued).

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.

Table 1.2. Genome sizes and estimated ploidy levels of cultivated camellias 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*					
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 ± 020	0.77	2[V]
		GrN	1.64 ± 0.13	0.82	
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*					

Table 1.2 (continued).

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

Table 1.2 (continued).

C. japonica	'Governor Mouton'	NCSU 2016-005	6.47 ± 0.39	3.24	2
C. japonica	'Irrational Exuberance'	GN	6.33 ± 0.41	3.17	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
		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

Table 1.2 (continued).

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
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

Table 1.2 (continued).

C. crapnelliana = octopetala		CF	6.76 ± 0.42	3.38	2
Section *Paracamellia*					
C. grijsii		CF	5.65 ± 0.51	2.83	2
C. hiemalis	'Rose of Autumn'	JCRA 070075	21.11 ± 1.59	3.52	6
C. grijsii var. *grijsii = odorata*		CF	16.33 ± 0.81	2.72	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. brevistyla var. *brevistyla = puniceiflora*		CGBG14	12.35 ± 0.50	3.09	4
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

Table 1.2 (continued).

C. sasanqua	'Green 94-035' October Magic® Orchid™	JCRA 110770	16.59 ± 1.45	2.77	6
C. sasanqua	'Green 99-031' Susy Dirr	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	'Rosey 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

Table 1.2 (continued).

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	2.71	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

Table 1.2 (continued).

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. *synaptica*	'Elina Cascade'	CF	7.11 ± 0.32	3.56	2
Genus *Polyspora*					
P. axillaris		GrN	11.32 ± 0.54	1.89	6
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]

Table 1.2 (continued).

***Unplaced in Ming & Barthlomew 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 when given indicate plant received as such.

[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, D.C.;

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

[W]1C*x* values were calculated as 2C value/ploidy level.

[V]Ploidy levels were confirmed by cytology.

Table 1.3. Monploid genome sizes (1C*x*), determined by flow cytometry, for Camellia and related taxa grouped by subfamily, section, genus, species within the Theaceae.

Subfamily	1C*x* (pg)[Z]	Genus	1C*x* (pg)[Z]	Subgenu	1C*x* (pg)	Section	1C*x* (pg)[Z]	Species	1C*x* (pg)[Z]
Gordoniae	0.84 A	*Franklinia*	0.81 D					*F. alatamaha*	0.81 N
		Gordonia	0.84 D					*G. lasianthus*	0.84 N
		Schima	0.84 D					*S. argentea*	0.85 M
								S. khasiana	0.83 N
								S. remotiserrata	0.91 MN
								S. sinensis	0.82 N
								S. superba	0.79 N
								S. wallichii	0.86 N
Stewartiae	2.50 B	*Stewartia*	2.50 B					*S. ovata*	2.34 J
								S. pseudocamellia	2.71 HIJ
								S. sp. (Hartia sp.)	2.61 IJ
Theeae	3.01 C	*Camellia*	3.14 A	Camellia	3.12 B	Camellia	3.10 AB	*C. azalea*	2.70 HIJ
								C. cheakiangoleosa	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

Table 1.3 (continued).

						C. reticulata	2.82 FGHI
						C. semiserrata	3.02 CDEFGHI
				Heterogenea	3.29 A	*C. crapnelliana*	3.29 ABCDE
				Paracamellia	3.11 AB	*C. brevistyla*	3.09 BCDEFGH
						C. drupifera	2.87 EFGHI
						C. grijsii	2.78 FGHIJ
						C. hiemalis	3.52 AB
						C. oleifera	3.11 BCDEFGH
						C. sasanqua	3.20 ABCDEF
		Thea	3.22 A	Archecamell	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	3.22 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 KL

Table 1.3 (continued).

		P. chrysandra	1.75 KL
		P. sp.	1.96 JK
		P. sp. (JCRA	1.70 KL
	Pyrenaria 1.39 C	*P. microcarpa*	1.42 KL
		P. spectabilis	1.33 LM

Values followed by different letters within a column are significantly different by Fisher's LSD test, $P \leq 0.05$.

Table 1.4. 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 1C*x* genome size (pg)[X]	Purported parental ploidy levels (*x*)	Est. ploidy (*x*)[W]
		Intraploid hybrids				
C. japonica ssp. *rusticana x lutchensis*	'Fragrant Joy'	NCSU 2016-096	6.52 ± 0.36	3.17	2 x 2	2
C. ×*williamsii*	'Freedom Bell'	CF	6.35 ± 0.41	2.96	2 x 2	2
C. japonica × *C. edithae*	'Heimodan'	CF	6.35 ± 0.45	3.12	2 x 2	2
C. ×*williamsii*	'Mary Christian'	JCRA xx0193	5.84 ± 0.48	2.96	2 x 2	2
C. pitardii × *C. japonica*	'Nicky Crisp'	NCSU 20015-134	5.85 ± 0.58	3.29	2 x 2	2
C. flava × *C. japonica*	'Optical Illusion'	CF	5.71 ± 0.46	2.89	2 x 2	2
C. japonica × *C. lutchuensis*	'Quintessence'	UF 20071130	6.11 ± 0.49	3.17	2 x 2	2
C. japonica × *C. sinensis*	'Robiraki'	CF	5.91 ± 0.53	3.20	2 x 2	2
C. xwilliamsii	'Taylor's Perfection'	CGBG1	6.35 ± 0.41	2.96	2 x 2	2
C. japonica 'Wendy' × *C. azalea*	'Wendzalea'	GN	6.17 ± 0.39	2.92	2 x 2	2
C. flava × *C. japonica* 'Snowman'	Unnamed selection	GN	5.91 ± 0.33	2.89	2 x 2	2
C. japonica × *C. flava*	Unnamed selection	GN	5.93 ± 0.36	2.89	2 x 2	2

Table 1.4 (continued).

C. amplexicaulis × *C. japonica* 'Royal Velvet'	Unnamed selection	GN	5.45 ± 0.33	2.67	2 x 2	2
C. amplexicaulis × *C. japonica* 'Kramer's Supreme'	Unnamed selection	GN	5.56 ± 0.31	2.67	2 x 2	2
Camellia japonica × *Franklinia alatamaha*	Unnamed selection	USNA 79387	5.94 ± 0.51[X]	1.97	2 x 2	2[V]
C. sasanqua 'Shikishima' × *C. oleifera* 'Plain Jane'	'Ashton's Ballet'	NCSU 2015-071	20.44 ± 0.82	3.09	6 x 6	6
C. sasanqua 'Shikishima' × *C. oleifera 'Plain Jane'*	'Ashton's Ballet'	USNA 82775	21.24 ± 0.99	3.09	6 x 6	6
C. oleifera 'Plain Jane' × *C. sasanqua* 'Santô-zaki'	'Ashton's Pride'	CF	18.67 ± 1.47	3.12	6 x 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 x 6	6

Table 1.4 (continued).

