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GENETIC AND CYTOLOGICAL STUDIES WITH CAMELLIA AND RELATED GENERA
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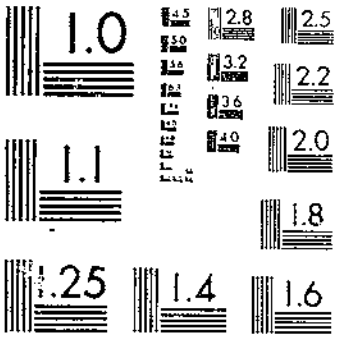

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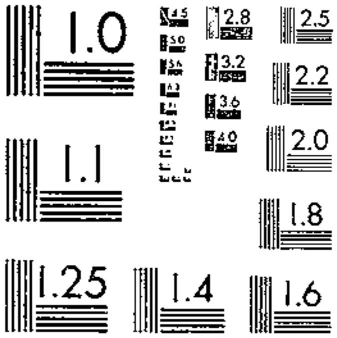

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# Genetic and Cytological Studies With *Camellia* and Related Genera

By William L. Ackerman

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# Genetic and Cytological Studies With *Camellia* and Related Genera

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## INTRODUCTION

Interest in the genus *Camellia* L. has been largely concerned with species of economic significance. In the Orient, camellias are important as ornamentals, for the oil of the seeds of certain species, and as the source of tea. In both Europe and the United States, camellias are important only as ornamentals. Introduction of species of *Camellia* into Europe from the Orient is generally accepted to have been about 1740 and was closely associated with the tea industry, based on *C. sinensis* (L.) O. Kuntze. A report by Meyer (*1959*)[1] indicates a much earlier introduction into Europe by Portuguese traders who brought *C. japonica* L. to Oporto, Portugal, about 1550. Introduction into the United States was during the latter part of the 18th century.

During Victorian times, camellias were grown as conservatory plants in both Europe and Northern United States and as garden specimens in Southeastern United States. Popularity of camellias waned near the turn of the century, and not until after World War II did they again gain prominence as ornamentals. Presently, the many cultivars of *C. japonica* and *C. sasanqua* Thunberg are grown rather widely as hardy evergreens in southern and Pacific coastal regions and, to a limited extent, in greenhouses in the North. *C. hiemalis* Nakai, *C. reticulata* Lindley, *C. saluenensis* Stapt ex Bean, and *C. vernalis* (Makino) Makino are less frequently cultivated species

*Camellia* belongs to the family Theaceae, tribe Gordonieae, along with eight other genera including *Franklinia, Gordonia, Laplacea,*

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[1] References to Literature Cited, p. 89, are herein indicated by the name of the author or authors followed by the year of publication in italic.

*Pyrenaria*, *Schima*, *Stewartia*, *Tutcheria*, and *Yunnanea*. *Camellia* is the largest of the genera within Gordonieae. Index Kewensis (Hooker and Jackson, *1895*) lists 80 species, whereas Sealy (*1958*) describes 82 recognized species and 16 others still too imperfectly known for their status to be decided. A wide variation in floral characters reflects a great diversity between species. In Sealy's (*1958*) revision of *Camellia* he divided the genus into 12 sections plus a miscellaneous group called Dubiae. Sealy's taxonomic classification is used as the basis of species separation in this study.

Extensive programs have been undertaken in intraspecific hybridization, particularly with *C. japonica*. Until recently, little attention was given to interspecific and intergeneric crosses. Anderson (*1961*) and Savige (*1967*) have both said that much of the useful intraspecific genetic variation has been exploited in *C. japonica*. Although interspecific and intergeneric hybridizations are frequently difficult or unsuccessful, a program of wide crosses was initiated in 1960 at the U.S. Plant Introduction Station, Glenn Dale, Md., in an attempt to develop hybrids with wider genetic variation.

Vegetative and floral limitations occur in *C. japonica* and *C. sasanqua*. Flower color in the wild *C. japonica* is confined to red, but in the horticultural varieties to white through red in both solid colors and variegated patterns. No yellow or blue camellias appear among the commonly grown species. Most varieties retain old withered flowers. Except for a few faintly scented cultivars, particularly of *C. sasanqua*, floral scent is lacking. Efforts to intensify this scent through intraspecific hybridization have been disappointing. The natural flowering season for the cultivated species is limited to the spring for *C. japonica* and *C. reticulata* and the fall for *C. sasanqua*. Improved cold hardiness is desirable because outdoor culture is now (1971) confined mostly to the Southeastern and West Coast States.

Lesser known species have all of the characters presently lacking in the cultivated species with the exception of blue flowers, although purple-flowered species do exist. Diversity within the genus and numbers of indigenous species suggest the center of origin to be in the region of southern China and North Vietnam. Many species described by early taxonomists were never successfully exported from this region and so are not presently available for hybridization. However, Hilsman (*1966*) states that approximately 25 to 30 species have been introduced into the United States. The Glenn Dale station has 26 species of *Camellia* in its collection, 20 of which have flowered and have been used as parents.

The basic chromosome number in the genus is 15. Chromosome numbers of 30, 45, 60, 75, and 90 have been reported for different species. Success in the development of new forms will depend upon the establishment of hybrids between species with different chromosome numbers as well as between species with the same number. Therefore, crosses have been made to obtain as many interspecific combinations as possible without consideration of the chomosome numbers of the parents. The chromosome numbers of interspecific hybrids can be variable, particularly if one or both parents are polyploids.

The purposes of this study were: (1) To investigate the compatibility relationships of various *Camellia* species and species of related genera in our collection by obtaining interspecific and intergeneric hybrids, (2) to determine the chromosome numbers of species and hybrids, (3) to determine the chromosome morphology of *Camellia* species where possible, and (4) to determine the breeding potential of interspecific and intergeneric hybrids. Previous reports on this subject have been made by the writer (*1963, 1970a, 1970b*).[2]

## MATERIALS AND METHODS

### Parental Species of *Camellia* and Related Genera

The Glenn Dale collection of *Camellia* and species of related genera is composed of wild species and cultivated varieties imported during the last two decades by the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture, through plant explorations throughout much of the Orient and, to a lesser extent, through exchange with European botanical gardens. A large number of these introductions have been the result of the joint Agricultural Research Service—Longwood Gardens cooperative ornamental exploration program.[3] J. L. Creech, ARS, has collected 47 camellia introductions during Longwood Gardens-sponsored plant explorations in the Orient. Plant breeders in the United States have contributed other species and varieties. Seventy-one introductions comprising 20 species of *Camellia* and four species of related genera were used as parents. The sources of the par-

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[2] Also, ACKERMAN, W. L. INTERSPECIFIC AND INTERGENERIC HYBRIDIZATION OF CAMELLIAS. 1969. (Unpublished Ph. D. thesis. Copy on file Univ. of Md. library, College Park.)

[3] Longwood Gardens of Longwood Foundation, Inc., Kennett Square, Pa. This cooperative exploration program has been responsible for 14 foreign plant explorations, including 8 to the Orient since 1956.

ents used are listed in table 1. Voucher specimens of all introductions included in the table, except for *C. taliensis* and *C. tenuiflora,* were submitted to the herbarium of the National Arboretum, Washington, D.C.

With the exception of outdoor specimens of *Franklinia alatamaha* and *Stewartia ovata,* all of the plants used as parents were grown on greenhouse benches. Daily temperature records have been maintained during the blooming season for the past 5 years. The houses have been kept at night temperatures of 50° to 56° F. during the blooming period. These temperatures are considered to be suitable for floral development.

## Experimental Procedures

### Hybridization

An effort was made to hybridize each species in as many different combinations as possible, including the reciprocal of each interspecific cross. However, several factors reduced the number of combinations from that first anticipated. Originally, there were many varieties of *Camellia japonica, C. rusticana,* and *C. sasanqua* and only one or a very few plants of most of the other species. Some of the more recent acquisitions were represented only by small plants bearing limited numbers of blossoms. Although these plants could be used as male parents, limited production of flowers precluded their extensive use as female parents. Another factor that reduced the number of combinations was the limitations in greenhouse space, which curtailed the numbers of parents and hybrid progenies that could be grown at one time.

### Methods of Pollination

The blooming season of most species of *Camellia* grown under greenhouse conditions at Glenn Dale extends from early October to late March, although a few bloom sporadically through late spring and summer. Flowers were emasculated by cutting horizontally around the flower bud with a razor blade to remove the apex half of the petals and stamens with attached anthers before dehiscence. To gain access to the pistil of semidouble peony-type flowers, we frequently had to cut and remove considerably more of the petals.

Both fresh and stored pollen were used for making controlled crosses. Where possible, fresh pollen of the desired male parent was collected and used the same or the next day. In many cases, the flowering seasons of two species to be hybridized did not overlap and pollen had to be collected in advance and stored for later use. In these cases, the pollen was dried at room temperature for 24 hours and then stored in cotton-stoppered glass vials over anhydrous calcium chloride at 45° F. Lengths of storage of pollen varied from less than 1 week to several months. Under the storage

TABLE 1.—*Inventory of species of* Camellia *and related genera used in hybridization studies*

| P.I. or B No.[1] | Scientific name | Source |
|---|---|---|
| 162476 | *C. fraterna* Hance | Kuling, China. |
| 251534 | *C. granthamiana* Sealy | Victoria, Hongkong. |
| B56995 | *C. hiemalis* Nakai, 'Shishi-Gashira' | A. Fendig, Brunswick, Ga. |
| B56996 | *C. hiemalis* 'Bill Wylam' | Do. |
| 229973 | *C. hongkongensis* Seem. | Victoria, Hongkong. |
| B56272 | *C. japonica* L., 'Ville de Nantes' | National Arboretum, Washington, D.C. |
| 226109 | *C. japonica* No. 6 | Angyo, Japan. |
| 227063 | *C. japonica* 'Bon-Shirotama' | Rokuji-Kai, Japan. |
| 228024 | *C. japonica* "Tsubaki' | Okayama-shi, Japan. |
| 230278 | *C. japonica* | Aichi-ken, Japan. |
| 231686 | *C. japonica* 'Hasumi-shiro' | Chiba, Japan. |
| 231687 | *C. japonica* 'Komyotai' | Do. |
| 231689 | *C. japonica* 'Moshio' | Do. |
| 231690 | *C. japonica* | Do. |
| 231694 | *C. japonica* 'Utamakura' | Do. |
| 231695 | *C. japonica* 'Yuki botan' | Do. |
| 231858 | *C. japonica* 'Beni botan' | Do. |
| 231859 | *C. japonica* 'Kanyo-tai' | Do. |
| 238725 | *C. japonica* 'Saudade de Martins Blanco' | Porto, Portugal. |
| 274530 | *C. japonica* No. 825 | Kyushu, Japan. |
| 274797 | *C. japonica* No. 870 | Do. |
| 274799 | *C. japonica* No. 872 | Do. |
| 275054 | *C. japonica* No. 913 | Kita-Ibaraki, Japan. |
| 275512 | *C. japonica* D | Miyako, Iwate Prefecture, Japan. |
| 309001 | *C. japonica* 'Le Lys' | Botanic Garden, Nantes, France. |
| 319283 | *C. japonica* K–20 | Cheju Island, Korea. |
| 252062 | *C. kissi* Wall. | Katmandu, Nepal. |
| 252064 | *C. kissi* | Do. |
| 226756 | *C. luchuensis* T. Ito | Kunigami, Okinawa. |
| 226704 | *C. miyagii* (Koidz.) Makino & Nemoto | Genka, Okinawa. |
| 231057 | *C. miyagii* | Ryukyu, Okinawa. |
| 162561 | *C. oleifera* Abel | Nanking, China. |
| 235500 | *C. oleifera* | Oshima Island, Japan. |
| B58296 | *C. pitardii* Cohen-Stuart var. *pitardii* | R. Cutter, Berkeley, Calif. |
| B51685 | *C. reticulata* Lindl. 'Crimson Robe' | W. Gotelli, East Orange, N.J. |

See footnote at end of table.

TABLE 1.—*Inventory of species of* Camellia *and related genera used in hybridization studies*—Continued

| P.I. or B No.[1] | Scientific name | Source |
|---|---|---|
| B51686 | *C. reticulata* 'Great Shot Silk' | Do. |
| B51689 | *C. reticulata* 'Chang's Temple' | Do. |
| B51690 | *C. reticulata* 'Large Cornelian' | Do. |
| B51694 | *C. reticulata* 'Lion's Head' | Do. |
| B58619 | *C. rosaeflora* Hooker | Berkeley, Calif. |
| 228187 | *C. rusticana Honda*, 'Yoshida' | Niigata, Japan. |
| 228188 | *C. rusticana* 'Hatano' | Do. |
| 228190 | *C. rusticana* 'Koshiji' | Do. |
| 233642 | *C. rusticana* B. White plena | Tokyo, Japan. |
| 310320 | *C. salicifolia* Champ. ex Benth. | Royal Botanic Gardens, Kew, England. |
| 243862 | *C. saluenensis* Stapf in Bean, No. 6093 | Cornwall, England. |
| 227624 | *C. sasanqua* Thumb. 'Kokinran' | Yamamato, Japan. |
| 228025 | *C. sasanqua* 'Sazanka' | Kotohira-eho, Japan. |
| 235568 | *C. sasanqua* | Rokko-san, Japan. |
| 237854 | *C. sasanqua* No. 791 | Yakushima, Japan. |
| 277763 | *C. sasanqua* 'Narumi-gata' | Winchester, England. |
| 319284 | *C. sasanqua* | Kurume City, Japan. |
| 319285 | *C. sasanqua* 'Onishiki' | Do. |
| 235570 | *C. sinensis* (L.) Kuntze, 'Tama-midori' | National Tea Experiment Station, Kanaya, Japan. |
| 235572 | *C. sinensis* Y-2 | Do. |
| 235573 | *C. sinensis* Z-1 | Do. |
| 304404 | *C. sinensis* No. 1 | Oruziya, U.S.S.R. |
| 304405 | *C. sinensis* No. 2 | Do. |
| 316471 | *C. sinensis* 'Beni-fuji' | Kanaya, Japan. |
| 316472 | *C. sinensis* 'Beni-Homare' | Do. |
| 316473 | *C. sinensis* 'Makinowara Wase' | Do. |
| 316476 | *C. sinensis* 'Yamatomidori' | Do. |
| 316477 | *C. sinensis* | Do. |
| 316478 | *C. sinensis* | Do. |
| B57043 | *C. taliensis* (W. W. Smith) Melchior | C. Parks, Los Angeles, Calif. |
| B57048 | *C. tenuiflora* (Hay.) Cohen-Stuart | Do. |
| 271683 | *C. tsaii* Hu | Hillier & Sons, England. |
| 69037 | *Franklinia alatamaha* Bartr. ex Marsh. | S. Baxter, Philadelphia, Pa. |

See footnote at end of table.

TABLE 1.—*Inventory of species of* Camellia *and related genera used in hybridization studies*—Continued

| P.I. or B No.[1] | Scientific name | Source |
|---|---|---|
| 104210 | *Stewartia ovata* (Cav.) Weatherby | Orleans, France. |
| 230368 | *Tutcheria spectabilis* (Champ.) Dunn | Victoria, Hongkong. |
| 229881 | *Tutcheria virgata* (Koidz.) Nakai | Genka Haneji-son, Okinawa. |

[1] P.I. refers to the accession number assigned to foreign introductions by the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture. B numbers are code numbers assigned to importations under postentry quarantine permit by the U.S. Plant Introduction Station, Glenn Dale, Md.

conditions used, pollen viability had decreased somewhat at the end of 2 months but not enough to seriously affect hybridizing results. Fresh pollen was most easily transferred by removing stamens from the male parent with forceps and using the anther as the applicator. Stored pollen was applied with a small camel's hair brush.

Most controlled crosses were made in greenhouses screened against insects. Therefore, emasculated flowers did not have to be protected from undesired pollination. The flowers of *Franklinia* and *Stewartia,* grown outdoors, were bagged with nylon netting for protection from pollination by insects. Approximately 2 months after pollination, successful development of capsules and failures were recorded. All capsules were individually enclosed in bags of nylon netting to prevent accidental loss.

### Embryo Culture

Seed capsules matured in late summer and early fall. Interspecific and intergeneric crosses frequently resulted in highly defective seeds. Many of these seeds were small and deformed and contained incompletely developed embryos with disorganized tissue development. Most of these seeds did not germinate when the routine moist sphagnum peat method was used for the germination of seeds of *Camellia*. Embryo culture methods were investigated and found more satisfactory and were adopted as standard procedure for germinating all seeds from interspecific and intergeneric crosses.

The seeds were prepared for embryo culture by carefully removing both the outer and inner seedcoats with a sharp knife. The outer seedcoat normally was very hard, and frequently a small area at the side of the seed had to be scraped with the knife blade held at an oblique angle until penetration was made. The size and location of the embryo could then be determined. In a normal seed, the embryo and associated endosperm fill the entire space within the seedcoat. In seeds of wide crosses, however, the embryos and endosperm occupy only 1/10 to 1/2 of the space. After the outer seedcoat was removed, the rest of the seed was placed in water for approximately 2 hours. The inner seedcoat softened and, in most cases, was not difficult to remove. The embryos and associated endosperm were then transferred under aseptic conditions to the sterilizing solution and gently agitated for 5 minutes before being transferred with sterilized forceps to culture bottles.

Several sterilizing solutions were tried, but the most successful was 5 percent sodium hypochlorite (Clorox). A drop of Tween 20 in 100 cc. of Clorox solution reduced surface tension and promoted wetting with the sterilant.

The nutrient agar used was that described by Tukey (*1934*) and later adapted for embryo culture of *Camellia* by Lammerts (*1950*). Transfers of the embryos were made during the first two seasons in a small homemade, glass-topped chamber, fitted with hand holes. Later, a larger, rigid plastic chamber was used until a transfer room could be constructed especially for embryo culture.

The culture bottles were then placed under fluorescent lights in a room with a near constant temperature of 68° F. The cultured embryos were maintained under these conditions until they had adequate root development and the first set of true leaves was at least partly unfolded.