(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 x 6	6
C. oleifera × *C. sasanqua*	'Carolina Moonmist'	NCSU 2014-166	20.98 ± 1.07	3.08	6 x 6	6
C. sasanqua 'Narumi gata' × *C. oleifera*	'CF21'	H2003-023-011	18.53 ± 1.51	3.16	6 x 6	6
(C. reticulata × *C. fraterna) OP*	'Crimson Candles'	JCRA	15.26 ± 0.94	2.92	6 x ?	6
C. 'Yume' (*C. yuhsienensis* × *C. hiemalis* 'Shishigashira') OP	'Dream Quilt'	NCSU 2015-003	18.73 ± 1.67	3.15	6 x ?	6
C. hiemalis 'Bill Wylam' x *C. oleifera*	'Frost Princess'	USNA 75304	20.64 ± 0.98	3.32	6 x 6	6
C. oleifera 'Plain Jane' × *C. sasanqua*	'Londontowne Blush'	USNA 73731	21.84 ± 1.44	3.12	6 x 6	6
C. 'Yume' (*C. yuhsienensis* × *C. hiemalis* 'Shishigashira') OP	'Marshall'	GN	17.56 ± 1.04	3.15	6 x ?	6

Table 1.4 (continued).

C. × 'Frost Princess' (*C. hiemalis* 'Bill Wylam' × *C. oleifera* 'Plain Jane') × *C. oleifera*	'Polar Ice'	CF	19.98 ± 1.94	3.22	6 x 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 x 6	6
C. sasanqua 'Narumi-gata' × *C. oleifera*	'Survivor'	CF	22.00 ± 1.52	3.08	6 x 6	6
C. sasanqua 'Takara-wase' × *C. oleifera*	'Winter's Charm'	CGBG17	20.40 ± 1.59	3.08	6 x 6	6
C. oleifera 'Plain Jane' × *C. sasanqua*	'Winter's Cupid'	USNA 69933	21.30 ± 1.02	3.12	6 x 6	6
C. hiemalis 'Shishigashira' × *C. oleifera*	'Winter's Darling'	USNA 75299	22.30 ± 1.08	3.32	6 x 6	6
(C. hiemalis 'Bill Wylam' × *C. hiemalis* 'Shishi-gashira') × *C. oleifera* 'Plain Jane'	'Winter's Fancy'	USNA 69934	19.78 ± .89	3.52	6 x 6	6
C. oleifera × *C.* × 'Frost Princess' (*C. hiemalis* 'Bill Wylam' × *C. oleifera* 'Plain Jane')	'Winter's Hope'	CF	19.65 ± 1.27	3.22	6 x 6	6
C. oleifera 'Plain Jane' × *C. sp.*	'Winter's Interlude'	CF	20.07 ± 2.03	3.12	6 x ?	6

Table 1.4 (continued).

(C. sasanqua 'Narumi-gata' × *C. sansaqua* 'Shishigashira') × *C. oleifera* 'Plain Jane'	'Winter's Joy'	CF	20.47 ± 1.69	3.16	6 x 6	6
(*C. sasanqua* 'Narumi-gata' × *C. sasanqua* 'Shishigashira') × *C. oleifera* 'Plain Jane'	'Winter's Peony'	CF	20.47 ± 1.69	3.16	6 x 6	6
C. sasanqua 'Shishigashira' × *C. oleifera* 'Lu Shan Snow'	'Winter's Red Rider'	CF	21.28 ± 0.99	3.16	6 x 6	6
C. oleifera 'Plain Jane' × *C. hiemalis* 'Otome'	'Winter's Rose'	CF	20.79 ± 1.37	3.32	6 x 6	6
C. oleifera × *C. hiemalis* 'Show-no-sakae'	'Winter's Star'	CGBG19	20.97 ± 1.50	3.32	6 x 6	6
C. oleifera × *C. hiemalis 'Show-no-sakae'*	'Winter's Star'	JCRA 090424	21.02 ± 1.02	3.32	6 x 6	6
Sport of 'Winter's Star'	'Winter's Star Light'	JCRA 960468	17.265 ± 1.45	3.32	6	6
C. oleifera × C. sasanqua	'Winter's Toughie'	CF	15.90 ± 1.48	3.16	6 x 6	6
C. oleifera × *C. sasanqua* 'Mine-no-yuki'	'Winter's Waterlily'	CF	20.74 ± 1.45	3.16	6 x 6	6
C. sasanqua 'Shishigashira' × *C. yuhsienensis*	'Yume'	CF	17.25 ± 1.51	2.93	6 x 6	6

Table 1.4 (continued).

C. 'Winter's Charm' (*C. sasanqua* 'Takara-wase' × *C. oleifera)* OP	Unnamed selection	H2003-022-002	20.96 ± 0.92	3.16	6 x ?	6
C. 'CF.21' (*C. sasanqua* 'Narumigata' × *C. oleifera*) OP	Unnamed selection	NCSU H2003-023-011	19.24 ± 1.61	3.16	6 x 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 x ?	6
C. 'Winter's Charm' (*C. sasanqua* 'Takara-wase' × *C. oleifera)* OP	Unnamed selection	H2003-024-005	18.74 ± 0.70	3.16	6 x ?	6
		Putative Interploid Hybrids				
C. ×*williamsii* 'November Pink' × *C. oleifera* 'Lu Shan Snow'	'Arctic Dawn'	USNA 82774	6.01 ± 0.44	3.04	2 x 6	2^V
C. japonica × *C. oleifera*	'Fire 'N Ice'	USNA 63544	6.05 ± 0.57	3.10	2 x 6	2^V
C. oleifera × *C. japonica*	'Ice Follies'	CF	6.27 ± 0.42	3.10	6 x 2	2^V
C. ×*williamsii* 'November Pink' × *C. oleifera* 'Lu Shan Snow'	'Pink Icicle'	CF	5.99 ± 0.56	3.04	2 x 6	2^V
C. oleifera × *C. japonica*	'Red Fellow'	CF	6.23 ± 0.44	3.10	6 x 2	2^V
C. japonica × *C. oleifera*	'Spring Cardinal'	CF	6.14 ± 0.51	3.10	2 x 6	2^V
C. japonica × *C. oleifera*	'Spring Circus'	USNA 73726	6.10 ± 0.52	3.10	2 x 6	2^V

Table 1.4 (continued).

C. oleifera 'Plain Jane' × *C.* ×*vernalis* 'Egao'	'Spring Frill'	CF	6.02 ± 0.49	3.14	6 x 4	2[v]
C ×*vernalis* 'Egao' OP	'Christmas Candy'	GrN	9.52 ± 0.69	3.17	4 x ?	3
C. ×*vernalis*	'Ginryu'	GrN	8.90 ± 0.48	2.97	2 x 6	3
C. ×*vernalis* 'Ginryu' OP	'Starman'	GrN	9.35 ± 0.64	3.17	3 x ?	3
C ×*vernalis* 'Star-Above-Star' OP	Unnamed selection	GrN 00-020	9.29 ± 0.92	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 05-017	9.93 ± 0.69	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-051	10.13 ± 0.72	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-052	8.45 ± 1.13*	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-053	9.85 ± 0.57	3.17	4 x ?	3
C ×*vernalis* 'Star-Above-Star' OP	Unnamed selection	GrN 07-054	9.73 ± 0.76	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-065	9.16 ± 0.69	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 07-066	9.86 ± 1.04*	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 08-054	8.91 ± 0.83	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 08-056	9.27 ± 0.87	3.17	4 x ?	3
C.×*vernalis* 'Ginryu' OP	Unnamed selection	GrN 08-070	9.78 ± 0.60	3.17	3 x ?	3

Table 1.4 (continued).