### General Culture

After the seedlings were removed from culture bottles, they were transplanted to 2-inch pots of milled sphagnum. The pots were set on gravel in a greenhouse bench and subjected to automatic mist for 1 minute each hour. After 2 weeks, the pots were plunged in peat moss in an open greenhouse bench until growth required transfer to larger pots. The seedlings were then continued in open gravel benches. During the first several seasons, the plants were transplanted to sterilized soil. Growth was not always satisfactory and other cultural methods were investigated. Tests showed that superior growth resulted from continuing the plants in milled sphagnum moss, fertilized once a month with a 20–20–20 liquid fertilizer. The night period from September to March was broken with incandescent light from 10:00 p.m. until 2:00 a.m. to help accelerate vegetative growth of young plants.

### Morphological Comparisons of Parents and Hybrids

Morphological observations were made for evidence of interspecific and intergeneric hybridity. Early observations of vegetative characters disclosed that some were strongly dominant in the progenies. These characters could thus serve as useful markers for hybridity when the particular species was used as a male parent. Taxonomic descriptions were recorded as presented by Sealy (*1958*) for the species used in successful crosses. The taxonomic characters of the parental species were compared with Sealy's descriptions and summarized in appendix table 21. We then compared pairs of parental species for differences in distinct, easily identifiable characters and observed these specific characters among the $F_1$ hybrid populations. $F_1$ plants possessing one or more vegetative or floral characters of the male parent and $F_1$ plants intermediate in appearance between the two parents were considered as valid hybrids.

### Determination of Pollen Abortion

Many of the hybrids were developed from rather wide interspecific or intergeneric crosses. Thus, reduced fertility in many of the hybrids was anticipated. Accordingly, percentages of filled and unfilled pollen were determined for the hybrids and the parents after the pollen was stained with acetocarmine.

A 1-millimeter square grid was scribed with a diamond-pointed pencil on microscope slides to facilitate making pollen counts. Pollen from parental species and the hybrids was stained with a 2-percent acetocarmine solution. The slides were allowed to stand at room temperature for approximately 10 minutes to allow for stain penetration before observation at a magnification of 125. Pollen abortion counts were based on 1,000 grains for each test if both normal (filled) and aborted grains were observed. If, however, no normal grains were observed in the first 500 examined, that hybrid was classified as completely male sterile.

Two classes of pollen, stainable and unstainable, were clearly evident. The stainable grains were smooth-surfaced in contrast to the shrunken, wrinkled, and unstainable aborted pollen. In most cases, shape alone would have been sufficient to distinguish the two classes of pollen, but the staining facilitated classification.

### Cytological Methods

Chromosome studies were made on both hybrids and species. Root tips were collected from mature plants, from cuttings rooted under intermittent mist, and from seedlings shortly after removal from embryo culture.

After collection, root tips were placed immediately in vials of tapwater. A prefixation treatment of 0.2-percent aqueous solution of colchicine for 2 hours at room temperature (68° F.) was used to shorten and spread the chromosomes. Prefixation for 3 hours was used on polyploid clones to facilitate counting, but longer treatment caused stickiness and clumping of chromosomes. A saturated aqueous solution of paradichlorobenzene for 3 hours at 45° F. was a good alternate prefixation treatment but not as consistent in results as the 0.2-percent solution of colchicine.

Root tips were fixed for 6 to 8 hours at room temperature in three parts of 95 percent ethyl alcohol and one part of glacial acetic acid and then stored at 32°F. Acetocarmine proved superior to acetoorcein and the Feulgen technique for staining the root tips and therefore was used routinely. Before the preparation of acetocarmine smears, the root tips were softened in one normal hydrochloric acid solution for 5 minutes at 68° F. to obtain a good spread of cells. This was followed by transfer to 70 percent ethyl alcohol for the same time at the same temperature (Darlington and La Cour, *1960*). Good spreads were indispensable because of the high number of chromosomes concentrated in rather small cells. Photomicrographs of good temporary slides were taken at 1525×. Some of these slides were made permanent, using the method of Zeilinga and Kroon (*1965*).

Seasonal variations in mitotic activity in the root tips were observed during 5 consecutive years. The lowest degree of mitotic activity was during the summer months, especially when the night temperature in the greenhouse was above 68° F. A gradual increase in activity began in early autumn and reached a peak during December and January. This peak was followed by a gradual decrease toward spring and reached a low point again in summer. Accordingly, after variation in mitotic activity became evident, most root tips were collected during the winter months.

The use of chromosome morphology as a method for distinguishing species and hybrids was investigated. Chromosomes were measured by taking photomicrographs, projecting the negative at a magnification of 2300×, and then tracing the enlarged chromosomes on paper. Also, glossy prints were made at this same magnification for comparative purposes. Chromosome configurations presented problems for accurate measurements. Soft copper wire was used to duplicate each chromosome configuration. Chromosome length and centromere position were marked on the wire with a sharp knife. The wire was then straightened and measured with a vernier caliper.

Few cells of any one species studied showed all chromosomes in a position where they could be followed accurately. A tentative karyotype, showing chromosomes in sequence of descending order of total chromosomal length, was first constructed for each species from the best cell available. The chromosomes of other cells were likewise placed in order of chromosomal length as closely as possible and then individual chromosomes were matched with those of the karyotype. This method was found convenient and reduced the possibility of having the same chromosome included twice in the karyotype to the exclusion of some other chromosome. Individual chromosomes from six cells were selected to construct the final karyotype for each species.

Methods of classification of chromosomes as median, submedian or subterminal on the basis of centromere position were investigated. A general lack of uniformity of methods described in the literature results in considerable overlapping between the various types of chromosomes. Shindo and Kamemoto (*1963*) and Kaneko (*1966*) used mean F% values derived by taking the percentages of the short arm length over the total length of a chromosome. Chromosomes were classified as subterminal, submedian, and median where the F% values fell within 0 to 30, 30 to 45, and 45 to 50, respectively. Bammi (*1965*) and Settle (*1967*) used long arm to short arm indices. Kawano and others (*1967*) and Murin (*1962*) used short arm to long arm indices. Ourecky (*1966*) used double indices of long arm to total length and short arm to total length. Other investigators, including Nakajima (*1963*), Jagathesan and Sreenivasan (*1967*), and Mallick and Sharma (*1966*), used alphabetical designations based on narrative descriptions. The resulting classifications appear arbitrary at best. For example, Bammi (*1965*) classified a chromosome as submedian with a long arm to short arm index of 3.7. If converted to the F% used by Shindo and Kamemoto (*1963*), the value is 21, which is well within their classification for subterminal chromosomes.

For the purposes of this study, long arm to short arm indices were used and chromosomes classified as median, submedian, and subterminal where index values were 1.00 to 1.20, 1.21 to 2.40, and 2.41 upward, respectively. This method of classification resulted in separations very closely comparable with the F% values of Shindo and Kamemoto (*1963*).

# RESULTS

## Interspecific Hybridization

Sufficient blooms were available on 16 *Camellia* species for use as female parents, and 20 species were used as male parents. A total of 8,741 controlled pollinations were made. These represented 219 interspecific combinations, including reciprocal crosses. A total of 459 hybrid plants from 5,862 pollinations in 106 combinations were obtained. In table 2, those interspecific combinations that resulted in hybrid plants are listed, along with the numbers of pollinations and the numbers and percentages per pollination of seed capsules produced, of seeds started in culture, and of hybrid plants. The interspecific crosses attempted, but which proved unsuccessful in the establishment of hybrid plants, are listed in appendix table 20. Chi-square values, based on the number of pollinations and hybrids obtained from reciprocal crosses, are listed in table 3. Six of the 54 reciprocal crosses were significantly or highly significantly different.

Seed capsule development after pollination is no assurance of eventually obtaining hybrid plants. In a substantial number of crosses, seed capsules developed to apparent maturity, but contained either no seeds or seeds with partly developed embryos. Poor seed is very common among interspecific and intergeneric crosses because incompatibility factors frequently exist where large differences are involved in the genetic complexes of the parental species. Many of these seeds either failed to germinate in culture or developed abnormally and subsequently died. Both normal and abnormal development in culture are illustrated in figure 1.

### Morphological Comparisons

One of the first indications of validity of a young hybrid plant is the comparison of its vegetative morphological characters with those of its parents. Because most seedlings do not flower before they are 2 to 4 years old, we had to rely heavily on vegetative characters rather than floral and seed characters. Characters selected were those described by Sealy (*1958*) and centered mostly on twigs and young shoots, leaves, and terminal vegetative buds. The chief characters used are summarized for each species in appendix table 21.

Validation of 211 interspecific hybrids, based on the characters described in table 21 and used specifically in the discussion and analysis in this study, is given in appendix table 22. Those seedlings that could not be proved to be valid hybrids on the basis of morphological comparisons, on pollen abortion, or on chromosome

TABLE 2.—*Interspecific crosses in* Camellia *resulting in hybrid plants*

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | | Hybrid plants | |
|---|---|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. fraterna* × *C. japonica* | 49 | 1 | 2.0 | 1 | 2.0 | 1 | 2.0 |
| Reciprocal | 105 | 6 | 5.7 | 16 | 15.2 | 10 | 9.5 |
| *C. fraterna* × *C. lutchuensis* | 79 | 1 | 1.3 | 1 | 1.3 | 1 | 1.3 |
| Reciprocal | 50 | 3 | 6.0 | 3 | 6.0 | 1 | 2.0 |
| *C. fraterna* × *C. reticulata* | 218 | 2 | 9.1 | 2 | 9.1 | 1 | .4 |
| Reciprocal | 24 | 2 | 8.3 | 4 | 16.7 | 3 | 12.5 |
| *C. hiemalis* × *C. kissi* | 16 | 2 | 12.5 | 3 | 18.8 | 1 | 6.3 |
| Reciprocal | 35 | 11 | 31.4 | 8 | 22.9 | 1 | 2.9 |
| *C. hiemalis* × *C. miyagii* | 30 | 5 | 16.7 | 5 | 16.7 | 4 | 13.3 |
| Reciprocal | 32 | 15 | 46.9 | 16 | 50.0 | 8 | 25.0 |
| *C. hiemalis* × *C. oleifera* | 9 | 3 | 33.3 | 2 | 22.2 | 1 | 11.1 |
| Reciprocal | 48 | 8 | 16.7 | 9 | 18.8 | 4 | 8.3 |
| *C. hiemalis* × *C. sasanqua* | 38 | 8 | 21.0 | 10 | 26.3 | 8 | 21.0 |
| Reciprocal | 50 | 10 | 20.0 | 12 | 24.0 | 6 | 12.0 |
| *C. hongkongensis* × *C. reticulata* | 20 | 9 | 45.0 | 9 | 45.0 | 3 | 15.0 |
| *C. hongkongensis* × *C. rusticana* | 41 | 7 | 17.1 | 13 | 31.7 | 5 | 12.2 |
| Reciprocal | 60 | 1 | 1.7 | 4 | 6.6 | 2 | 3.3 |
| *C. hongkongensis* × *C. salicifolia* | 54 | 2 | 3.7 | 2 | 3.7 | 1 | 1.9 |
| *C. hongkongensis* × *C. sinensis* | 67 | 2 | 2.9 | 5 | 7.4 | 2 | 2.9 |
| *C. japonica* × *C. granthamiana* | 75 | 1 | 1.3 | 4 | 5.3 | 3 | 4.0 |
| *C. japonica* × *C. hiemalis* | 48 | 1 | 2.1 | 1 | 2.1 | 1 | 2.1 |
| *C. japonica* × *C. hongkongensis* | 111 | 2 | 1.8 | 8 | 7.2 | 7 | 6.3 |

TABLE 2.—*Interspecific crosses in* Camellia *resulting in hybrid plants*—Continued

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | | Hybrid plants | |
|---|---|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. japonica* × *C. kissi* | 44 | 2 | 4.5 | 5 | 11.4 | 2 | 4.5 |
| Reciprocal | 59 | 7 | 11.9 | 10 | 16.9 | 5 | 8.5 |
| *C. japonica* × *C. lutchuensis* | 551 | 28 | 5.1 | 86 | 15.6 | 62 | 11.2 |
| Reciprocal | 245 | 4 | 1.6 | 4 | 1.6 | 2 | .8 |
| *C. japonica* × *C. miyagii* | 20 | 1 | 5.0 | 3 | 15.0 | 2 | 10.0 |
| *C. japonica* × *C. pitardii* var. *pitardii* | 22 | 1 | 4.5 | 2 | 9.1 | 2 | 9.1 |
| Reciprocal | 24 | 1 | 4.2 | 1 | 4.2 | 1 | 4.2 |
| *C. japonica* × *C. reticulata* | 150 | 4 | 2.7 | 6 | 4.0 | 5 | 3.3 |
| Reciprocal | 69 | 6 | 8.7 | 7 | 10.1 | 7 | 10.1 |
| *C. japonica* × *C. rosaeflora* | 38 | 1 | 2.6 | 1 | 2.6 | 1 | 2.6 |
| *C. japonica* × *C. rusticana* | 20 | 3 | 15.0 | 4 | 20.0 | 4 | 20.0 |
| Reciprocal | 57 | 8 | 14.0 | 17 | 20.0 | 13 | 22.8 |
| *C. japonica* × *C. saluenensis* | 41 | 12 | 29.3 | 15 | 36.6 | 12 | 29.3 |
| Reciprocal | 13 | 1 | 7.7 | 2 | 15.4 | 1 | 7.7 |
| *C. japonica* × *C. sinensis* | 44 | 4 | 9.1 | 10 | 22.7 | 3 | 6.8 |
| Reciprocal | 41 | 5 | 12.2 | 4 | 9.8 | 1 | 2.4 |
| *C. japonica* × *C. taliensis* | 30 | 1 | 3.3 | 1 | 3.3 | 1 | 3.3 |
| *C. japonica* × *C. tsaii* | 86 | 6 | 7.0 | 11 | 12.8 | 6 | 7.0 |
| *C. kissi* × *C. miyagii* | 52 | 15 | 28.8 | 13 | 25.0 | 8 | 15.4 |
| Reciprocal | 37 | 3 | 8.1 | 2 | 5.4 | 2 | 5.4 |
| *C. kissi* × *C. oleifera* | 53 | 13 | 24.5 | 15 | 28.3 | 9 | 16.9 |
| Reciprocal | 42 | 6 | 14.3 | 6 | 14.3 | 3 | 7.1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *C. kissi* × *C. reticulata* | 56 | 5 | 8.9 | 3 | 5.4 | 1 | 1.8 |
| *C. kissi* × *C. rosaeflora* | 36 | 5 | 13.9 | 6 | 16.7 | 4 | 11.1 |
| *C. kissi* × *C. rusticana* | 35 | 2 | 5.6 | 2 | 5.6 | 1 | 2.8 |
| Reciprocal | 27 | 1 | 3.7 | 2 | 7.4 | 1 | 3.7 |
| *C. kissi* × *C. salicifolia* | 63 | 21 | 33.3 | 10 | 15.9 | 2 | 3.2 |
| *C. kissi* × *C. sasanqua* | 46 | 21 | 45.7 | 26 | 56.5 | 14 | 30.4 |
| Reciprocal | 33 | 12 | 36.4 | 12 | 36.4 | 7 | 21.2 |
| *C. kissi* × *C. sinensis* | 44 | 13 | 29.5 | 9 | 20.5 | 4 | 9.1 |
| Reciprocal | 45 | 8 | 17.8 | 6 | 13.3 | 4 | 8.9 |
| *C. lutchuensis* × *C. pilardii* var *pilardii* | 50 | 1 | 2.0 | 2 | 4.0 | 1 | 2.0 |
| Reciprocal | 27 | 2 | 7.4 | 3 | 11.1 | 2 | 7.4 |
| *C. lutchuensis* × *C. rusticana* | 67 | 1 | 1.5 | 1 | 1.5 | 1 | 1.5 |
| Reciprocal | 280 | 12 | 4.3 | 41 | 14.6 | 24 | 8.6 |
| *C. lutchuensis* × *C. salicifolia* | 42 | 10 | 23.8 | 6 | 14.3 | 4 | 9.5 |
| *C. miyagii* × *C. fraterna* | 17 | 3 | 17.6 | 1 | 5.9 | 1 | 5.9 |
| *C. miyagii* × *C. hongkongensis* | 44 | 5 | 11.4 | 2 | 4.5 | 1 | 2.3 |
| *C. miyagii* × *C. lutchuensis* | 112 | 6 | 5.4 | 8 | 7.2 | 4 | 3.6 |
| *C. miyagii* × *C. oleifera* | 33 | 16 | 48.5 | 21 | 63.6 | 13 | 39.4 |
| Reciprocal | 19 | 2 | 10.6 | 4 | 21.1 | 3 | 15.8 |
| *C. miyagii* × *C. reticulata* | 37 | 4 | 10.8 | 3 | 8.1 | 1 | 2.7 |
| *C. miyagii* × *C. salicifolia* | 69 | 8 | 11.6 | 5 | 7.2 | 2 | 2.9 |
| *C. miyagii* × *C. sasanqua* | 40 | 18 | 45.0 | 15 | 37.5 | 9 | 22.5 |
| Reciprocal | 33 | 2 | 6.1 | 6 | 18.2 | 4 | 12.1 |
| *C. oleifera* × *C. salicifolia* | 43 | 4 | 9.3 | 2 | 4.7 | 1 | 2.3 |
| *C. oleifera* × *C. sasanqua* | 29 | 14 | 48.3 | 27 | 93.1 | 18 | 62.1 |
| Reciprocal | 31 | 7 | 22.6 | 26 | 83.9 | 16 | 51.6 |
| *C. oleifera* × *C. sinensis* | 63 | 6 | 9.5 | 4 | 6.3 | 2 | 3.1 |
| Reciprocal | 64 | 4 | 6.3 | 8 | 12.5 | 5 | 7.8 |

TABLE 2.—*Interspecific crosses in* Camellia *resulting in hybrid plants*—Continued