C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 08-071	9.68 ± 0.47	3.17	4 x ?	3
C ×*vernalis* 'Egao' OP	Unnamed selection	GrN 13-007	9.92 ± 0.38	3.17	4 x ?	3
C. japonica x C. oleifera	'Ashton's Pink'	NCSU 2015-066	12.87 ± 0.67	3.13	2 x 6	4
C ×*vernalis* 'Star-Above-Star' OP	'Dabney's Star'	GrN	12.84 ± 0.78	3.17	4 x ?	4
C. ×*vernalis* 'Ginryu' OP	Unnamed selection	GrN 08-080	12.90 ± 0.72	3.17	3 x ?	4
C. 'Christmas Candy' (*C.* ×*vernalis* 'Egao' OP) OP	Unnamed selection	GrN J-031	12.10 ± 0.38	3.17	3 x ?	4
C. × *vernalis*	'Egao'	GrN	13.08 ± 0.81	3.08	2 x 6	4
Sport of *C.* ×*vernalis* 'Egao'	'Egao Corkscrew'	JCRA	12.81 ± 0.92	3.08	2 x 6	4^{U}
C. japonica 'Mrs. Bertha A. Harms' × *C. oleifera* 'Plain Jane'	'Elaine Lee'	CF	13.47 ± 0.94	3.17	2 x 6	4
C. japonica 'Frost Queen' × *C. oleifera*	'Fairweather Favorite'	USNA 73958	13.19 ± 0.91	12.2	2 x 6	4
C. ×*vernalis*	'Star Above Star'	NCSU 2017-104	12.23 ± 0.63	3.17	2 x 6	4
C. japonica 'Billie McCaskill' × *C. oleifera* 'Plain Jane'	'Winter's Beauty'	CGBG21	12.92 ± 0.61	3.17	2 x 6	4

Table 1.4 (continued).

C. japonica × *C. yushienensis*	Unnamed selection	CF	12.12 ± 0.62	2.88	2 x 6	4
C. 'Christmas Candy' (*C.* ×*vernalis* OP) OP	Unnamed selection	GrN J-081	12.52 ± 0.73	3.17	3 x ?	4
C. ×*williamsii* 'William's Lavender' × *C. reticulata* 'Purple Gown'	'Scarlet Temptations'	CF	14.27 ± 0.94	2.89	2 x 6	5 [V]
C. sasanqua × *C. tenuiflora*	'Starry Pillar'	NCSU 2016-102	14.94 ± 1.01	3.15	6 x 2	5[V]
C. ×*vernalis* 'Takarazuka' × *C.* 'Frost Prince' (*C. hiemalis* 'Shishigashira' × *C. oleifera*)	'Winter's Fire'	CGBG23	16.17 ± 1.14	3.09	4 x 6	5
C. ×*vernalis* 'Egao' OP	'Egao Spring Snowfall'	GrN	17.33 ± 1.35	3.17	4 x ?	6
C. ×*vernalis* 'Ginryu' OP	'Eos'	GrN	19.43 ± 1.94	3.17	3 x ?	6
C. 'Eos' (*C.* ×*vernalis* 'Ginryu' OP) OP	Unnamed selection	GrN 10-005	18.74 ± 0.88	3.17	6 x ?	6
C. 'Dabney's Star' (*C* ×*vernalis* 'Star-Above-Star' OP) OP	Unnamed selection	GrN 12-001	18.07 ± 0.76	3.17	4 x ?	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,

Table 1.4 (continued).

Savannah, GA; NCSU = North Carolina State University Mountain Horticultural Crops Research and Extension Center, Mills River, NC. OP = open pollinated.

Table 1.4 (continued).

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

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

[W]Estimated ploidys were calculated as 2C genome size / weighted 1C*x*.

[V]Ploidy and/or genome size is inconsistent with reported parentage.

[U]Ploidy confirmed with cytology.

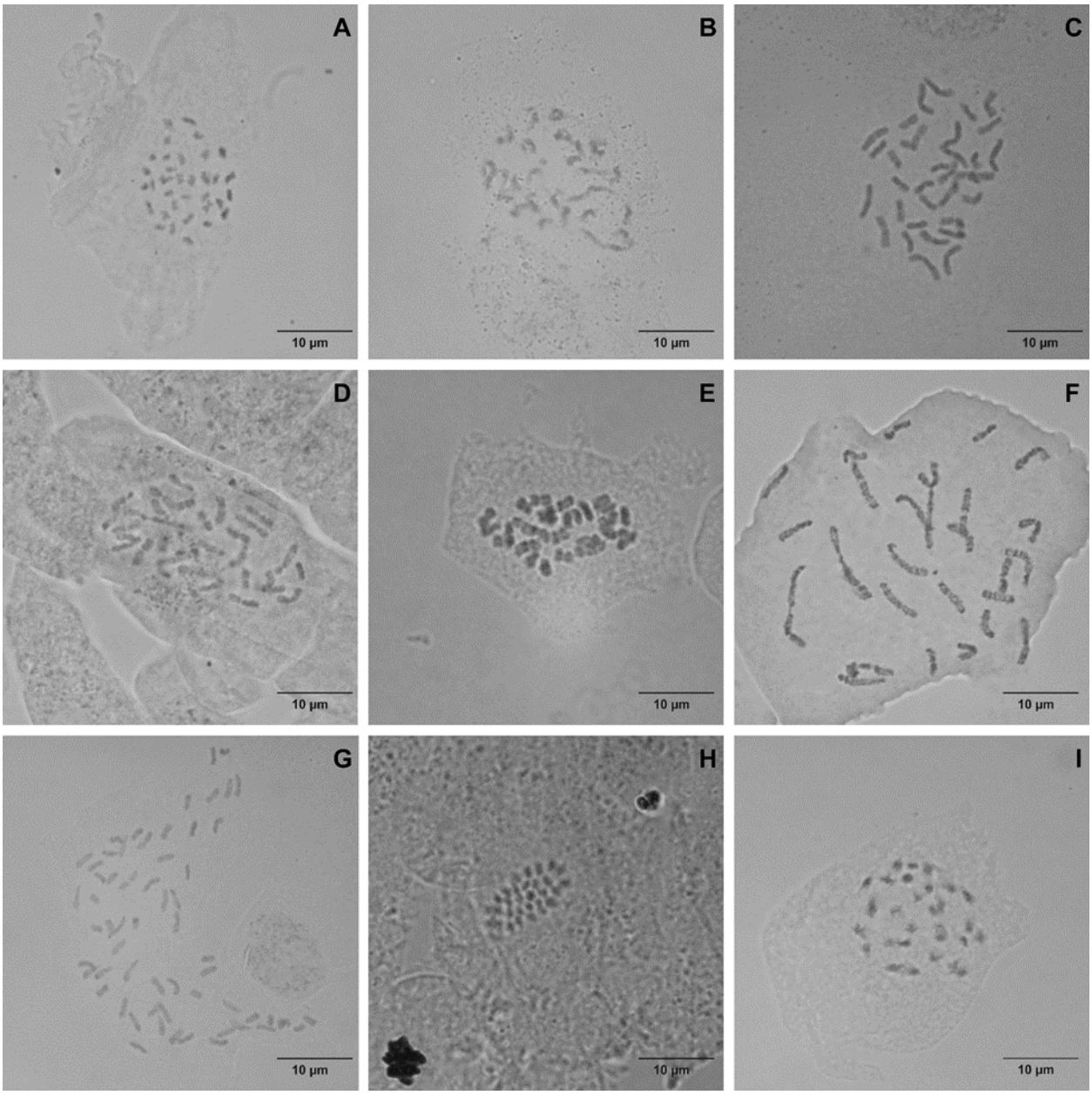

Figure 1.1. Photomicrographs of condensed, stained chromosomes of Theaceae.(A): *Gordonia lasianthus* 2006-220, 2*n* 2*x* = 36 (B): *Schima superba* 2018-009, 2*n* = 2*x* = 36 (C): *Stewartia pseudocamellia* 2018-111, 2*n* = 2*x* = 34 (D): *Camellia japonica* 'Dr. JC Raulston' 2017-060, 2*n* = 2*x* = 30 (E): *Camellia sinensis* 'Red Leaf' 2017-111, 2*n* = 2*x* = 30 (F): *Camellia azalea* 2018-063, 2*n* = 2*x* = 30 (G): *Camellia* ×*vernalis* 'Egao Corkscrew' 2017-062, 2*n* = 4*x* = 60 (H): *Polyspora chrysandra* 2015-114, 2*n* = 2*x* = 30 (I): *Pyrenaria spectabilis* 2018-008 2*n* = 2*x* = 30.

CHAPTER 2: Identification, Genome Sizes, and Ploidy of *Deutzia*

William G. Hembree[1] and Thomas G. Ranney[2]

Mountain Crop Improvement Laboratory, Department of Horticultural Science, Mountain Horticultural Crops Research and Extension Center, North Carolina State University, 455 Research Drive, Mills River, NC 28759

Brian E. Jackson[3]

Department of Horticultural Science, North Carolina State University, Campus Box 7609, Raleigh, NC, 27695-7609

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[1]Graduate Research Assistant.

[2]JC Raulston Distinguished Professor and corresponding author, Email: tom_ranney@ncsu.edu

[3]Associate Professor.

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Identification, Genome Sizes, and Ploidy of *Deutzia*

Additional index words. cytogenetics, cytology, DNA content, flow cytometry, Hydrangeaceae, plant breeding, polyploidy, taxonomy

Abstract. **The genus *Deutzia*, in the Hydrangeaceae, includes about sixty species that range in ploidy from diploid (2*x*) to tetradecaploid (14*x*). There have been extensive breeding efforts in *Deutzia*, but this has been limited to the use of only a few parental species. Although there have been numerous studies into the cytogenetics of some species of *Deutzia*, the ploidy level of many species remains unknown and there is very little cytogenetic data available for *Deutzia* hybrids and cultivars. The purpose of this study was to validate identification and determine the genome sizes and ploidy of a diverse collection of *Deutzia* species, hybrids, and cultivars using cytology and flow cytometry. Accessions were identified using the most current taxonomic key and voucher specimens were deposited for each at the North Carolina State University herbarium. Corrected and updated species names are provided for all cultivars and accessions studied. Traditional cytology was performed on roots of representative taxa to calibrate genome size with ploidy level. Genome size and estimated ploidy was determined for 46 accessions using flow cytometry. Ploidy levels were reported for the first time for three species of *Deutzia* included *D. calycosa* (2*n* = 4*x* = 52), *D. paniculata* (2*n* = 4*x* = 52) and *D. glauca* (2*n* = 12*x* = 156). Base, monoploid genome size (1C*x*) was relatively conserved and ranged from 1.20 to 2.05 pg for these species. Ploidy of all interspecific hybrid taxa was consistent with and had the same ploidy as the reported parents except for *D.* ×*myriantha* 2014-116, which was found to be an octoploid while the purported parental species were most likely diploid, indicating incorrect parentage. No interploid hybrids were documented suggesting the presence of an interploid block. The information produced from this study should benefit future curation, research, development and improvement of this genus with corrected nomenclature and clone-specific data on cytogenetics.**

Deutzia are a valuable group of temperate landscape plants grown primarily for their profusions of showy white to pink flowers produced in late spring. Several species have been widely cultivated in Europe since the first *Deutzia* were imported from Japan in the early 18th century. *Deutzia* gained added global popularity early in the 19th century, due to the introduction of additional Asian species into cultivation (Styer and Stern, 1979). With access to this diverse germplasm, many additional *Deutzia* hybrids and cultivars were developed through the breeding and selection efforts of Victor Lemoine, his family, and the Lemoine Nursery staff in the 19th and early-mid 20th century in Nancy, France (Wyman, 1971). Development of new hybrids and cultivars has continued since.

The taxonomic history of *Deutzia* has seen it placed within both the *Saxifragaceae* and the *Philadelphaceae* families, though it is currently accepted to be a member of the *Philadelpheae* within the *Hydrangeaceae* (Soltis et al., 1995; Stevens, 2001 onwards). *Deutzia* is most closely allied with *Kirengoshoma*, a small genus of rhizomatous perennials that share a few morphological traits with *Deutzia* (Hufford et al., 2001). *Deutzia* represents a disjunct genus with species occurring in eastern Asia and central America. The genus has traditionally been divided into three sections based on morphological differences, with the Asian sections *Deutzia* and *Mesodeutzia* differing in the aestivation of the petals - valvate/induplicate in Sec. *Deutzia* and imbricate in Sec. *Mesodeutzia*. The central American *Neodeutzia*, rarely treated as a separate genus, differs from its Asian relatives in the number of stamens with 12 to 15 in *Neodeutzia* compared to 10 in *Deutzia* and *Mesodeutzia* (Hwang, 1993; Styer and Stern, 1979; Zaikonnikova, 1966; 1975). Kim et al. (2015) constructed a phylogeny of the genus and suggested that polyphyletic sections *Deutzia* and *Mesodeutzia* be merged into a single monophyletic section (*Deutzia*/*Mesodeutzia*), reducing the number of sections to two.