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | | Hybrid plants | |
|---|---|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. pitardii* var. *pitardii* × *C. fraterna* | 21 | 2 | 9.5 | 7 | 33.3 | 2 | 9.5 |
| *C. pitardii* var. *pitardii* × *C. granthamiana* | 25 | 1 | 4.0 | 2 | 8.0 | 2 | 8.0 |
| *C. pitardii* var. *pitardii* × *C. reticulata* | 25 | 1 | 4.0 | 2 | 8.0 | 1 | 4.0 |
| Reciprocal | 42 | 4 | 9.5 | 5 | 11.9 | 4 | 9.5 |
| *C. pitardii* var. *pitardii* × *C. saluenensis* | 20 | 1 | 5.0 | 2 | 10.0 | 1 | 5.0 |
| Reciprocal | 19 | 2 | 10.5 | 3 | 15.8 | 1 | 5.2 |
| *C. pitardii* var. *pitardii* × *C. tsaii* | 76 | 8 | 10.5 | 11 | 14.5 | 4 | 5.3 |
| *C. reticulata* × *C. granthamiana* | 39 | 1 | 2.5 | 2 | 5.1 | 1 | 2.5 |
| *C. reticulata* × *C. rosaeflora* | 35 | 1 | 2.9 | 1 | 2.9 | 1 | 2.9 |
| *C. reticulata* × *C. rusticana* | 12 | 1 | 8.3 | 1 | 8.3 | 1 | 8.3 |
| *C. reticulata* × *C. saluenensis* | 24 | 2 | 8.3 | 5 | 20.8 | 3 | 12.5 |
| Reciprocal | 28 | 1 | 3.6 | 2 | 7.1 | 2 | 7.1 |
| *C. rosaeflora* × *C. fraterna* | 36 | 1 | 2.8 | 2 | 5.6 | 2 | 5.6 |
| *C. rusticana* × *C. fraterna* | 162 | 2 | 1.2 | 6 | 3.7 | 3 | 1.9 |
| *C. rusticana* × *C. oleifera* | 63 | 8 | 12.7 | 7 | 11.1 | 3 | 4.8 |
| *C. rusticana* × *C. rosaeflora* | 46 | 5 | 10.9 | 8 | 17.4 | 3 | 6.5 |
| *C. rusticana* × *C. salicifolia* | 53 | 4 | 7.5 | 8 | 15.1 | 5 | 9.4 |
| *C. rusticana* × *C. saluenensis* | 13 | 1 | 7.7 | 1 | 7.7 | 1 | 7.7 |
| *C. saluenensis* × *C. fraterna* | 24 | 1 | 4.2 | 1 | 4.2 | 1 | 4.2 |
| *C. saluenensis* × *C. granthamiana* | 21 | 1 | 4.8 | 1 | 4.8 | 1 | 4.8 |
| *C. saluenensis* × *C. hongkongensis* | 12 | 1 | 8.3 | 2 | 16.6 | 1 | 8.3 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *C. saluenensis* × *C. lutchuensis* | 19 | 1 | 5.2 | 1 | 5.2 | 1 | 5.2 |
| *C. saluenensis* × *C. rosaeflora* | 24 | 2 | 8.3 | 3 | 12.5 | 1 | 4.2 |
| *C. saluenensis* × *C. taliensis* | 23 | 1 | 4.3 | 2 | 8.7 | 1 | 4.3 |
| *C. sasanqua* × *C. granthamiana* | 60 | 1 | 1.7 | 2 | 3.4 | 2 | 3.4 |
| *C. sasanqua* × *C. japonica* | 46 | 1 | 2.2 | 3 | 6.5 | 3 | 6.5 |
| *C. sasanqua* × *C. reticulata* | 88 | 2 | 2.3 | 5 | 5.7 | 3 | 3.4 |
| *C. sasanqua* × *C. tenuiflora* | 16 | 1 | 6.2 | 2 | 12.5 | 2 | 12.5 |
| *C. sinensis* × *C. fraterna* | 32 | 7 | 21.9 | 6 | 18.8 | 1 | 3.1 |
| *C. sinensis* × *C. hiemalis* | 66 | 14 | 21.2 | 8 | 12.1 | 5 | 7.6 |
| *C. sinensis* × *C. miyagii* | 58 | 5 | 8.6 | 18 | 31.0 | 10 | 17.2 |
| *C. sinensis* × *C. rosaeflora* | 51 | 5 | 9.8 | 5 | 9.8 | 3 | 5.9 |
| *C. sinensis* × *C. salicifolia* | 49 | 3 | 6.1 | 1 | 2.0 | 1 | 2.0 |
| *C. sinensis* × *C. sasanqua* | 52 | 10 | 19.2 | 10 | 19.2 | 7 | 13.5 |

TABLE 3.—*Chi-square values for reciprocal interspecific crosses where one or both reciprocals produced hybrid* Camellias[1]

| Interspecific crosses | Pollinations | Hybrid plants | Chi-square value |
|---|---|---|---|
| | *Number* | *Number* | |
| *C. fraterna* × *C. japonica* | 49 | 1 | 2.52 |
| Reciprocal | 105 | 10 | |
| *C. fraterna* × *C. lutchuensis* | 79 | 1 | .11 |
| Reciprocal | 50 | 1 | |
| *C. fraterna* × *C. reticulata* | 218 | 1 | 19.29** |
| Reciprocal | 24 | 3 | |
| *C. hiemalis* × *C. kissi* | 16 | 1 | .34 |
| Reciprocal | 35 | 1 | |
| *C. hiemalis* × *C. miyagii* | 30 | 4 | 1.35 |
| Reciprocal | 32 | 8 | |
| *C. hiemalis* × *C. oleifera* | 9 | 1 | .07 |
| Reciprocal | 48 | 4 | |
| *C. hiemalis* × *C. sasanqua* | 38 | 8 | 1.32 |
| Reciprocal | 50 | 6 | |
| *C. hongkongensis* × *C. reticulata* | 20 | 3 | 3.09 |
| Reciprocal | 19 | 0 | |
| *C. hongkongensis* × *C. rusticana* | 41 | 5 | 2.97 |
| Reciprocal | 60 | 2 | |
| *C. japonica* × *C. granthamiana* | 75 | 3 | .46 |
| Reciprocal | 11 | 0 | |
| *C. japonica* × *hiemalis* | 40 | 1 | .33 |
| Reciprocal | 13 | 0 | |
| *C. japonica* × *C. hongkongensis* | 111 | 7 | 1.20 |
| Reciprocal | 18 | 0 | |
| *C. japonica* × *C. kissi* | 44 | 2 | .61 |
| Reciprocal | 59 | 5 | |
| *C. japonica* × *C. lutchuensis* | 551 | 62 | 24.98** |
| Reciprocal | 245 | 2 | |
| *C. japonica* × *C. miyagii* | 20 | 2 | 2.21 |
| Reciprocal | 21 | 0 | |
| *C. japonica* × *C. pitardii* var. *pitardii* | 22 | 2 | .46 |
| Reciprocal | 24 | 1 | |
| *C. japonica* × *C. reticulata* | 150 | 5 | 4.23* |
| Reciprocal | 69 | 7 | |
| *C. japonica* × *C. rusticana* | 20 | 4 | .07 |
| Reciprocal | 57 | 13 | |

See footnotes at end of table.

TABLE 3.—*Chi-square values for reciprocal interspecific crosses where one or both reciprocals produced hybrid* Camellias [1]—Continued

| Interspecific crosses | Pollinations | Hybrid plants | Chi square value |
|---|---|---|---|
| *C. japonica* × *C. saluenensis* | 41 | 12 | 2.51 |
| Reciprocal | 13 | 1 | |
| *C. japonica* × *C. sinensis* | 44 | 3 | .91 |
| Reciprocal | 41 | 1 | |
| *C. kissi* × *C. miyagii* | 52 | 8 | 2.16 |
| Reciprocal | 37 | 2 | |
| *C. kissi* × *C. oleifera* | 53 | 9 | 2.06 |
| Reciprocal | 42 | 3 | |
| *C. kissi* × *C. reticulata* | 56 | 1 | .33 |
| Reciprocal | 18 | 0 | |
| *C. kissi* × *C. rosaeflora* | 36 | 4 | 4.01* |
| Reciprocal | 34 | 0 | |
| *C. kissi* × *C. rusticana* | 35 | 1 | .04 |
| Reciprocal | 27 | 1 | |
| *C. kissi* × *C. sasanqua* | 46 | 14 | .84 |
| Reciprocal | 33 | 7 | |
| *C. kissi* × *C. sinensis* | 44 | 4 | .01 |
| Reciprocal | 45 | 4 | |
| *C. lutchuensis* × *C. pitardii* var. *pitardii* | 50 | 1 | 1.02 |
| Reciprocal | 27 | 2 | |
| *C. lutchuensis* × *C. rusticana* | 67 | 1 | 4.05* |
| Reciprocal | 280 | 24 | |
| *C. miyagii* × *C. fraterna* | 17 | 1 | 2.93 |
| Reciprocal | 49 | 0 | |
| *C. miyagii* × *C. hongkongensis* | 44 | 1 | .48 |
| Reciprocal | 21 | 0 | |
| *C. miyagii* × *C. lutchuensis* | 112 | 4 | 1.85 |
| Reciprocal | 49 | 0 | |
| *C. miyagii* × *C. oleifera* | 33 | 13 | 3.15 |
| Reciprocal | 19 | 3 | |
| *C. miyagii* × *C. sasanqua* | 40 | 9 | 1.33 |
| Reciprocal | 33 | 4 | |
| *C. oleifera* × *C. sasanqua* | 29 | 18 | .67 |
| Reciprocal | 31 | 16 | |
| *C. oleifera* × *C. sinensis* | 63 | 2 | 1.31 |
| Reciprocal | 64 | 5 | |

See footnotes at end of table.

TABLE 3.—*Chi-square values for reciprocal interspecific crosses where one or both reciprocals produced hybrid* Camellias [1]—Continued

| Interspecific crosses | Pollinations | Hybrid plants | Chi square value |
|---|---|---|---|
| | *Number* | *Number* | |
| *C. pilardii* var. *pilardii* × *C. fraterna* | 21 | 2 | 2.49 |
| Reciprocal | 25 | 0 | |
| *C. pilardii* var. *pilardii* × *C. reticulata* | 25 | 1 | .69 |
| Reciprocal | 42 | 4 | |
| *C. pilardii* var. *pilardii* × *C. saluenensis* | 20 | 1 | .01 |
| Reciprocal | 19 | 1 | |
| *C. reticulata* × *C. rosaeflora* | 35 | 1 | .99 |
| Reciprocal | 34 | 0 | |
| *C. reticulata* × *C. rusticana* | 12 | 1 | 4.07* |
| Reciprocal | 48 | 0 | |
| *C. reticulata* × *C. saluenensis* | 24 | 3 | .43 |
| Reciprocal | 28 | 2 | |
| *C. rosaeflora* × *C. fraterna* | 36 | 2 | 1.49 |
| Reciprocal | 26 | 0 | |
| *C. rusticana* × *C. fraterna* | 162 | 3 | .94 |
| Reciprocal | 50 | 0 | |
| *C. saluenensis* × *C. fraterna* | 24 | 1 | 1.06 |
| Reciprocal | 25 | 0 | |
| *C. saluenensis* × *C. hongkongensis* | 12 | 1 | 3.06 |
| Reciprocal | 36 | 0 | |
| *C. saluenensis* × *C. lutchuensis* | 19 | 1 | .76 |
| Reciprocal | 14 | 0 | |
| *C. sasanqua* × *C. granthamiana* | 60 | 2 | .21 |
| Reciprocal | 6 | 0 | |
| *C. sasanqua* × *C. japonica* | 46 | 3 | 1.97 |
| Reciprocal | 29 | 0 | |
| *C. sasanqua* × *C. reticulata* | 88 | 3 | 1.08 |
| Reciprocal | 31 | 0 | |
| *C. sinensis* × *C. fraterna* | 32 | 1 | .86 |
| Reciprocal | 27 | 0 | |
| *C. sinensis* × *C. hiemalis* | 66 | 5 | .89 |
| Reciprocal | 11 | 0 | |
| *C. sinensis* × *C. miyagii* | 58 | 10 | 3.38 |
| Reciprocal | 17 | 0 | |
| *C. sinensis* × *C. sasanqua* | 52 | 7 | .02 |
| Reciprocal | 12 | 0 | |

[1] Statistical calculations based on Snedecor and Cochran (*1967*), pp. 215–226.

*Indicates significant difference (0.05). **Indicates highly significant difference (0.01).

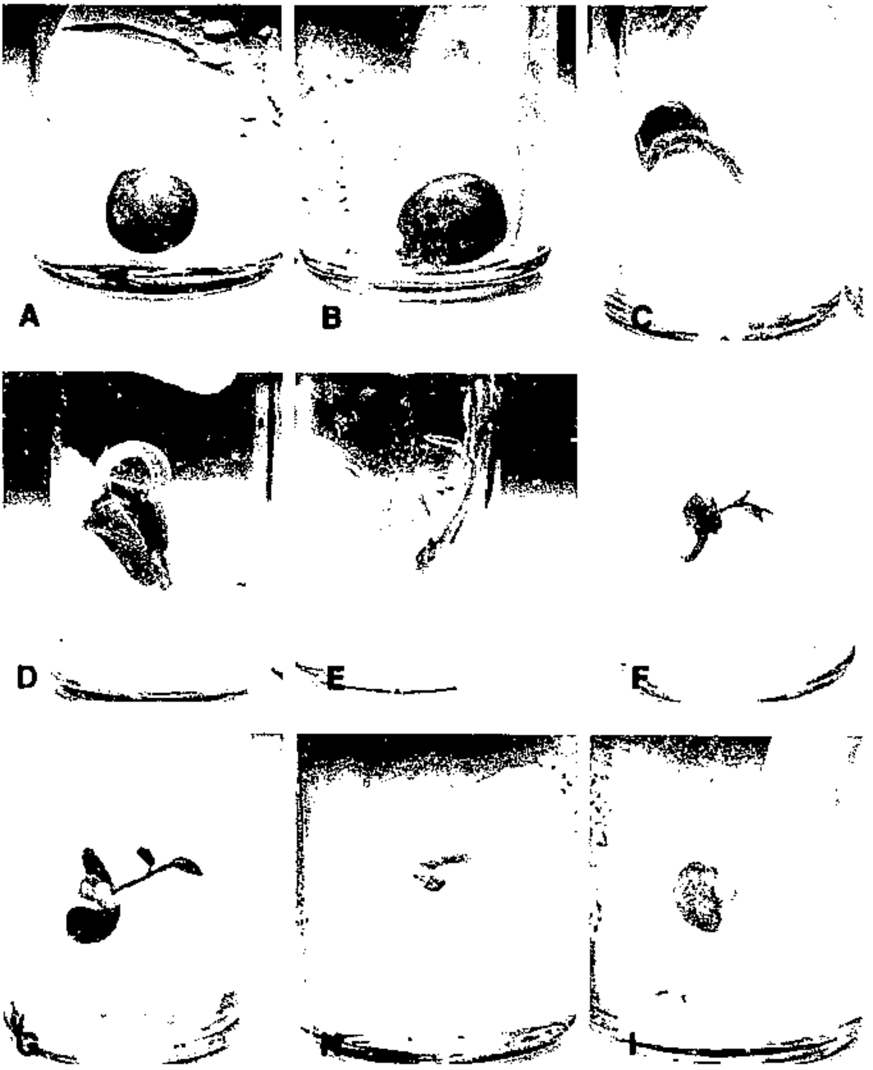

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FIGURE 1.—Normal and abnormal development in *Camellia* embryo culture. *A* through *E* show normal development and *F* through *I* show abnormal: *A*, Two days after placement in culture jar. *B*, Five days in culture; early stage of development of radicle. *C*, Ten days in culture; development of radicle. *D*, Four weeks in culture; radicle is developed but partly hidden; hypocotyl arched over cotyledons. *E*, Six weeks in culture; normally developed seedling with primary leaves unfolding; at proper stage for transfer from culture. *F*, Six weeks in culture; stunted radicle and hypocotyl; however, seedling developed sufficiently after 6 months for transfer from culture. *G*, Six weeks in culture; no radicle development; stunted hypocotyl; radicle never developed and seedling finally died. *H*, Ten weeks in culture; very small embryo; normal radicle but no hypocotyl; no further development. *I*, Ten weeks in culture; embryo very much shriveled at time of culturing, but expanded in culture before abortion.

counts were omitted from this study. In table 22, each hybrid is listed separately and identified by its code number. Future references to code numbers of hybrids are based on this table.

Species possessing strongly dominant characters can be extremely useful to the plant breeder in ascertaining the validity of the hybrids when those species are used as male parents. Specific characters that appeared to be dominant among the $F_1$ progeny are as follows:

(1) The pubescent stem character was dominant over the glabrous. Hybrids resulting from female parents with glabrous stems crossed with males having pubescent stems were consistently pubescent stemmed, indicating homozygosity of the pubescent stem character in the Glenn Dale parental species used. Thus, 62 hybrids of C *japonica* × C. *lutchuensis*, 24 of C. *rusticana* × C. *lutchuensis*, 10 of C. *japonica* × C. *fraterna*, three of C. *rusticana* × C. *fraterna, three* of C. *reticulata* × C. *fraterna*, three of C. *japonica* × C. *granthamiana*, two of C. *japonica* × C. *kissi*, and one of C. *reticulata* × C. *granthamiana* had pubescent stems like their male parents. When both parents had glabrous stems, all of the progeny also had glabrous stems.

(2) Hybrids from crosses where C. *granthamiana* was the male parent consistently showed highly raised midrib and veination on the lower surface of the leaves, which appeared as deep indentations from the upper surface. Illustrations of the leaves of both parents and progeny are shown in figure 2 where pollen of C. *granthamiana* was used on C. *japonica*, C. *pitardii* var. *pitardii*, C. *reticulata*, and C. *saluenensis*.

(3) Hybrids from crosses where C. *hongkongensis* was the male parent showed a distinct resemblance to this species by having narrow, elongate leaves. Illustrations of the leaves of both parents and progeny are shown in figure 3, where pollen of C. *hongkongensis* was used on C. *japonica*, C. *saluenensis*, and C. *rusticana*.