Polyploidy has played an important role in the evolution and divergence of angiosperms (Soltis et al., 2015; Wendel, 2015). These repeated cycles of whole genome duplication (sometimes coupled with hybridization) can lead to reproductive isolation, genomic rearrangements, enzymatic multiplicity, epigenetic changes, and novel phenotypes that contribute to biodiversity and speciation (Adams and Wendel, 2005; Chen and Ni, 2006; Chen and Yu, 2013; Hegarty and Hiscock, 2008; Laport and Ng, 2017; Madlung, 2013). For plant breeders, knowledge of ploidy is particularly important as it influences reproductive compatibility, fertility of hybrids, and gene expression (Ranney, 2006). There have been numerous cytological studies into *Deutzia* beginning with Sax (1931) at the Arnold Arboretum. Compared to other genera within the *Philadelpheae*, *Deutzia* exhibits extreme variability in ploidy, with $2n = 2x = 26$ to $2n = 14x = 182$ (Table 1), possibly with ploidy variation within species. The other

speciose genus in this tribe, *Philadelphus*, has a similar number of species (about 65) as *Deutzia* (Dirr, 2009). However, unlike in *Deutzia*, polyploidy is not found in *Philadelphus.* The greater ploidy variation in *Deutzia* may contribute to its higher degree of morphological variation when compared to other genera in this tribe (Sax, 1931). Both *Deutzia* and *Philadelphus*, as well as *Fendlerella,* also of the *Philadelpheae,* have a base chromosome number of $x = 13$ (Sax, 1931; Ward, 1984).

Genome size (base DNA content) can reflect biodiversity traits, genome evolution, and taxonomic relationships (Laport and Ng, 2017; Ranney et al., 2018; Rounsaville and Ranney, 2010; Soltis et al., 2015). Genome size data can also be used to estimate ploidy in closely related taxa when properly calibrated with known cytological standards (Jones et al., 2007; Lattier et al., 2014; Parris et al., 2010; Rounsaville and Ranney, 2010; Shearer and Ranney, 2013). The single previous report of genome size in *Deutzia* was also the first report of genome size in the Hydrangeaceae. Using Feulgen densitometry, Hanson et al. (2001) determined the 1C genome size of *D. prunifolia* to be 1.9 pg. The more recent development of flow cytometry provides a more accurate and efficient method to determine genome size (Doležel et al., 2007). We are not aware of other reports of genome size in *Deutzia* using flow cytometry.

Despite the extensive use and wide cultivation of *Deutzia,* correct identification of species is challenging and problematic and differentiation between species is often subtle (Dirr, 2009). With over sixty species of *Deutzia*, it is possible that many species and cultivars have been traded under incorrect names for years. However, an excellent key for *Deutzia* was developed by Zaikonnikova (1975) that provides clear distinctions between taxa.

The broad genetic diversity and array of desirable commercial traits found in *Deutzia* provide a valuable base for further breeding and development of future cultivars. However, confusion over proper identity and lack of information on cytogenetics of particular accessions and cultivars constrains the development of informed breeding strategies. The objectives of this study were to validate identification and determine genome sizes and estimated ploidy for an extensive collection of *Deutzia* species, hybrids, and cultivars.

Materials and Methods

Plant Material. Plant material was collected from arboreta and botanical gardens within the United States in June 2014. Plants were propagated, accessioned, and incorporated into the research collection at the Mountain Horticulture Crops Research and Extension Center in Mills River, NC. Accessions were planted in the fall of 2014.

Flowering and vegetative material of mature plants from each accession were collected and pressed in May 2018. For root tip collections, selected taxa were propagated, containerized, and grown using standard horticultural practices. All accessions were identified following Zaikonnikova's key as translated by Airy Shaw (1975). Herbarium specimens for each accession were prepared and deposited in the North Carolina State University Herbarium (NCSC) in Gardner Hall, Raleigh, NC.

Genome size/Ploidy Determination. Flow cytometry and cytology were used in concert to determine genome size and ploidy of each accession. For flow cytometry, samples were prepared from fully expanded leaf tissue. Approximately 0.5 cm^2 of leaf tissue was placed in a petri dish with 500 µl nuclei extraction buffer (CyStain PI Absolute P Nulclei Extraction Buffer, Sysmex Partec, Görlitz, Germany) and finely chopped with a razorblade. The resulting solution was filtered through a 50 µm nylon mesh filter (CellTrics, SysmexPartec) into a 3.5 ml polystyrene tube. Following filtration, 2 mL of nuclei staining buffer (CyStain PI Absolute P, Sysmex Partec), 6 µl RNAse A (Sysmex Partec), and 12 µl propidium iodide (Sysmex Partec) was added to the mixture. The solution was then incubated at 4°C in a refrigerator for at least 30 minutes. The incubated samples were analyzed using a Partec PA II Flow Cytometer (Partec). A minimum of 3000 counts were recorded for each sample. Two subsamples were prepared for each accession. Mean fluorescence for each sample was compared to an internal standard, either *Pisum sativum* 'Ctirad' (2C = 8.76 pg) or *Magnolia virginiana* 'Jim Wilson' (2C = 3.92 pg) (Doležel et al., 1998; Parris et al., 2010). Genome size (2C) was calculated as (DNA content of the standard) x (mean fluorescence of the sample / mean fluorescence of the standard). 1C*x* monoploid genome size was calculated as (2C genome size / ploidy).

To calibrate genome size with ploidy levels, chromosome counts were performed on root tips from selected accessions. Root tips from actively growing roots were collected from containerized plants. Root tips were placed in 2mM 8-hydroxyquinoline + 70 mg L-1 cycloheximide to arrest mitosis. Roots were left for 3 hours at room temperature (20°C) in the dark before being moved to a refrigerator to incubate at 4°C for an additional 3 hours. After the cold incubation period, the roots were triple-washed in cold, distilled water before being transferred to a 1:3 fixative solution of propionic acid and 95% ethanol and stored at room temperature overnight. The following morning the roots were transferred to a storage solution of 70% EtOH. Fixed roots were hydrolyzed in a 1:3 solution of 12M hydrochloric acid and 95% ethanol for 90 seconds. The roots were moved to a slide where the tips were excised before being transferred to a new slide with a drop of modified carbol fuchsin. After several minutes, a

cover slip was placed over the root tips and they were then squashed and viewed with a light microscope at 1000x magnification. Highly resolved cells were observed and photographed for each counted accession.

Results and Discussion

Forty-six accessions were included in this study representing 13 unique species and 6 unique interspecific hybrids including 24 named cultivars (Tables 2 and 3). Of the taxa studied, species designations on 18 were inconsistent with the key created by Zaikonnikova (1966) (Table 2). The names in the Zaikonnikova key were compared with current taxonomy in *Deutzia*, updated where appropriate (The Plant List, 2018), and species names were corrected when appropriate (Table 2). There were many possible factors that could have contributed to these discrepancies. As Zaikonnikova (1966) stated at the beginning of her key, *Deutzia* are "a difficult group" that present many "problems of identification". It is difficult to know how many of our germplasm sources have been revisited and reexamined since the date of their initial accessions, and it is likely that the concept and scope of the genus *Deutzia* and species designations has changed considerably since then. It is often the case, particularly in commerce, that species names are accepted without question, especially when there are no resident experts at the receiving institution. In this way, plants may be widely shared and distributed, and even come to be known by a name which is taxonomically incorrect.

Estimated ploidy levels of the *Deutzia* included in this study ranged from 2*x* to 12*x*. The first known ploidy estimates of *D. calycosa* (2*n* = 4*x* = 52), *D. paniculata* (2*n* = 4*x* = 52), and *D. glauca* (2*x* = 12*x* = 156) were also determined. For *D. parviflora*, *D. naseana*, and *D. longifolia*, ploidy levels were found which were inconsistent with the past literature. It is likely that previous cytological studies in *Deutzia* were challenged by the same taxonomic issues and difficulty in correctly identifying species that were encountered in this study. As such, it is difficult to know for certain which taxa specifically were being used in these studies and if the species designations were correct as herbarium vouchers generally don't exist for these studies. The difficulties surrounding the identification of members of this group are omnipresent and influence the results of virtually all studies thereof. Without the ability to confirm which species have been studied previously, it is sometimes difficult to validate the results of prior studies of *Deutzia*.

Several species of Deutzia have been reported as having ploidy series according to the literature, including *D. bungoensis, D. corymbosa,* and *D. uniflora*, as well as two species included in our study, *D crenata and D.*

scabra. In this study ploidy series were not found in these species but was found in Deutzia schneideriana, which has not been previously reported as having a ploidy series. If the accessions in this study were not keyed and verified, our results would have been quite different. For example, *D. gracilis* 'Pink Minor' ($2n = 2x = 26$), *D. crenata* 'Codsall Pink' ($2n = 10x = 130$), *D. crenata* 'Candidissima' ($2n = 10x = 130$) and *D. naseana* 2014-111 ($2n = 10x = 130$) were all received as *D. scabra* before being keyed out. *D. scabra* and *D. crenata* have shared a close and confusing taxonomic and horticultural history. The common name Pride of Rochester, which is sometimes used as a cultivar name, is variously ascribed to both species (Clapham, 1959; Clarke, 2007). Additionally, *D. crenata* has at times been considered a synonym of *D. scabra* (Hillier Nurseries, 1974), and the Flora of China (Huang et al., 2001) recognizes *Deutzia crenata* as being synonymous with *D. scabra* var. *crenata*. Kim et al. (2015) showed the two to be very closely related as sister species in his phylogenetic study of the genus, adding to the confusion surrounding the circumscription of the putative taxa.

The accessions received as *D. scabra* var. *prunifolium* 2014-111 and *D. parviflora* 2014-073 both keyed to *D. scabra* var. *latifolia*, which is a synonym of the currently accepted *D. naseana* that has been reported as tetraploid (Funamoto and Nakamura, 1992; Ohba and Akiyama, 1992). Both accessions were found to be $2n = 10x = 130$, which has been reported for *D. scabra* (Singhal et al., 1980), but not *D. naseana*.

Most of the accessions received as *D. scabra* were cultivars, including 'Candidissima' and 'Codsall Pink', two decaploids, and 'Pink Minor', a diploid. 'Candidissima' and 'Codsall Pink' were keyed to *D. crenata*. Both *D. crenata* and *D. scabra* have been reported to be decaploids (Niu and Ohba, 2000; Singhal et al., 1980). 'Pink Minor' was keyed to be *D. gracilis*, consistent with all other diploid *D. gracilis* included in this study.

Two of the three accessions that were identified as *D. discolor* were received under other names, *D. vilmoriniae* and *D. globosa*. The ploidy of both *D. vilmoriniae* and *D. globosa* is unreported in past literature. Flow cytometry data estimated both to be octoploid, which is consistent with prior reports *D. discolor* (Darlington and Wylie, 1955; Fedorov, 1974).

The two accessions of *D. parviflora*, reported to be diploid by Darlington and Wylie (1955) and Fedorov (1974), were found to have genome sizes consistent with other tetraploids. The accession of *D. ogatai*, which has been reported as decaploid (Niu and Ohba, 2003), was found to be tetraploid through flow cytometry and chromosome counts.

The one accession of *D. longifolia* had a genome size equivalent to other decaploids, even though it is reported as an octoploid in the literature (Cave, 1959). In *D. schneideriana*, which has been reported as decaploid, there was a considerable difference in the genome sizes between our two accessions. *D. schneideriana* 2014-102, received as *D. schneideriana* var. *laxiflora*, had a genome size consistent with other decaploids. *D. schneideriana* 2014-122, however, had a genome size in the range expected of a dodecaploid, which has not been reported in *Deutzia*. *Deutzia glauca* had a similarly large genome size as *D. schneideriana* 2014-122, but its ploidy has not been reported in the literature. Despite considerable effort, we were unable to confirm chromosome numbers of these putative dodecaploids with cytology.

The ploidy levels of hybrids were generally consistent and the same as their reported parents with the exception of *D. ×myriantha* (Table 3). Our accession of *Deutzia ×myriantha* 2014-116 had a genome size consistent with an octoploid, but inconsistent with any of its supposed parents. Different sources claim *D. ×myriantha* is either the result of a cross between *D. parviflora* × *setchuenensis* or *D. gracilis* × *purpurascens*. It is unlikely that any of these species are parents of our accession as they all have a lower ploidy level than *D. ×myriantha*. The lack of any interploid hybrids points to the probability of incompatibility of interploid crosses. Some efforts have been made to create interploid hybrids (e.g., *D. ×hybrida* × *D. gracilis*, Ranney, pers. comm.), but no successes further reinforce the likelihood of an interploid block in *Deutzia*.

The proportion of plants used in this study that were determined to be misidentified underscores the challenges of *Deutzia* taxonomy. The correct identification and determination of genome sizes and ploidy of a wide range of *Deutzia* species and hybrids will provide a valuable resource for breeders and curators. As the most current comprehensive key, Zaikonnikova's work (1965) is now over a half century old. There have been numerous taxonomic changes in the genus and an updated and revised key with referenced voucher specimens is essential for the continued understanding of *Deutzia*. In addition to the phylogeny of *Deutzia* (Kim et al., 2015), this data will help inform decisions on potential interspecific crosses with greater potential for success.