(4) Hybrids from crosses where C. *fraterna* was the male parent showed similarity to this species in a rather substantial number of characters. These include willowy, spreading plant habit with thin,

highly pubescent young shoots, dull grey-green foliage, and shape of the leaves characteristic of *C. fraterna*. Illustrations of the last character are shown in figure 4. Figure 4, *A*, *B*, and *C* show the dominance of *C. fraterna* as the male parent with respect to the shape of the leaves. As shown in figure 4, *D*, similar dominance was expressed when *C. fraterna* was used as the female parent. In the latter case, subsequent chromosome counts proved the validity of the hybrid. *C. fraterna* is extremely floriflerous, and it is not unusual for a mature plant to have six to eight flower buds per node along the entire length of each branchlet. This trait, illustrated in figure 4, *E*, appeared in all 18 hybrids involving this species which have flowered to date.

(5) Among the hybrids of *C. japonica* × *C. lutchuensis* and *C. rusticana* × *C. lutchuensis*, the male parent *C. lutchuensis*, showed dominance of pink to red coloration of young shoots and leaves over the light-green coloration of *C. japonica* or *C. rusticana;* dominance of short, stout, bluntly pointed, silky terminal buds typical of *C. lutchuensis* over long, sharply pointed, glabrous terminal buds of *C. japonica* or *C. rusticana;* and dominance of leaf veination patterns of *C. japonica* or *C. rusticana* over those of *C. lutchuensis.*

Not all species transmitted such distinct dominance, and the hybrids were intermediate in character. Hybrids of this type are illustrated in figure 5. Here, additional proof of hybridity was obtained by chromosome counts or determinations of percentages of aborted pollen.

Floral characters proved to be a valuable supplement to vegetative characters and were especially helpful in some otherwise questionable cases of hybridity. Flower size and form were most frequently intermediate between that of the parents. However, where small-flowered, wild species such as *C. fraterna*, *C. kissi*, *C. lutchuensis*, or *C. miyagii* were crossed with large flowered cultivated varieties of *C. japonica*, *C. reticulata*, *C. rusticana*, or *C. sasanqua*, the small-flowered species appeared to exert the greater influence on the progeny.

Certain species transmitted their floral characters more strongly than others. This was true of *C. granthamiana*, which transmitted large, frilled petals to the majority of its progeny. Figure 6 shows the nature of the petals in this species and in typi-

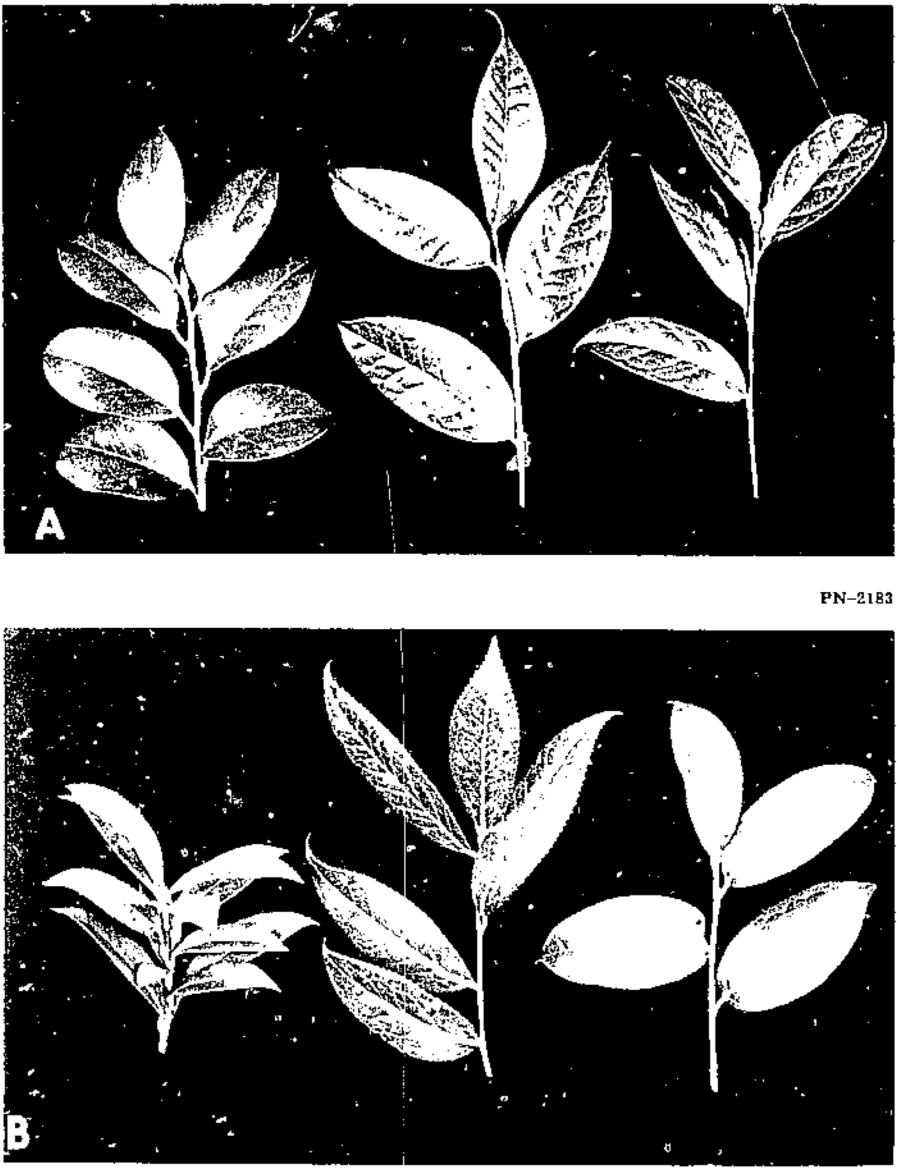

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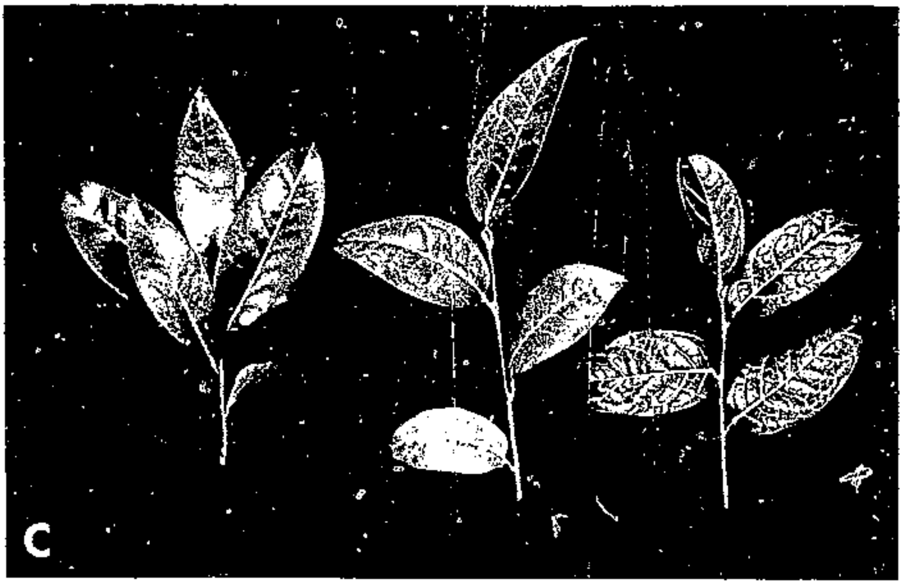
FIGURE 2.—Leaf veination of parents and hybrids from crosses where *C. granthamiana* was the male parent. Hybrids show indented veination of leaves similar to *C. granthamiana*: *A*, Left, *C. japonica*, female parent; center, hybrid B-3; right, *C. granthamiana*, male parent. *B*, Left, *C. pitardii* var. *pitardii*, female parent; center, hybrid B–6; right, *C. granthamiana*, male parent. *C*, Left, C. *reticulata*, female parent; center, hybrid B-5; right, *C. granthamiana*, male parent. *D*, Left, *C. saluenensis*, female parent; center, hybrid B-2; right, *C. granthamiana*, male parent.



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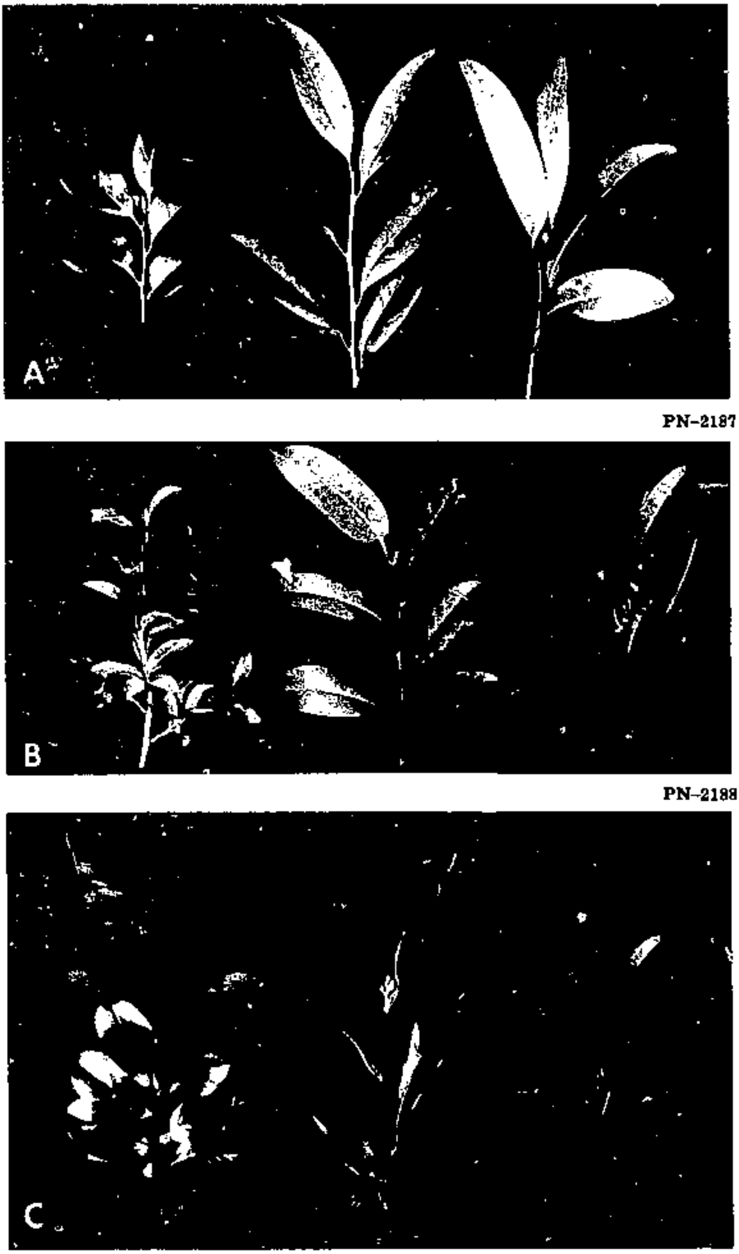

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FIGURE 3.—Leaf shape of parents and hybrids from crosses where *C. hongkongensis* was the male parent. Hybrids show elongate leaves similar to *C. hongkongensis*: *A*, Left, *C. japonica*, female parent; center, hybrid 5-47; right, *C. hongkongensis*, male parent. *B*, Left, *C. saluenensis*, female parent; center, hybrid P-48; right, *C. hongkongensis*, male parent. *C*, Left, *C. rusticana*, female parent; center, hybrid 7-1; right, *C. hongkongensis*, male parent.

cal hybrids. *C. hongkongensis* has trumpet-shaped flowers and rough, grey perules, which are also common characters in many of its hybrids. The floral form characteristic of *C. hongkongensis* and its hybrids is shown in figure 7. The floral petals of *C. saluenensis* have an illuminative quality that is also present in most of its progeny.

Floral scent is rather rare in the genus and is not generally present in the cultivated species. In addition to *C. sasanqua*, which has only a few faintly scented cultivars, six other species, *C. fraterna*, *C. kissi*, *C. lutchuensis*, *C. miyagii*, *C. oleifera*, and *C. tsaii*, are scented. Only *C. lutchuensis* and *C. tsaii* have a scent that is pleasant to most people. The scent of the other five species is described as being musky and unpleasant. Floral scent appears to be transmitted to a large percentage of the hybrid progeny. Because this character is unique in these species, its presence in hybrid progenies provided a valuable marker. Among 59 *C. lutchuensis* hybrids, 55 were scented. Only 16 *C. fraterna* hybrids have flowered to date, but all except one were scented. All eight *C. miyagii* hybrids observed have the scent characteristic of this species. Nine out of 21 *C. sasanqua* hybrids were scented. None of the hybrids involving *C. kissi*, *C. oleifera*, or *C. tsaii* have flowered as yet.

Several of the scented hybrids are of considerable ornamental interest. One hybrid selection, a cross between *C. rusticana* 'Yoshida' (P.I. 228187)[4] and *C. lutchuensis* (P.I. 226756) was named 'Fragrant Pink' by the Plant Science Research Division in 1966 and has since been distributed to the nursery trade. This is a loose, peony-type flower, 2¼ inches by 1¼ inches, medium pink, with 10 petals and 12 petaloids. The scent of the flowers is similar to that of *C. lutchuensis* and it represents an improvement in flower size and form from that of *C. lutchuensis*, which is 1¼ inches across, white, and single. Although no claim is made that 'Fragrant Pink' is commercially outstanding, it appears to be a definite step in the right direction. Figure 8 illustrates four of the more scented ornamental hybrids.

### Determination of Pollen Abortion

Early in the interspecific hybridization program, the question of the selection of suitable parents arose, especially in regard to species represented solely by commercial varieties. The flowers of many cultivated varieties are frequently almost sterile because of distorted nonfunctional styles and aborted pollen. Thus, it was necessary to evaluate all prospective parents for quality of the pollen

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[4] P.I. refers to the accession number assigned to foreign introductions by the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture.

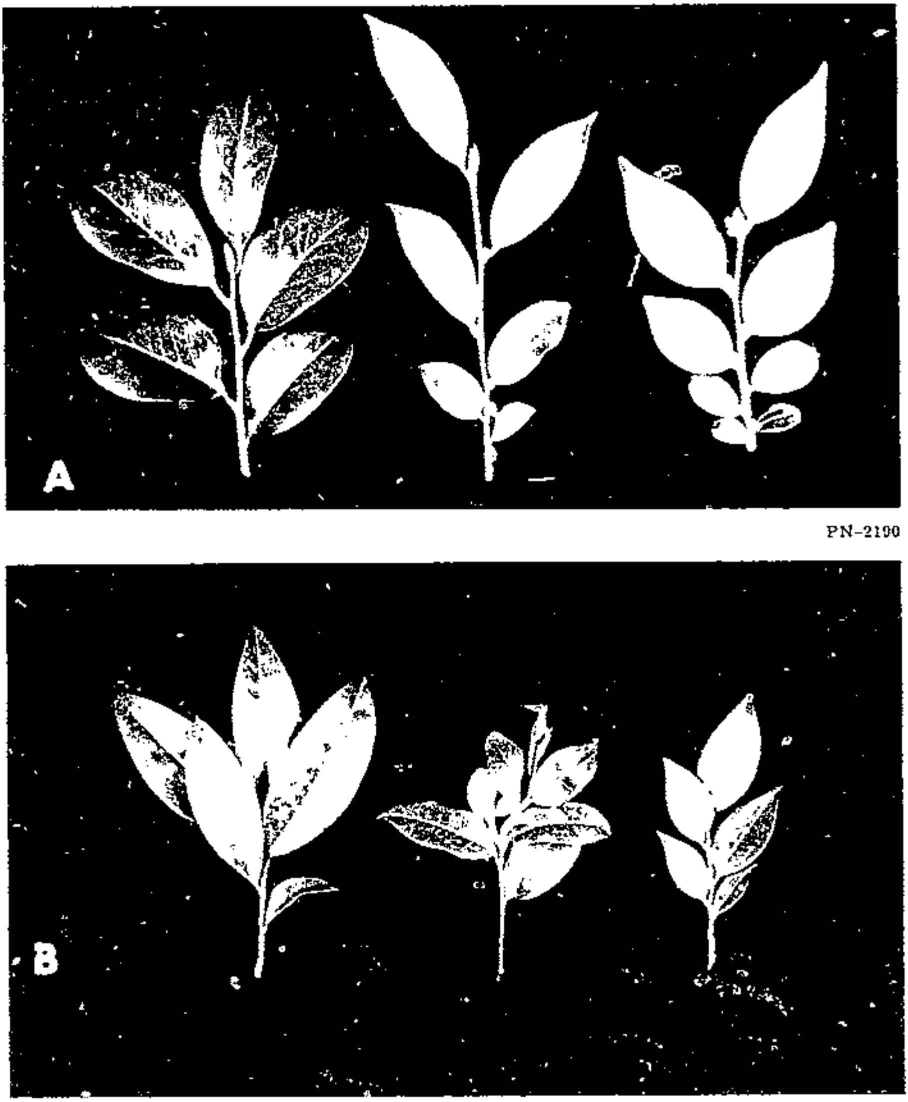

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FIGURE 4. Dominant foliar and floral bud characters transmitted by *C. fraterna* to its hybrids. *A* through *D* show dominant leaf shape of *C. fraterna* and *E* shows the prolific floral buds characteristic of *C. fraterna* and its hybrids: *A*, left, *C. japonica*, female parent; center, hybrid 4-7; right, *C. fraterna*, male parent. *B*, Left, *C. reticulata*, female parent; center, hybrid 2-7; right, *C. fraterna*, male parent. *C*, Left, *C. rusticana*, female parent; center, hybrid 3-2; right, *C. fraterna*, male parent. *D*, Left, *C. fraterna*, female parent; center, hybrid B-7; right, *C. japonica*, male parent. *E*, Flowering branches illustrating typical floriferous nature of *C. fraterna* and its hybrids: Left, *C. fraterna*; right, hybrid 4-4 of *C. japonica* × *C. fraterna*.

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FIGURE 5. Leaf shape of parents and hybrids showing intermediate nature of the hybrids. *A*, Left, *C. oleifera*, female parent; center, hybrid C-1; right, *C.* [illegible], male parent. *B*, Left, *C. japonica*, female parent; center, hybrid 5-C; right, *C. saluenensis*, male parent. *C*, Left *C. japonica*, female parent; center, hybrid 7-250; right, *C. sinensis*, male parent. *D*, Left, *C. sasanqua*, female parent; center, hybrid 5-52; right, *C. miyagii*, male parent. *E*, Left, *C. sasanqua*, female parent; center, hybrid B-1; right, *C. oleifera*, male parent.

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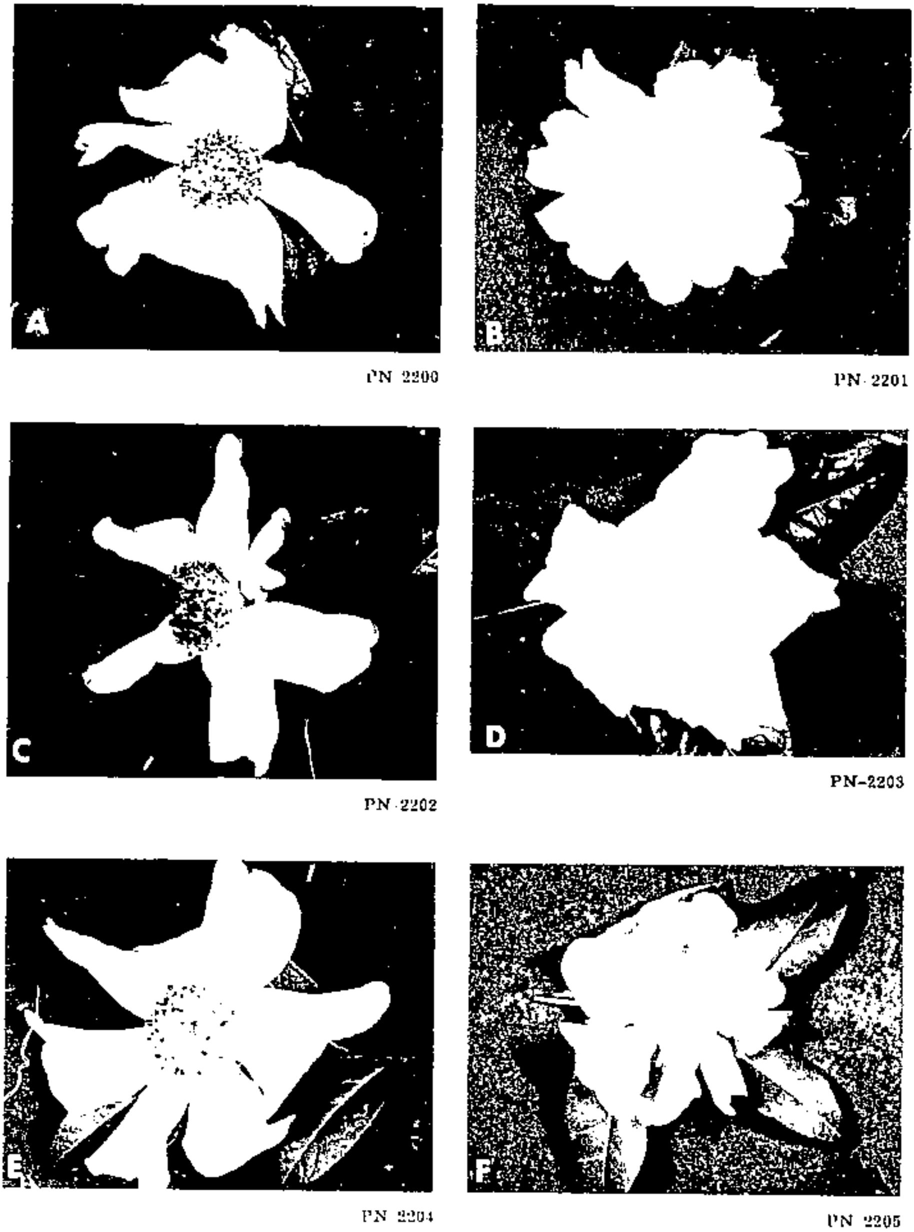

FIGURE 6.—Flowers of *C. granthamiana* and hybrids showing transmission of frilled petals from *C. granthamiana* when it was used as the male parent: *A*, *C. granthamiana*; *B*, hybrid B-3 of *C. japonica* × *C. granthamiana*; *C*, hybrid B-6 of *C. pitardii* var. *pitardii* × *C. granthamiana*; *D*, hybrid B-5 of *C. reticulata* × *C. granthamiana*; *E*, hybrid B-2 of *C. saluenensis* × *C. granthamiana*; *F*, hybrid B-4 of *C. sasanqua* × *C. granthamiana*.

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FIGURE 7.—Flowers of *C. hongkongensis* and hybrids showing transmission of trumpet-shaped floral form when *C. hongkongensis* was used as the male parent: *A*, *C. hongkongensis;* B, hybrid 5-12 of *C. japonica* × *C. hongkongensis; C*, hybrid 7-1 of *C. rusticana* × *C. hongkongensis.*

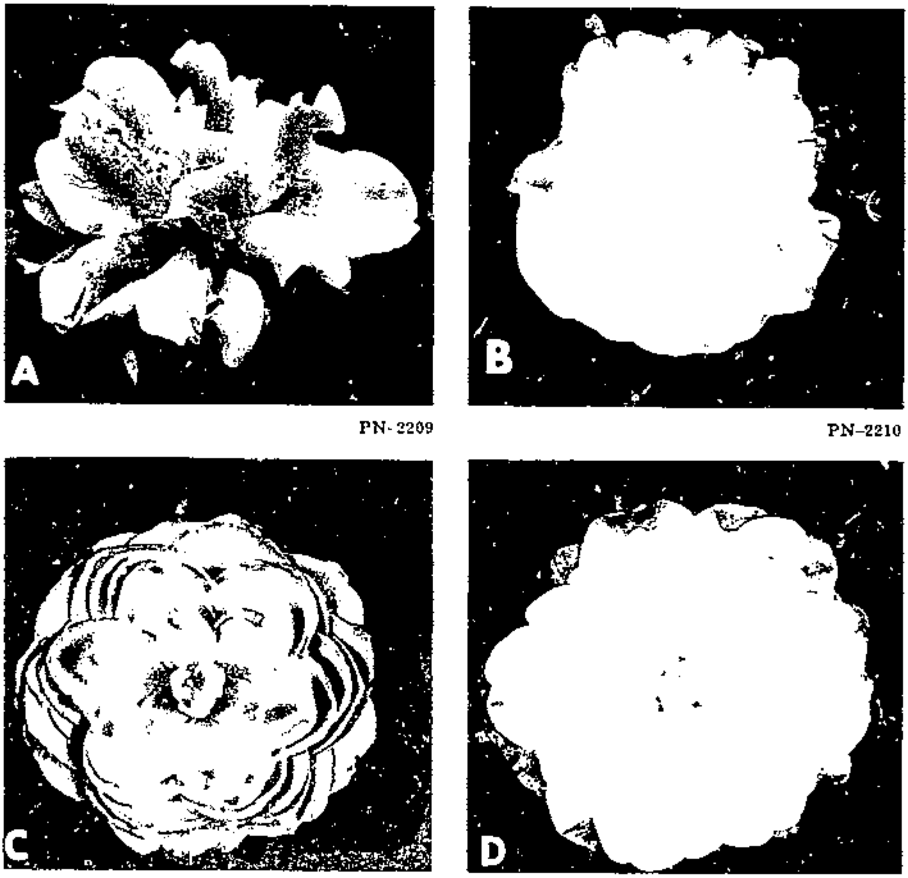

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FIGURE 8.—Flowers of scented hybrids of possible ornamental value: *A*, Hybrid, 'Fragrant Pink,' of *C. rusticana* × *C. lutchuensis*; *B*, highly scented hybrid 3-12 of *C. japonica* × *C. lutchuensis*; *C*, mildly scented hybrid 3-4 of *C. rusticana* × *C. fraterna*; *D*, strongly scented hybrid 5-56 of *C. sasanqua* × *C. miyagii*.

before any meaningful interspecific hybridization program could be undertaken. Table 4 lists percentages of aborted pollen for the parents used in interspecific crosses. The percentages of aborted pollen ranged among the species from 3 percent to 58 percent. Introductions with higher percentages of aborted pollen were omitted from the breeding program. Figure 9, *A* shows uniform, filled, stainable pollen and figure 9, *B* shows shriveled, empty, unstainable aborted pollen.

TABLE 4.—*Percentages of aborted and large, presumably unreduced pollen, based on observations of 1,000 grains from a minimum of six anthers for each species or clone of* Camellia

| P.I. or B No.[1] | Species | Aborted pollen | Large pollen |
|---|---|---|---|
| | | *Percent* | *Percent* |
| 162476 | *C. fraterna* | 22 | 3 |
| 251534 | *C. granthamiana* | 55 | 1 |
| B56995 | *C. hiemalis* | 11 | 7 |
| B56996 | do | 29 | 6 |
| 229973 | *C. hongkongensis* | 19 | 0 |
| B56272 | *C. japonica* | 17 | 3 |
| 226109 | do | 22 | 5 |
| 227063 | do | 19 | 3 |
| 228024 | do | 12 | 2 |
| 230278 | do | 21 | 3 |
| 231686 | do | 24 | 3 |
| 231687 | do | 28 | 1 |
| 231689 | do | 7 | 2 |
| 231690 | do | 8 | 5 |
| 231694 | do | 13 | 1 |
| 231695 | do | 3 | 4 |
| 231858 | do | 4 | 4 |
| 231859 | do | 48 | 2 |
| 238725 | do | 25 | 18 |
| 274530 | do | 51 | 2 |
| 274797 | do | 7 | 2 |
| 274799 | do | 12 | 2 |
| 275054 | do | 4 | 3 |
| 275512 | do | 21 | 22 |
| 309001 | do | 13 | 13 |

See footnote at end of table.

TABLE 4.—*Percentages of aborted and large, presumably unreduced pollen, based on observations of 1,000 grains from a minimum of six anthers for each species or clone of* Camellia—Continued

| P.I. B No.[1] | Species | Aborted pollen | Large pollen |
|---|---|---|---|
| | | Percent | Percent |
| 319283 | *C. japonica* | 20 | 5 |
| 252062 | *C. kissi* | 53 | 1 |
| 252064 | do | 9 | 2 |
| 226756 | *C. lutchuensis* | 21 | 1 |
| 226704 | *C. miyagii* | 22 | 1 |
| 231057 | do | 17 | 1 |
| 162561 | *C. oleifera* | 37 | 0 |
| 235500 | do | 11 | 2 |
| B58296 | *C. pitardii* var. *pitardii* | 33 | 9 |
| B51685 | *C. reticulata* | 33 | 1 |
| B51686 | do | 15 | 1 |
| B51689 | do | [illegible] | 1 |
| B51690 | do | 11 | 2 |
| B51694 | do | 14 | 4 |
| B58619 | *C. rosaeflora* | 26 | 2 |
| 228187 | *C. rusticana* | 34 | 1 |
| 228188 | do | 21 | 0 |
| 228190 | do | 11 | 2 |
| 233642 | do | 58 | 3 |
| 310320 | *C. salicifolia* | 14 | 9 |
| 243862 | *C. saluenensis* | 21 | 2 |
| 227624 | *C. sasanqua* | 22 | 2 |
| 228025 | do | 16 | 2 |
| 235568 | do | 19 | 2 |
| 237854 | do | 27 | 3 |
| 277763 | do | 17 | 2 |
| 319284 | do | 24 | 2 |
| 319285 | do | 25 | 2 |
| 235570 | *C. sinensis* | 4 | 2 |
| 235572 | do | 6 | 2 |

See footnote at end of table.

TABLE 4.—*Percentages of aborted and large, presumably unreduced pollen, based on observations of 1,000 grains from a minimum of six anthers for each species or clone of* Camellia—Continued

| P.I. or B No.[1] | Species | Aborted pollen | Large pollen |
|---|---|---|---|
| | | *Percent* | *Percent* |
| 235573 | *C. sinensis* | 3 | 0 |
| 304404 | do | 6 | 1 |
| 304405 | do | 10 | 1 |
| 316471 | do | 14 | 5 |
| 316472 | do | 8 | 3 |
| 316473 | do | 26 | 4 |
| 316476 | do | 13 | 3 |
| 316477 | do | 22 | 1 |
| 316478 | do | 10 | 1 |
| B57043 | *C. taliensis* | 15 | 0 |
| B57048 | *C. tenuiflora* | 28 | 5 |

[1] P.I. refers to the accession number assigned to foreign introductions by the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture. B numbers are code numbers assigned to importations under postentry quarantine permit by the U.S. Plant Introduction Station, Glenn Dale, Md.

Observation of the pollen also disclosed that the production of large grains with presumably unreduced chromosome numbers is very common in the genus. All but five of 66 introductions observed produced at least some large pollen as shown in table 4. Figure 9, *C* shows the presence of large pollen. Although germination tests unfortunately were not made on large pollen grains, indirect evidence from chromosome counts of parents and hybrids indicate that at least some unreduced pollen grains and egg cells are viable. The chromosome numbers observed for two hybrids of *C. reticulata* × *C. japonica* (see p. 62) appear to be the result of the functioning of unreduced pollen grains, and the chromosome number observed for one hybrid of *C. pitardii* var. *pitardii* × *C. granthamiana* (see p. 57) appears to be the result of an unreduced egg.

The use of hybrids in the interspecific transfer of desirable characters depends upon fertility. Furthermore, a greatly increased frequency of aborted pollen produced by a presumptive hybrid in comparison with the frequencies produced by the parents provides corroborative evidence of hybridity. Pollen abortion among the hybrids varied from 100 percent to percentages similar to those of

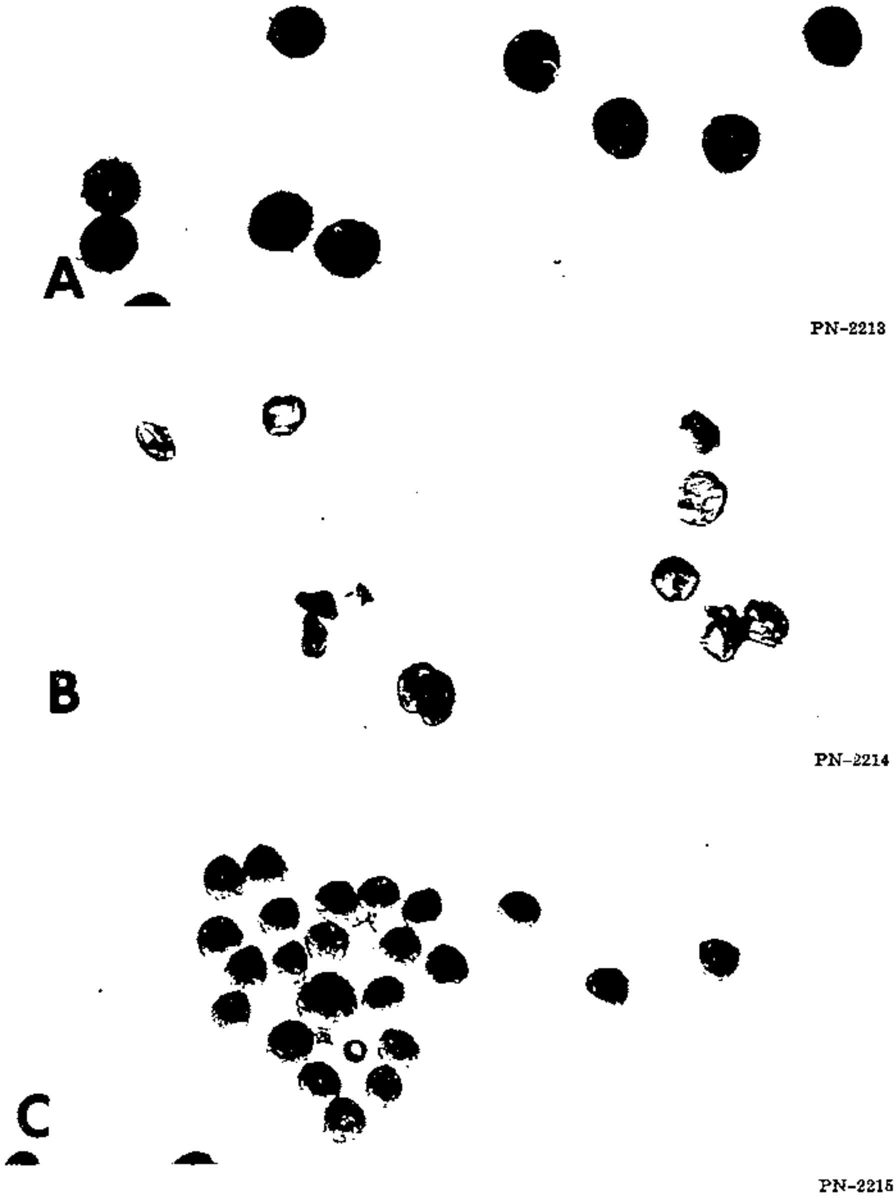

FIGURE 9.—Filled, empty, and large pollen following staining with acetocarmine (125×): *A*, Uniform, filled, stainable pollen. *C. japonica*, P.I. 231695; *B*, shriveled, empty, unstainable aborted pollen. Hybrid 4-4 from *C. japonica* × *C. fraterna*; *C*, large, presumably unreduced pollen occurring among filled and aborted grains of normal size. Hybrid A-2 from *C. reticulata* × *C. japonica*.

the parental species. Table 5 summarizes the pollen abortion determinations of flowering hybrids. As expected, the percentages of aborted pollen produced by the hybrids were generally greater than the percentages produced by the parental species. Large, presumably unreduced pollen was also observed in 112 of the 134 hybrids examined.

## Intergeneric Hybridization

As an extension of the interspecific hybridization program, attempts were made to hybridize several *Camellia* species with species of related genera. This was initiated in a limited fashion with crosses of *Camellia* with *Tutcheria spectabilis* and *T. virgata*. Some early success encouraged the later expansion of hybridizing to include outdoor plants of *Franklinia alatamaha* and *Stewartia ovata*.

The intergeneric crosses attempted are listed in table 6, along with the number of pollinations and the number and percentage per pollination of capsules produced, of seeds started in culture, and of hybrid plants. A total of 1,064 controlled pollinations were made. These represented 24 intergeneric combinations, including reciprocal crosses. Eleven plants judged to be valid hybrids were secured from *T. virgata* × *C. granthamiana*, *T. virgata* × *C. miyagii*, and *C. pitardii* var. *pitardii* × *T. spectabilis*. In addition, six as yet unvalidated plants were secured from *F. alatamaha* × *C. hongkongensis*.