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Table 2.1. Previous cytological results for *Deutzia* species

Taxa	Chromosome Number	References
D. baroniana	2*n* = 4x = 52	Fedorov, 1974; Hanson et al. 2001
D. bungoensis	2*n* = 4x = 52	Niu and Ohba, 2000
	2n = 6x = 78	Niu and Ohba, 2003
D. compacta	2*n* = 2*x* = 26	Fedorov, 1974
D. corymbosa	2*n* = 2*x* = 26	Sandhu and Mann, 1989
	2*n* = 14*x* = 182	Chatterjee et al. 1989
D. crenata	2*n* = 6*x* = 78	Funamoto and Nakamura, 1994
	2*n* = 8*x* = 104	Darlington and Wylie, 1955; Fedorov, 1974; Funamoto and Nakamura, 1994; Niu and Ohba 2000; Terasaka and Tanaka, 1974
D. discolor	2*n* = 6*x* = 78	Darlington and Wylie, 1955; Fedorov, 1974
D. floribunda	2*n* = 2*x* = 26	Niu and Ohba, 2000
D. gracilis	2*n* = 2*x* = 26	Funamoto and Nakamura, 1992; Darlington and Wylie, 1955; Fedorov, 1974
D. hypoglauca	2*n* = 8*x* = 104	Darlington and Wylie, 1955
D. longifolia	2*n* = 2*x* = 26	Cave, 1959
D. maximowicziana	2*n* = 6*x* = 78	Funamoto and Nakamura, 1992; Niu and Ohba, 2000
D. mollis	2*n* = 4*x* = 52	Darlington and Wylie, 1955; Fedorov, 1974

Table 2.1 (continued).

D. naseana	2*n* = 4*x* = 52	Funamoto and Nakamura, 1992; Ohba and Akiyama, 1992
D. naseana var. amanoi	2*n* = 10*x* = 130	Ohba and Akiyama, 1992
D. ogatai	2*n* = 2*x* = 26	Niu and Ohba, 2003
D. parviflora	2*n* = 8*x* = 104	Darlington and Wylie, 1955; Fedorov, 1974
D. pulchra	2*n* = 2*x* = 26	Cave, 1964
D. purpurascens	2*n* = 2*x* = 26	Darlington and Wylie, 1955
D. scabra	2*n* = 2*x* = 26	Singhal et al., 1980
	2*n* = 10*x* = 130	Funamoto and Nakamura, 1992; Niu and Ohba, 2000
D. scabra var. sieboldiana	2*n* = 10*x* = 130	Niu and Ohba, 2000
D. schneideriana	2*n* = 2*x* = 26	Darlington and Wylie, 1955
D. staminea	2*n* = 2*x* = 26	Cave, 1963; Sandhu and Mann, 1989
D. uniflora	2*n* = 2*x* = 26	Cave, 1959; Fedorov, 1974
	2*n* = 6*x* = 78	Funamoto and Nakamura, 1992; Niu and Ohba, 2000
D. yaeyamensis	2*n* = 2*x* = 26	Niu and Ohba, 2000; Ohba and Akiyama, 1992
D. ×candelabrum (gracilis x scabra)	2*n* = 2*x* = 26	Fedorov, 1974

Table 2.2. Genome sizes and estimated ploidy levels of *Deutzia* species and cultivars.

Taxa	Received as	Accession / NCSC Voucher ID	Source/ID	2C Genome Size (pg) ± SEM	1C Genome Size (pg)	Est. Ploidy (*x*)
D. gracilis						
'Nikko'	*gracilis*	2014-068/ Hembree 2	MCIL	2.87 ± 0.14	1.43	2
'Nikko Dawn' [w]	*gracilis*	2014-057/ Hembree 48	JCRA 100404	2.84 ± 0.15	1.42	2
'Pink Minor' [z]	*scabra*	2014-100/ Hembree 4	Cornell BG	2.93 ± 0.15	1.46	2
D. hypoglauca [z]	*rubens*	2014-134/ Hembree 6	USNA 67798	2.85 ± 0.16	1.42	2
D. calycosa [z]	*monbeigii*	2014-074/ Hembree 13	USNA 59699	6.76 ± 0.29	1.68	4
D. calycosa [z]	*ningpoensis*	2014-067/ Hembree 11	USNA 59620	6.75 ± 0.27	1.68	4
D. ogatai [wv]	*gracilis* var. *ogatai*	2018-060/ Hembree 49	JCRA 130638	5.45 ± 0.31	1.36	4

Table 2.2 (continued).

D. paniculata						
'Dippon' [zw]	*gracilis*	2014-098/ Hembree 12	Chicago Botanic Gardens	8.20 ± 0.27	2.05	4
D. parviflora [zv]	*sp.*	2014-065/ Hembree 14	USNA 64514	7.48 ± 0.26	1.87	4
D. discolor [x]	*vilmoriniae*	2014-107/ Hembree 19	Arnold Arboretum 296-2000A	10.25 ± 0.39	1.28	8
D. discolor [w]	*discolor*	2014-125/ Hembree 17	USNA 67633	10.71 ± 0.34	1.34	8
D. discolor	*globosa*	2014-105/ Hembree 38	Arnold Arboretum 957-86-A	11.80 ± 0.45	1.48	8
D. pulchra [z]	*taiwanensis*	2014-133/ Hembree 21	UGA	11.05 ± 0.37	1.38	8
D. crenata [z]	*coreana*	2014-119/ Hembree 24	Arnold Arboretum 460-73-A	11.95 ± 0.56	1.20	10

Table 2.2 (continued).

D. crenata		2014-066/ Hembree 39	USNA 72020	12.86 ± 0.44	1.29	10
'Candidissima' [z]	*scabra*	2014-112/ Hembree 29	Arnold Arboretum 923-81-A	12.70 ± 0.44	1.27	10
'Codsall Pink' [z]	*scabra*	2014-108/ Hembree 26	MCIL	12.45 ± 0.60	1.25	10
'Summer Snow'	*crenata*	2014-058/ Hembree 27	JCRA xx0228	12.51 ± 0.59	1.25	10
'Variegata' [z]	*gracilis*	2014-056/ Hembree 25	JCRA xx0591	12.56 ± 0.48	1.26	10
'White Splashed'	*crenata*	2014-099/ Hembree 32	Cornell BG	12.15 ± 0.44	1.22	10
D. longifolia						
'Elegans' [v]	*longifolia*	2014-106/ Hembree 33	Arnold Arboretum 850-80-A	12.70 ± 0.71	1.27	10
D. naseana [zv]	*parviflora*	2014-073/ Hembree 40	JCRA 001389	13.18 ± 0.46	1.32	10

Table 2.2 (continued).

D. glauca[z]	*glabrata*	2014-069/ Hembree 42	MCIL	16.15 ± 0.65	1.35	~12
D. schneideriana[x]	*schneideriana* var. *laxiflora*	2014-102/ Hembree 41	Morris Arboretum 1943-020*A	12.72 ± 0.52	1.27	10
D. schneideriana[v]	*schneideriana*	2014-122/ Hembree 23	Arnold Arboretum 196-96-A	17.10 ± 0.74	1.43	~12

[z] Indicates keyed to new species.

[x] Indicates keyed to same species as received, but taxon has been reclassified as noted here.

[w] Ploidy confirmed with chromosome counts.

[v]Ploidy inconsistent with the literature.

Table 2.3. Genome size and estimated ploidy levels of *Deutzia* hybrids.