### Morphological Comparisons

Hybrid validity was based initially on comparison of vegetative characters of parents and hybrids (appendix tables 23 and 24) and subsequently corroborated by floral characters, pollen abortion determinations, and chromosome counts of the parents and progeny. In figure 10, foliar characters are shown for *T. virgata* × *C. granthamiana*, *T. virgata* × *C. miyagii*, and *C. pitardii* var. *pitardii* × *T. spectabilis*. The hybrids illustrated for both *T. virgata* crosses are similar to the male parent, whereas the hybrid of *T. spectabilis* appears intermediate.

The floral characters, especially petal shape, of the hybrids of *T. virgata* × *C. miyagii* are shown in figure 11, along with those of the parental species. The petals of two hybrids (fig. 11, *D* and *E*) were distinctly similar to the male parent, four (fig. 11, *C*, *F*, *H*, and *I*) were intermediate, and one (fig. 11, *G*) was similar to the female parent. Figure 12 shows the floral characters of the hybrid of *C. pitardii* var. *pitardii* × *T. spectabilis* and its parents. None of the hybrids of *T. virgata* × *C. granthamiana* have flowered yet.

TABLE 5.—*Percentages of aborted and presumably unreduced pollen produced by interspecific* Camellia *hybrids. Observations of 1,000 grains from a minimum of six anthers were made for each hybrid having some filled pollen; 500 grains were examined in completely male-sterile hybrids*

| Interspecific crosses | Hybrids counted | Aborted pollen | | | Presumably unreduced pollen | | |
|---|---|---|---|---|---|---|---|
| | | Range | | Mean | Range | | Mean |
| | | Low | High | | Low | High | |
| | *Number* | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* |
| *C. fraterna* × *C. japonica* | 1 | 84 | 84 | 84 | 1.0 | 1.0 | 1.0 |
| Reciprocal | 8 | 48 | 98 | 78 | 0 | 3.0 | 2.2 |
| *C. fraterna* × *C. reticulata* | 1 | 91 | 91 | 91 | .5 | .5 | .5 |
| Reciprocal | 3 | 23 | 67 | 39 | 0 | 1.6 | .9 |
| *C. japonica* × *C. hongkongensis* | 6 | 80 | 97 | 92 | 0 | 5.2 | 2.1 |
| *C. japonica* × *C. kissi* | 1 | 83 | 83 | 83 | .4 | .4 | .4 |
| *C. japonica* × *C. lutchuensis* | 45 | 82 | 100 | 96 | 0 | 3.5 | 1.1 |
| *C. japonica* × *C. miyagii* | 2 | 93 | 96 | 94 | 0 | 1.2 | .6 |
| *C. japonica* × *C. reticulata* | 2 | 54 | 99 | 76 | 0 | 4.0 | 2.0 |
| Reciprocal | 6 | 58 | 93 | 83 | .3 | 7.2 | 4.7 |
| *C. japonica* × *C. rusticana* | 3 | 7 | 46 | 22 | 1.1 | 6.0 | 3.0 |
| *C. japonica* × *C. saluenensis* | 4 | 76 | 82 | 80 | 0 | 1.8 | 1.3 |
| Reciprocal | 1 | 77 | 77 | 77 | 0 | 0 | 0 |
| *C. japonica* × *C. sinensis* | 3 | 91 | 94 | 92 | 0 | 2.1 | 1.7 |
| *C. oleifera* × *C. hiemalis* | 1 | 95 | 95 | 95 | .3 | .3 | .3 |
| *C. oleifera* × *C. miyagii* | 2 | 91 | 97 | 94 | .2 | 1.2 | .7 |
| *C. pitardii* var. *pitardii* × *C. granthamiana* | 1 | 89 | 89 | 89 | 1.6 | 1.6 | 1.6 |
| *C. pitardii* var. *pitardii* × *C. japonica* | 1 | 86 | 86 | 86 | .1 | .1 | .1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *C. pitardii* var. *pitardii* × *C. lutchuensis* | 1 | 92 | 92 | 92 | 1.2 | 1.2 | 1.2 |
| *C. pitardii* var. *pitardii* × *C. saluenensis* | 2 | 88 | 93 | 90 | .2 | 1.2 | .7 |
| *C. reticulata* × *C. granthamiana* | 2 | 63 | 88 | 75 | 3.6 | 5.8 | 4.7 |
| *C. reticulata* × *C. saluenensis* | 2 | 49 | 75 | 62 | 2.0 | 3.7 | 2.8 |
| *C. rusticana* × *C. fraterna* | 3 | 12 | 99 | 51 | 0 | 9.3 | 4.7 |
| *C. rusticana* × *C. lutchuensis* | 20 | 82 | 100 | 95 | 0 | 6.0 | 2.4 |
| *C. saluenensis* × *C. granthamiana* | 1 | 100 | 100 | 100 | 0 | 0 | 0 |
| *C. saluenensis* × *C. hongkongensis* | 1 | 84 | 84 | 84 | 1.3 | 1.3 | 1.3 |
| *C. saluenensis* × *C. lutchuensis* | 1 | 88 | 88 | 88 | .7 | .7 | .7 |
| *C. sasanqua* × *C. granthamiana* | 2 | 19 | 25 | 22 | 1.6 | 2.9 | 2.2 |
| *C. sasanqua* × *C. miyagii* | 4 | 5 | 88 | 46 | .3 | 1.5 | .8 |
| *C. sasanqua* × *C. oleifera* | 1 | 44 | 44 | 44 | 1.6 | 1.6 | 1.6 |
| *C. sasanqua* × *C. reticulata* | 3 | 16 | 43 | 27 | .7 | 2.1 | 1.3 |

TABLE 6.—*Intergeneric crosses:* Franklinia alatamaha, Stewartia ovata, Tutcheria spectabilis, *and* T. virgata *crossed with species of* Camellia

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | | Hybrid plants | |
|---|---|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. japonica* × *T. spectabilis* | 95 | 2 | 2.1 | 3 | 3.2 | 0 | 0 |
| *C. pitardii* var. *pitardii* × *T. spectabilis* | 83 | 1 | 1.2 | 2 | 2.4 | 1 | 1.2 |
| *C. japonica* × *T. virgata* | 28 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. miyagii* × *T. virgata* | 59 | 3 | 5.1 | 0 | 0 | 0 | 0 |
| *C. reticulata* × *T. virgata* | 15 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. rusticana* × *T. virgata* | 26 | 1 | 3.8 | 1 | 3.8 | 0 | 0 |
| *C. sasanqua* × *T. virgata* | 16 | 0 | 0 | 0 | 0 | 0 | 0 |
| *F. alatamaha* × *C. granthamiana* | 25 | 4 | 16.0 | 0 | 0 | 0 | 0 |
| *F. alatamaha* × *C. hongkongensis* | 53 | 3 | 5.6 | 23 | 43.4 | 6 | 11.3 |
| *F. alatamaha* × *C. japonica* | 25 | 5 | 20.0 | 0 | 0 | 0 | 0 |
| *F. alatamaha* × *C. miyagii* | 23 | 1 | 4.3 | 0 | 0 | 0 | 0 |
| *F. alatamaha* × *C. oleifera* | 23 | 2 | 8.6 | 0 | 0 | 0 | 0 |
| *F. alatamaha* × *C. sinensis* | 51 | 8 | 15.7 | 0 | 0 | 0 | 0 |
| *S. ovata* × *C. japonica* | 25 | 0 | 0 | 0 | 0 | 0 | 0 |
| *S. ovata* × *C. kissi* | 28 | 1 | 3.6 | 1 | 3.6 | 0 | 0 |
| *S. ovata* × *C. miyagii* | 31 | 0 | 0 | 0 | 0 | 0 | 0 |
| *S. ovata* × *C. oleifera* | 26 | 0 | 0 | 0 | 0 | 0 | 0 |
| *T. virgata* × *C. granthamiana* | 106 | 5 | 4.7 | 3 | 2.8 | 3 | 2.8 |
| *T. virgata* × *C. hongkongensis* | 29 | 0 | 0 | 0 | 0 | 0 | 0 |
| *T. virgata* × *C. japonica* | 48 | 1 | 2.1 | 2 | 4.2 | 0 | 0 |
| *T. virgata* × *C. lutchuensis* | 27 | 1 | 3.7 | 1 | 3.7 | 0 | 0 |
| *T. virgata* × *C. miyagii* | 152 | 3 | 2.0 | 7 | 4.6 | 7 | 4.6 |
| *T. virgata* × *C. rusticana* | 45 | 4 | 8.9 | 2 | 4.4 | 0 | 0 |
| *T. virgata* × *C. sinensis* | 25 | 2 | 8.0 | 5 | 20.0 | 0 | 0 |

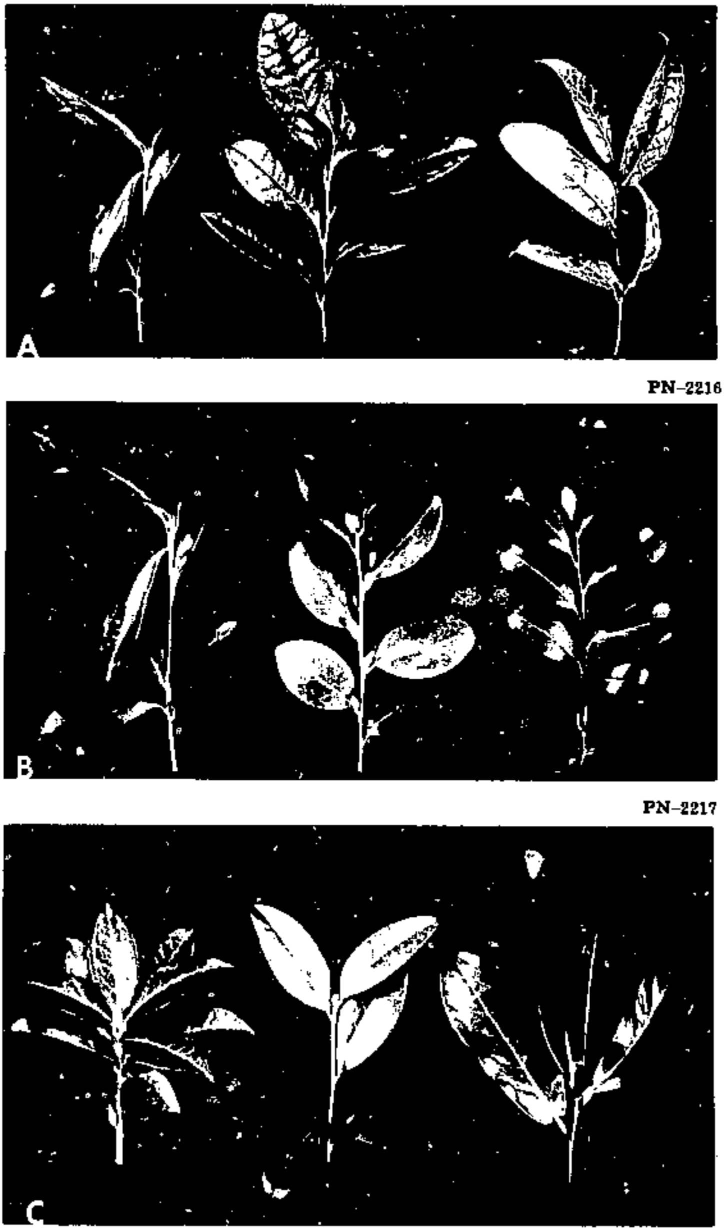

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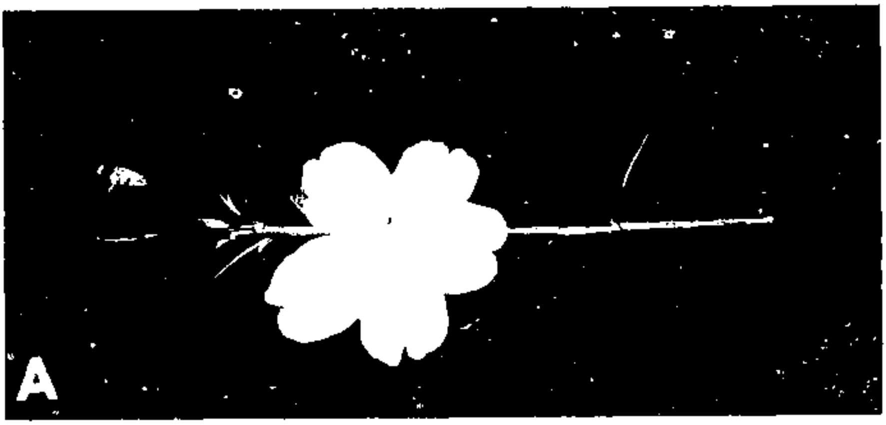
FIGURE 10.—Foliar characters of parents and hybrids involving intergeneric crosses: *A*, Left, *Tutcheria virgata*, female parent; center, hybrid 7-233, showing indented veination of male parent; right, *Camellia granthamiana*, male parent. *B*, Left, *T. virgata*, female parent; center, hybrid 5-62, showing leaf shape similar to male parent; right, *C. miyagii*, male parent. *C*, Left, *C. pitardii* var. *pitardii*, female parent; center, hybrid A-19, intermediate in leaf shape bewteen parents; right, *T. spectabilis*, male parent.



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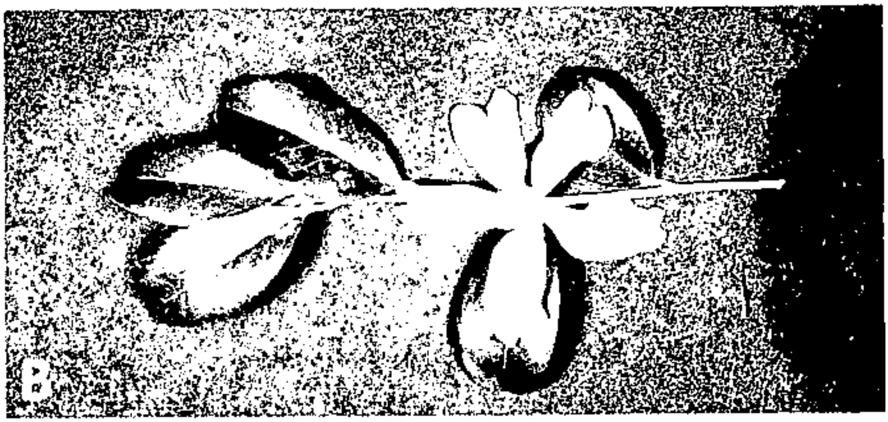

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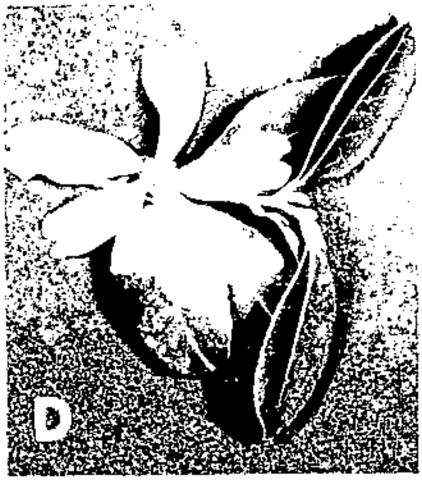

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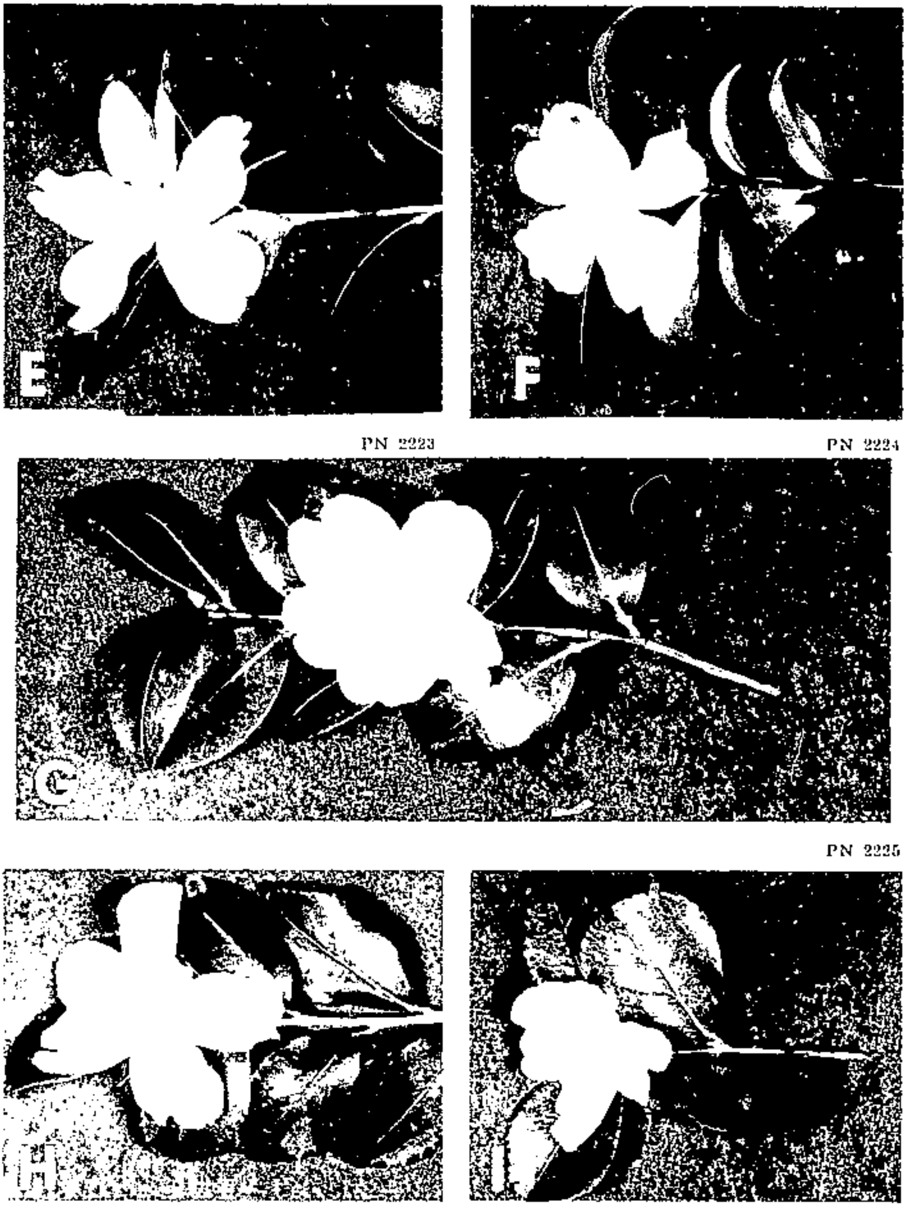