Taxa	Accession Number / NCSC Voucher ID	Source/ID	2C Genome Size	1C*x* Genome Size	Esti-mated Ploidy	Reported parental ploidy levels (x)
D. ×*elegantissima* (*D. purpurascens* × *D. scabra* var. *sieboldiana*) 'Rosalind'	2014-109 / Hembree 9	MCIL	2.67 ± 0.16	1.33	2	(2 x 2)
D. 'NCDX1' (*D.* ×*rosea* × *D. gracilis*)	H2007-190-001 / Hembree 50	MCIL	2.83 ± 0.12	1.41	2	(2 x 2)
D. 'NCDX2'[z] (*D.* ×*rosea* × *D. gracilis*)	H2010-310-034 / Hembree 51	MCIL	2.76 ± 0.14	1.38	2	(2 x 2)
D. ×*rosea* (*D. gracilis* × *D. purpurascens*)	2014-114 / Hembree 5	Longwood Gardens 1985-0281	2.92 ± 0.14	1.46	2	(2 x 2)
'Carminea'	2014-096 / Hembree 7	Cornell	2.87 ± 0.16	1.43	2	(2 x 2)
'Nikko Blush'	2014-063 / Hembree 3	USNA 74356	2.89 ± 0.14	1.44	2	(2 x 2)
D. ×*kalmiiflora*[z] (*D. parviflora* × *D. purpurascens*)	2014-064 / Hembree 10	USNA 59578	4.97 ± 0.17	2.49	2	(2 x 2)

Table 2.3 (continued).

D. ×*magnifica* (*D. scabra* × *D. discolor*)	2014-121 / Hembree 34	Arnold Arboretum 920-81-A	11.64 ± 0.48	1.46	8	(8 x 8)
'Nancy'[z]	2014-101 / Hembree 15	Cornell	9.11 ± 0.42	1.52	6[x]	(8 x 8)
'Rubra'	2014-075 / Hembree 16	USNA 59622	10.96 ± 0.41	1.37	8	(8 x 8)
'Superba'	2014-110 / Hembree 30	Arnold Arboretum 841-80-C	11.55 ± 0.50	1.44	8	(8 x 8)
'Eburnea'	2014-120 / Hembree 31	Holden Arboretum 69-25-85 via Morton Arboretum	11.55 ± 0.51	1.44	8	(8 x 8)
'Formosa'	2014-113 / Hembree 35	Arnold Arboretum 922-81-A	11.75 ± 0.53	1.47	8	(8 x 8)
D. ×*hybrida* (*D. longifolia* × *D. discolor*)						
'Strawberry Fields'	2014-131 / Hembree 20	JCRA 001170	10.25 ± 0.39	1.28	8	(8 x 8)

Table 2.3 (continued).

'Tourbillon Rouge'	2014-070 / Hembree 18	JCRA 020130	11.22 ± 0.42	1.40	8	(8 x 8)
'Magicien'	2014-124 / Hembree 22	Holden Arboretum 99-249	11.30 ± 0.41	1.41	8	(8 x 8)
'Pink Pompom'	2014-097 Hembree 36	Chicago Botanic Gardens	11.55 ± 0.44	1.44	8	(8 x 8)
D. ×*myriantha* (*D. parviflora* × *D. setchuenensis [*Hillier and Lancaster, 2014*]* or *D. gracilis* × *D. purpurascens* [Sargent, 1924])	2014-116 / Hembree 37	Arnold Arboretum 9-87-A	11.73 ± 0.52	1.47	8[x]	(2 x ?) or (2 x 2)

[z]Ploidy confirmed with chromosome counts.

[x]Ploidy inconsistent with reported parentage

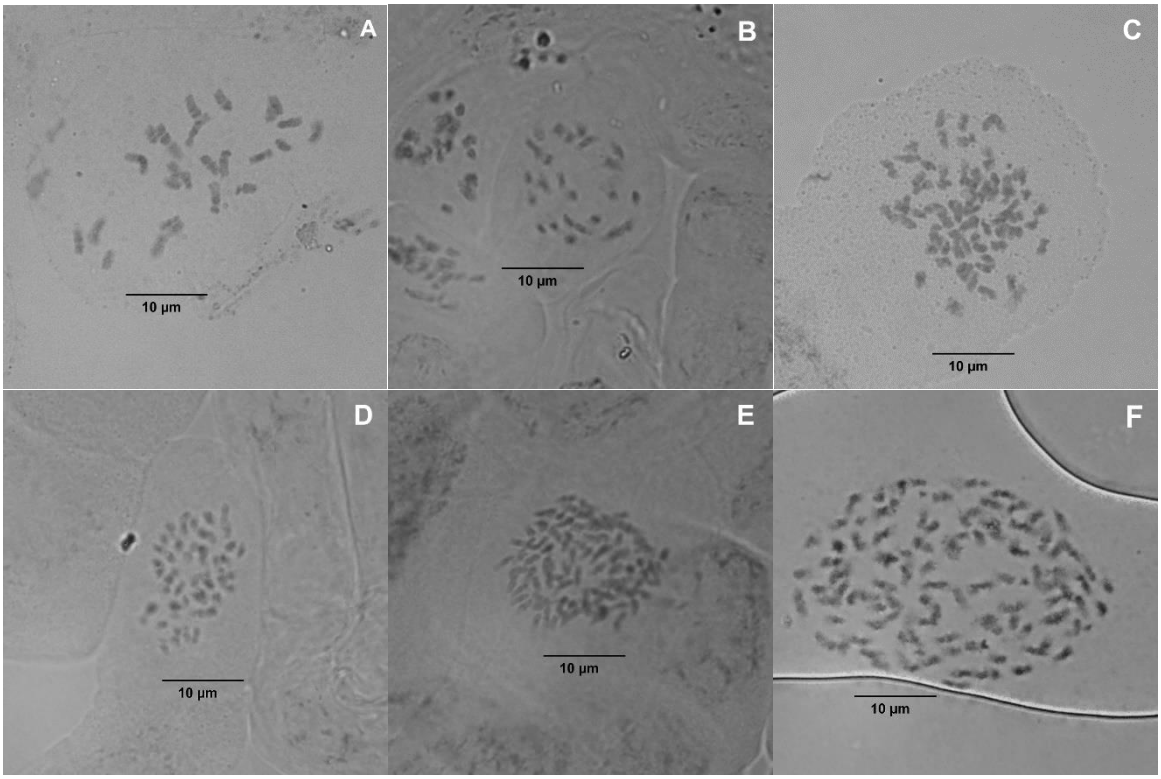

Figure 2.1. Photomicrographs of condensed chromosomes of *Deutzia* taxa. (A): *D. gracilis* 'Nikko Dawn', 2*n* = 2*x* = 26; (B): *D.* ×*kalmiiflora*, 2*n* = 2*x* = 26; (C):*D. paniculata* 'Dippon', 2*n* = 4*x* = 52; (D): *D. ogatai*, 2*n* = 4*x* = 52; (E): *D.* ×*magnifica* 'Nancy', 2*n* = 6*x* = 78; (F:) *D. discolor*, 2*n* = 8*x* = 104.