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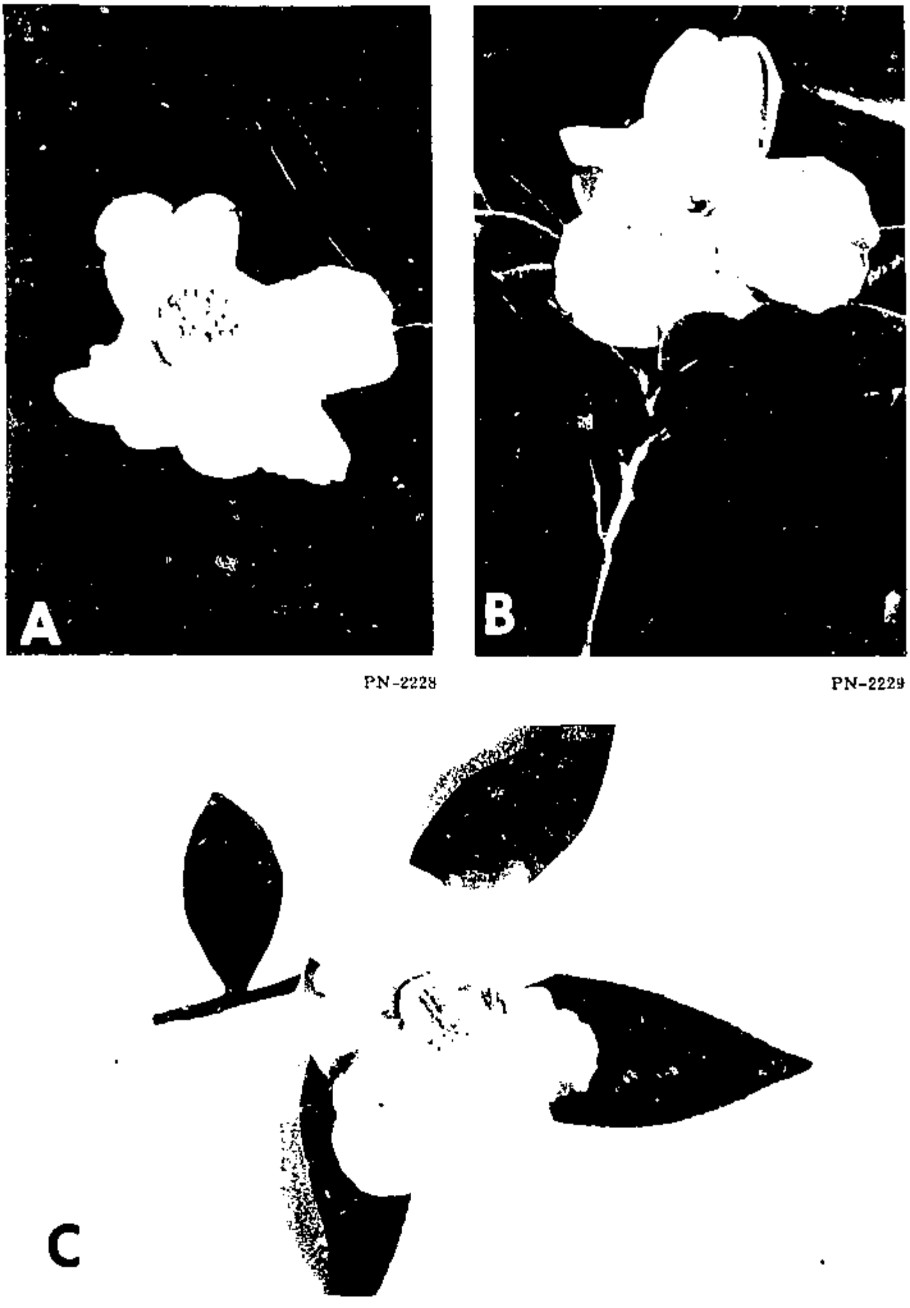
FIGURE 11. Floral characters of parents and hybrids involving intergeneric crosses; *A*, *Tutcheria virgata*, female parent, with broad petals; *B*, *Camellia miyagii*, male parent, with narrow reflexed petals; *C*, hybrid 5-62, intermediate between parents; *D*, hybrid 5-70, similar to male parent; *E*, hybrid 5-76, similar to male parent; *F*, hybrid 5-77, intermediate between parents; *G*, hybrid 5-80, similar to female; *H*, hybrid 5-81, intermediate between parents; *I*, hybrid 5-82, intermediate between parents.



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PN-2229

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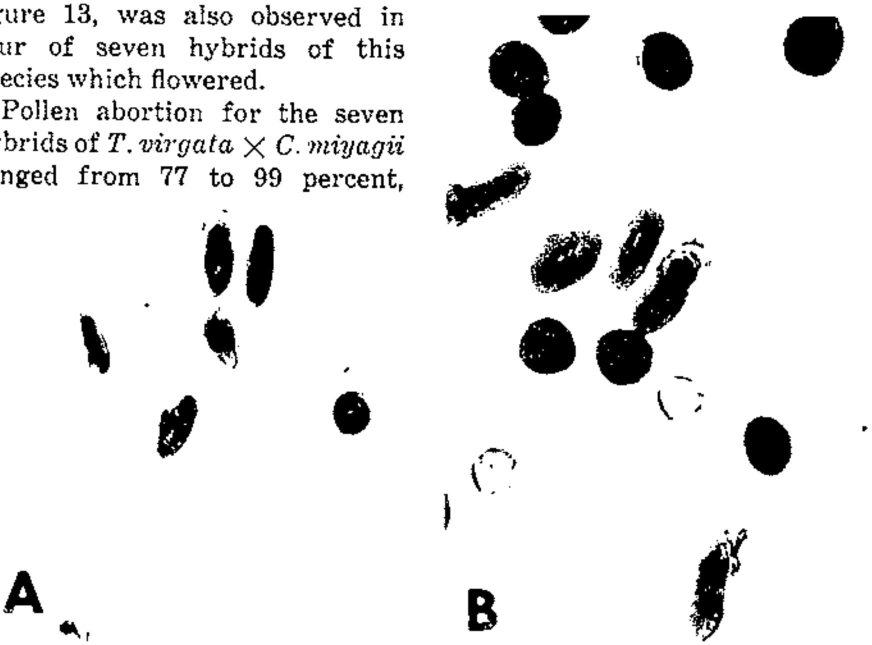
FIGURE 12.—Floral characters of parents and hybrid involving an intergeneric cross: *A*, *Camellia pitardii* var. *pitardii*, female parent; *B*, *Tutcheria spectabilis*, male parent; *C*, hybrid A-19.

### Determinations of Pollen Abortion

The parental plants of the genera related to *Camellia* showed considerable variation in percentages of aborted pollen. Counts disclosed that *F. alatamaha* had 34 percent aborted pollen, *S. ovata* had 69 percent, *T. spectabilis* had 26 percent, and *T. virgata* had 9 percent. Large pollen was found only in the two *Tutcheria* species. *T. spectabilis* had 1 percent and *T. virgata* 8 percent large pollen. In addition, approximately 4 percent of the pollen of *T. virgata* had an unusual elongate shape. This odd form of pollen, shown in figure 13, was also observed in four of seven hybrids of this species which flowered.

Pollen abortion for the seven hybrids of *T. virgata* × *C. miyagii* ranged from 77 to 99 percent, with a mean of 86 percent. Pollen abortion for the one hybrid of *C. pitardii* var. *pitardii* × *T. spectabilis* was 77 percent. Although these percentages appear to be sufficiently high to give reasonable certainty of hybridity, enough fertility is indicated to warrant the use of the intergeneric hybrids in further crosses.

Large pollen was found in five of seven hybrids of *T. virgata* × *C. miyagii*. The range was from 0 to 2.3 percent, with a mean of 0.7 percent. The one hybrid of *C. pitardii* var. *pitardii* × *T. spectabilis* did not have any large pollen.



PN–2231

PN–2232

FIGURE 13.—Pollen of *Tutcheria virgata* and hybrid, stained with acetocarmine (× 125): *A*, Pollen of *T. virgata* showing normal pollen and unusual elongate pollen; *B*, pollen of hybrid 5-70, typical of four of seven hybrids of *T. virgata* × *Camellia miyagii*, showing normal pollen, aborted pollen, and unusual elongate pollen.

## Species Compatibility Relationships

Sealy (*1958*) divided the genus *Camellia* into 12 sections of 82 species plus an unplaced group, Dubiae, of 16 species. Representative species of only six of the 12 sections plus the Dubiae group are presently grown in the United States and in the Glenn Dale collection. These six sections are: Camellia, Camelliopsis, Heterogenea, Paracamellia, Thea, and Theopsis. Species relationships in this study are based on these sections.

Hilsman (*1966*) and Savige (*1967*) have proposed that for breeding purposes the most successful interspecific crosses will be found within a section, particularly species with the same ploidy. Hybridizing results generally substantiate this assumption, but there are notable exceptions. Also, certain sections are more closely related than others, based on the cross compatibility between their representative species.

The number of valid hybrids in relation to the total number of reciprocal cross-pollinations for each parental combination afforded a rough indication of the degree of compatibility. Neither the number of representative species in each section nor the number of intrasectional or intersectional combinations was equal, so the data can only suggest relationships. In general, all hybrids had greater percentages of aborted pollen than did their parents. Pollen sterility of hybrids, a valid criterion of compatibility relations between species, was also used as a criterion in this study where possible, but many hybrids have not yet flowered. The data are presented primarily as a possible guide to plant breeders to illustrate those combinations that may be expected to produce hybrids successfully.

The largest amount of information for intrasectional hybridization was available within the section Camellia. Here, six species, *C. hongkongensis*, *C. japonica*, *C. pitardii* var. *pitardii*, *C. reticulata*, *C. rusticana*, and *C. saluenensis*, were intercrossed in a substantial number of combinations. Figure 14 summarizes the successful and unsuccessful combinations within the section. Most of the interspecific combinations, with the possible exception of those involving *C. hongkongensis*, could be made without particular difficulty. The compatibility ratio of the number of hybrids divided by the total number of cross-pollinations within the section was 9 percent.

The following crosses failed: *C. honkongensis* with *C. pitardii* var. *pitardii; C. hongkongensis* as the female parent with *C. japonica* and with *C. saluenensis; C. hongkongensis* as the male parent with *C. reticulata;* and *C. rusticana* as the female parent with *C. reticulata.*

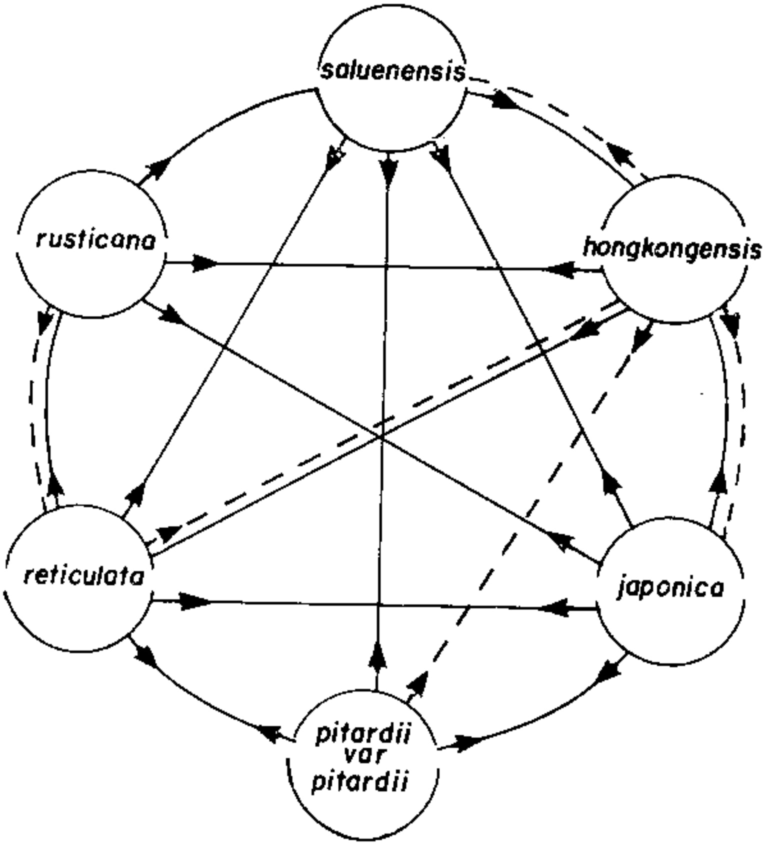


FIGURE 14.—Compatibility between species within the section Camellia: Solid lines denote successful combinations and dotted lines, unsuccessful. Arrows point in direction of male parent for each cross.

The section Paracamellia was represented by three species, *C. kissi*, *C. oleifera*, and *C. sasanqua*. All three of these species hybridized very readily with each other. The compatibility ratio of hybrids in relation to total cross-pollinations was 29 percent, the highest within any of the sections.

The section Theopsis was represented by four species, *C. fraterna*, *C. lutchuensis*, *C. rosaeflora*, and *C. tsaii*. One hybrid each was obtained from 79 *C. fraterna* × *C. lutchuensis* crosses and 50 reciprocal crosses. These hybrids were weak in growth and have not flowered. Two hybrids were obtained from 36 crosses of *C. rosaeflora* × *C. fraterna*, but no seed capsules were produced by 26 crosses of the reciprocal. Insufficient blossoms prevented testing of other combinations within this section. The compatibility ratio was 2 percent.

The unplaced group, Dubiae, of 16 species was represented by *C. hiemalis*, *C. miyagii*, and *C. tenuiflora*. *C. hiemalis* and *C. miyagii* were very readily hybridized in either direction. Their compatibility ratio was 19 percent. Insufficient blossoms prevented testing *C. tenuiflora* with either of the other species.

Compatibility between species of different subgeneric sections is summarized in figure 15. As shown in the figure, most intersectional combinations resulted in at least some hybrids, but successful crosses were much more easily made between certain sections than between others. The width of the solid lines between sections is proportionate to the compatibility ratio. The greater the width, the greater the compatibility between sections. Broken lines denote unsuccessful combinations.

Species within section Camellia produced hybrids with some representative species of all other sections, including Dubiae. Sec-

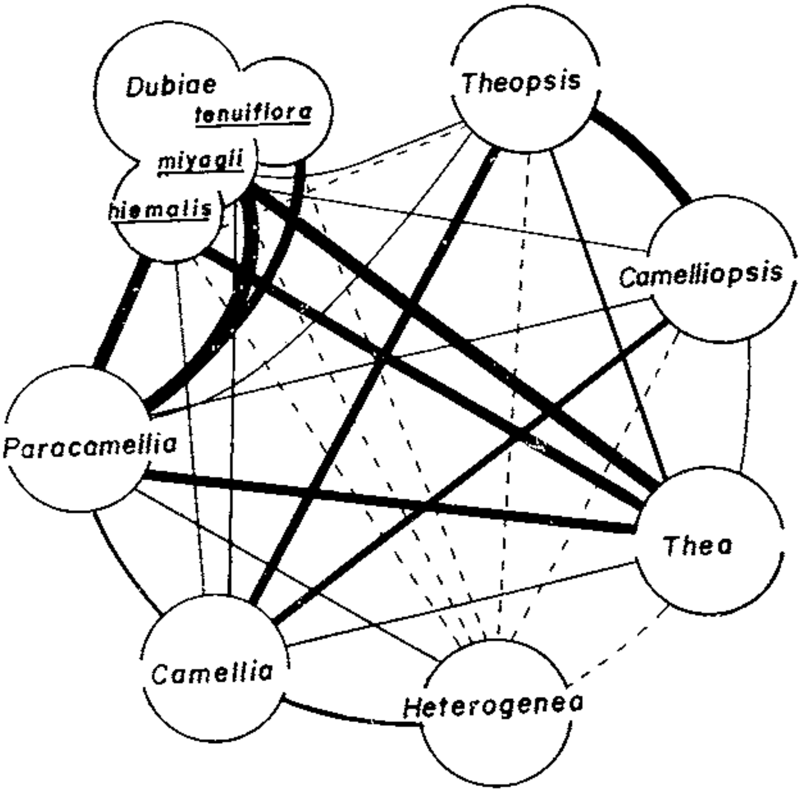


FIGURE 15.—Compatibility between species of different subgeneric sections: The width of the solid lines between sections denotes the relative ease of hybridization and dotted lines denote unsuccessful combinations.

tion Camellia hybridized more easily with Camelliopsis, Heterogenea, and Theopsis than with any other section. However, hybrids resulting from crosses with Heterogenea and Theopsis were highly sterile, mostly with 80 percent or more abortive pollen. None of the hybrids involving Camelliopsis have flowered yet.

Camelliopsis species produced hybrids with some representative species of all sections except Heterogenea. Camelliopsis hybridized more easily with Theopsis and with Camellia than with species of any other section.

In addition to producing hybrids with some representative species of section Camellia, *C. granthamiana* of section Heterogenea produced two hybrids with *C. sasanqua* of Paracamellia, but none with any other section.

Paracamellia species produced hybrids with some representative species of all other sections. Paracamellia hybridized with *C. hiemalis* and *C. miyagii* of Dubiae as easily as when intrasectional crosses were made within Paracamellia. Also, Paracamellia hybridized more easily with Thea than with any other section and only with considerable difficulty with Camelliopsis, Heterogenea, and Theopsis.

Thea species produced hybrids with some representative species of all other sections except Heterogenea. Thea hybridized more easily with Paracamellia and with *C. hiemalis* and *C. miyagii* of Dubiae than with any other section.

Theopsis species hybridized more easily with Camellia and Camelliopsis than with any other section. Successful crosses with Paracamellia and with *C. miyagii* of Dubiae were difficult to achieve, and crosses with Heterogenea and with *C. hiemalis* of Dubiae failed.

## Chromosome Numbers

### Chromosome Numbers of Parents

Chromosome numbers for most of the species used in this study have already been reported by the following: Darlington and Janaki Ammal (*1945*), Darlington and Wylie (*1961*), Janki Ammal (*1952*), Longley and Tourje (*1959, 1960*), Morinaga and others (*1929*), Morinaga and Fukushima (*1931*), Patterson, Longley, and Robertson (*1950*), and Simura (*1935*). However, it was necessary to establish the chromosome numbers of the particular clones used as parents. The importance of establishing these numbers is illustrated by Longley and Tourje (*1959, 1960*) who listed chromosome numbers for 59 *C. japonica* varieties; 47 were diploids and 12 were triploids. Thus, one must be certain of the chromosome number of each parent before determining numbers in the hybrids.

Table 7 gives determinations of root-tip chromosome numbers of *Camellia* species and species of related genera used as parents;

TABLE 7.—*Determinations of root-tip chromosome numbers of* Camellia *species and species of related genera used as parents*

| P.I. or B No.[1] | Scientific name | Root-tip chromosomes |
|---|---|---|
| | | *Number* |
| 162476 | *C. fraterna* | 90 |
| 251534 | *C. granthamiana* | 60 |
| B56995 | *C. hiemalis* 'Shishi-Gashira' | 90 |
| B56996 | *C. hiemalis* 'Bill Wylam' | 90 |
| 229973 | *C. hongkongensis* | 30 |
| 226109 | *C. japonica* No. 6 | 30 |
| 227063 | *C. japonica* 'Bon-Shirotama' | 30 |
| 228024 | *C. japonica* 'Tsubaki' | 30 |
| 230278 | *C. japonica* | 30 |
| 231686 | *C. japonica* 'Hasumi-Shiro' | 30 |
| 231687 | *C. japonica* 'Komyotai' | 30 |
| 231689 | *C. japonica* 'Moshio' | 30 |
| 231690 | *C. japonica* | 30 |
| 231694 | *C. japonica* 'Utamakura' | 30 |
| 231695 | *C. japonica* 'Yuki botan' | 30 |
| 231858 | *C. japonica* 'Beni botan' | 30 |
| 231859 | *C. japonica* 'Kanyo tai' | 30 |
| 238725 | *C. japonica* 'Saudade de Martins Blanco' | 30 |
| 274530 | *C. japonica* No. 825 | 30 |
| 274797 | *C. japonica* No. 870 | 30 |
| 274799 | *C. japonica* No. 872 | 30 |
| 275054 | *C. japonica* No. 913 | 30 |
| 275512 | *C. japonica* D | 30 |
| 309001 | *C. japonica* 'Le Lys' | 30 |
| 319283 | *C. japonica* K–20 | 30 |
| 252062 | *C. kissi* | 30 |
| 252064 | do | 30 |
| 226756 | *C. lutchuensis* | 30 |
| 226704 | *C. miyagii* | 90 |
| 231057 | do | 90 |

See footnote at end of table.

TABLE 7.—*Determinations of root-tip chromosome numbers of* Camellia *species and species of related genera used as parents*—Continued

| P.I. or B No.[1] | Scientific name | Root-tip chromosomes |
|---|---|---|
| | | *Number* |
| 162561 | *C. oleifera* | 90 |
| 235500 | do | 90 |
| B58296 | *C. pitardii* var. *pitardii* | 30 |
| B58619 | *C. rosaeflora* | 90 |
| 228187 | *C. rusticana* 'Yoshida' | 30 |
| 228188 | *C. rusticana* 'Hatano' | 30 |
| 228190 | *C. rusticana* 'Koshiji' | 30 |
| 233642 | *C. rusticana* B White plena | 30 |
| 243862 | *C. saluenensis* No. 6093 | 30 |
| 227624 | *C. sasanqua* 'Kokinran' | 90 |
| 228025 | *C. sasanqua* 'Sazanka' | 90 |
| 235568 | *C. sasanqua* | 90 |
| 237854 | *C. sasanqua* No. 791 | 90 |
| 319284 | *C. sasanqua* | 90 |
| 319285 | *C. sasanqua* 'Onishiki' | 90 |
| 235570 | *C. sinensis* 'Tama-midori' | 30 |
| 235572 | *C. sinensis* Y–2 | 30 |
| 235573 | *C. sinensis* Z–1 | 30 |
| 304404 | *C. sinensis* No. 1 | 30 |
| 304405 | *C. sinensis* No. 2 | 30 |
| 316471 | *C. sinensis* 'Benji-Fuji' | 30 |
| 316472 | *C. sinensis* 'Beni-Homare' | 30 |
| 316473 | *C. sinensis* 'Makinowara Wase' | 30 |
| 316476 | *C. sinensis* 'Yamatomidori' | 30 |
| 316477 | *C. sinensis* | 45 |
| 316478 | do | 60 |
| 230368 | *Tutcheria spectabilis* | 30 |
| 229881 | *T. virgata* | 75 |

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[1] P.I. refers to the accession number assigned to foreign introductions by the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture. B numbers are code numbers assigned to importations under postentry quarantine permit by the U.S. Plant Introduction Station, Glenn Dale, Md.

table 8 gives the chromosome numbers of parents not directly determined but recorded from the literature. All of the *C. japonica* clones were diploids. Although chromosome counts were not made of clones excluded as parents because of high percentages of pollen abortion, quite probably at least some of these clones were triploids. Among the *C. sinensis* clones, all were diploids except for one triploid and one tetraploid. No previous chromosome counts were found in the literature for the diploid species *C. lutchuensis* and the hexaploid species C. *miyagii* and *C. rosaeflora*. Figure 16 shows the chromosomal complements of these three species.

*Tutcheria spectabilis* and *T. virgata* are both recorded by Longley and Tourje (*1959*) as diploids. However, neither genus nor species was fully determined for *T. virgata*. In the current study, the diploid chromosome number was confirmed for *T. spectabilis*, but *T. virgata* was found to be pentaploid with 75 chromosomes. The authenticity of the Glenn Dale specimen was established through Takasi Tuyama, Department of Biology, Ochanomizu University, Tokyo, Japan. Figure 17 shows the chromosomal complements of *T. spectabilis* and *T. virgata*.

TABLE 8.—*Chromosome numbers of* Camellia *species and species of related genera used as parents*

| Scientific Name | Root-tip chromosomes | Source [1] |
|---|---|---|
| | *Number* | |
| *C. japonica* 'Ville de Nantes' | 30 | Patterson, Longley, and Robertson (*1950*) |
| *C. reticulata* 'Crimson Robe' | 90 | Longley and Tourje (*1959*) |
| *C. reticulata* 'Great Shot Silk' | 90 | Longley and Tourje (*1959*) |
| *C. reticulata* 'Chang's Temple' | 90 | Longley and Tourje (*1959*) |
| *C. reticulata* 'Large Cornellian' | 90 | Longley and Tourje (*1959*) |
| *C. reticulata* 'Lion's Head' | 90 | Longley and Tourje (*1959*) |
| *C. sasanqua* 'Narumi-gata' | 75 | Longley and Tourje (*1960*) |
| *C. taliensis* | 30 | Janaki Ammal (*1952*) |
| *C. tenuiflora* | 60 | Longley and Tourje (*1960*) |
| *Franklinia alatamaha* | 36 | Santamour (*1963*) |
| *Stewartia ovata* | 30 | Santamour (*1963*) |

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[1] Chromosome numbers are not directly determined in this study; recorded from literature.

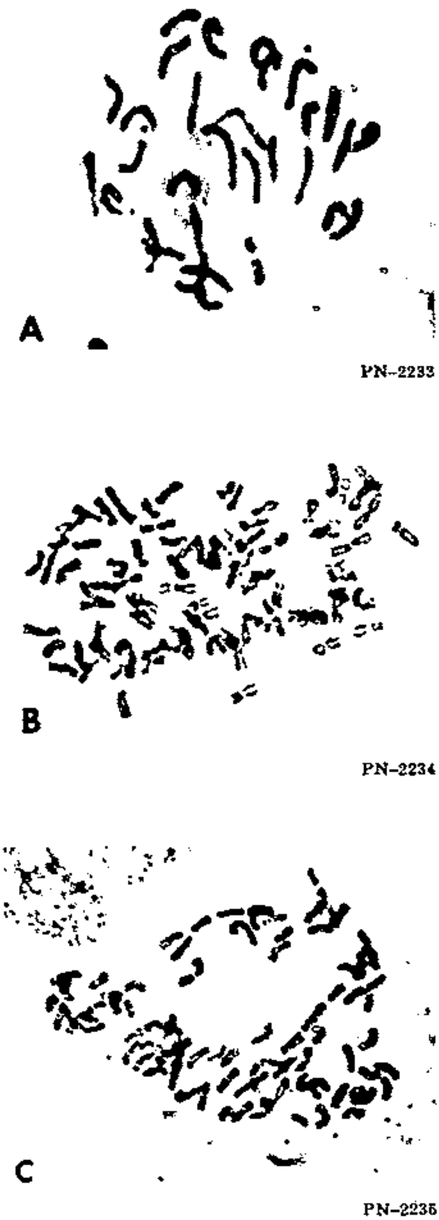


FIGURE 16.—Root-tip chromosomes of *C. lutchuensis*, *C. miyagii*, and *C. rosaeflora* (× 2,300): *A*, *C. lutchuensis*, 2x=30; *B*, *C. miyagii*, 6x=90; *C*, *C. rosaeflora*, 6x= 90.

FIGURE 17.—Root-tip chromosomes of *Tutcheria spectabilis* and *T. virgata* (× 2,300): *A*, *T. spectabilis*, 2x =30; *B*, *T. virgata*, 5x=75.

## Chromosome Numbers of Interspecific Hybrids

Table 9 gives determinations of root-tip chromosome numbers of the 88 interspecific hybrids of *Camellia* that produced root tips suitable for study. Hybrids resulting from crosses between diploid species were in all but one case also diploid. Figure 18 shows the chromosomal complements of representative diploid hybrids, including *C. japonica* × *C. honkongensis*, *C. japonica* × *C. lutchuensis*, *C. japonica* × *C. saluenensis*, *C. ja-*

TABLE 9.—*Determinations of root-tip chromosome numbers of 88 interspecific hybrids of* Camellia

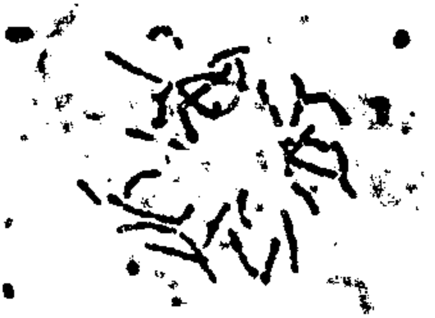
| Crosses | Hybrids | Root-tip chromosomes |
|---|---|---|
| | *Number* | *Number* |
| Diploid × diplid (30 × 30): | | |
| *C. japonica* × *C. hongkongensis* | 4 | 30 |
| *C. japonica* × *C. kissi* | 1 | 30 |
| *C. japonica* × *C. lutchuensis* | 9 | 30 |
| *C. japonica* × *C. lutchuensis* | 1 | 28 |
| *C. japonica* × *C. pitardii* var. *pitardii* | 1 | 30 |
| Reciprocal | 1 | 30 |
| *C. japonica* × *C. rusticana* | 2 | 30 |
| Reciprocal | 1 | 30 |
| *C. japonica* × *C. saluenensis* | 1 | 30 |
| Reciprocal | 1 | 30 |
| *C. japonica* × *C. sinensis* | 2 | 30 |
| *C. japonica* × *C. taliensis* | 1 | 30 |
| *C. kissi* × *C. rusticana* | 1 | 30 |
| Reciprocal | 1 | 30 |
| *C. pitardii* var. *pitardii* × *C. saluenensis* | 1 | 30 |
| Reciprocal | 1 | 30 |
| *C. rusticana* × *C. hongkongensis* | 1 | 30 |
| *C. rusticana* × *C. lutchuensis* | 6 | 30 |
| Diploid × tetraploid (30 × 60): | | |
| *C. japonica* × *C. granthamiana* | 2 | 45 |
| *C. pitardii* var. *pitardii* × *C. granthamiana* | 1 | 45 |
| *C. pitardii* var. *pitardii* × *C. granthamiana* | 1 | 60 |
| *C. saluenensis* × *C. granthamiana* | 1 | 45 |
| Diploid × hexaploid (30 × 90) | | |
| *C. japonica* × *C. fraterna* | 5 | 60 |
| *C. japonica* × *C. fraterna* | 1 | 56 |
| *C. japonica* × *C. fraterna* | 1 | 59 |
| *C. japonica* × *C. hiemalis* | 1 | 60 |
| *C. japonica* × *C. miyagii* | 1 | 60 |
| *C. japonica* × *C. reticulata* | 2 | 60 |
| *C. japonica* × *C. rosaeflora* | 1 | 60 |
| *C. pitardii* var. *pitardii* × *C. fraterna* | 1 | 60 |
| *C. pitardii* var. *pitardii* × *C. reticulata* | 1 | 60 |
| *C. rusticana* × *C. fraterna* | 1 | 60 |
| *C. saluenensis* × *C. fraterna* | 1 | 60 |
| *C. saluenensis* × *C. reticulata* | 2 | 60 |

TABLE 9.—*Determinations of root-tip chromosome numbers of 88 interspecific hybrids of* Camellia—Continued

| Crosses | Hybrids | Root-tip chromosomes |
|---|---|---|
| | *Number* | *Number* |
| Hexaploid × diploid (90 × 30): | | |
| *C. fraterna* × *C. japonica* | 1 | 60 |
| *C. reticulata* × *C. japonica* | 3 | 60 |
| *C. reticulata* × *C. japonica* | 2 | 75 |
| *C. reticulata* × *C. pitardii* var. *pitardii* | 1 | 60 |
| *C. reticulata* × *C. rusticana* | 1 | 60 |
| *C. reticulata* × *C. saluenensis* | 1 | 60 |
| *C. sasanqua* × *C. japonica* | 2 | 60 |
| *C. sasanqua* × *C. tenuiflora* | 1 | 60 |
| Pentaploid × tetraploid (75 × 60): | | |
| *C. sasanqua* 'Narumi-gata' × *C. granthamiana* | 1 | 60 |
| Pentaploid × hexaploid (75 × 90): | | |
| *C. sasanqua* 'Narumi-gata' × *C. reticulata* | 1 | 90 |
| Hexaploid × hexaploid (90 × 90): | | |
| *C. fraterna* × *C. reticulata* | 1 | 90 |
| Reciprocal | 2 | 90 |
| *C. oleifera* × *C. hiemalis* | 1 | 90 |
| *C. oleifera* × *C. miyagii* | 2 | 90 |
| *C. reticulata* × *C. sasanqua* | 1 | 90 |
| *C. sasanqua* × *C. hiemalis* | 1 | 90 |
| *C. sasanqua* × *C. miyagii* | 3 | 90 |
| *C. sasanqua* × *C. miyagii* | 1 | 86 |
| *C. sasanqua* × *C. oleifera* | 1 | 90 |
| *C. sasanqua* × *C. reticulata* | 2 | 90 |

*ponica* × *C. taliensis*, *C. kissi* × *C* *rusticana*, *C. rusticana* × *C. lutchuensis*, *C. saluenensis* × *C. japonica*, and *C. pitardii* var. *pitardii* × *C. saluenensis*. One aneuploid hybrid with 28 chromosomes occurred from a cross of *C. japonica* × *C. lutchuensis*. This plant was very weak in growth and has subsequently died. Figure 19 shows the chromosomal complement of this aneuploid hybrid.

Hybrids resulting from crosses between diploid female parents and tetraploid male parents resulted in triploids in four out of five hybrids studied. One of the two hybrids resulting from crosses between *C. pitardii* var. *pitardii* (2x=30) × *C. granthamiana* (4x=60) was tetraploid. This hybrid was probably the result of the functioning of an unreduced egg cell from *C. pitardii*



A

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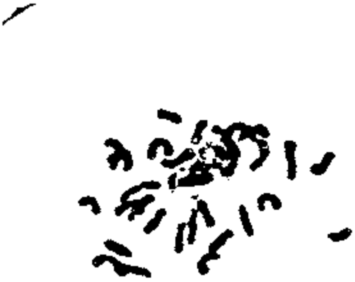
B

PN-2239

C

PN-2240



D

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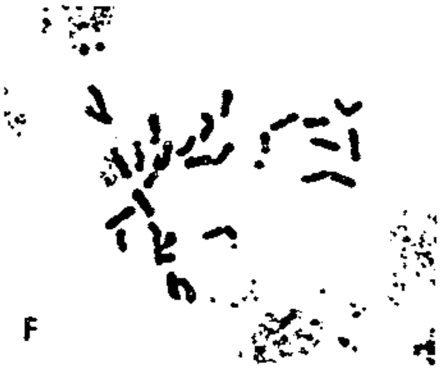
E

PN-2242



F

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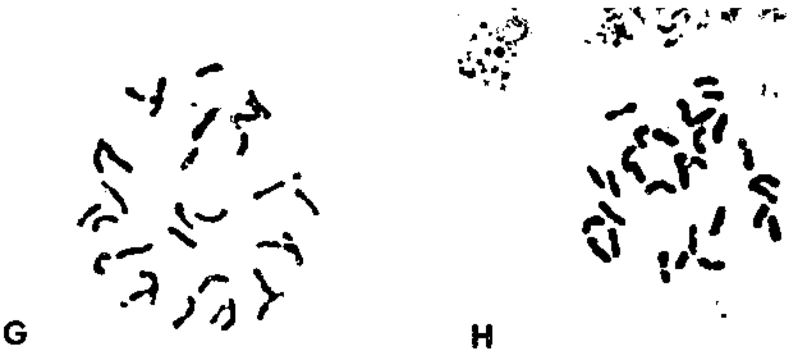


PN-2244 PN-2245

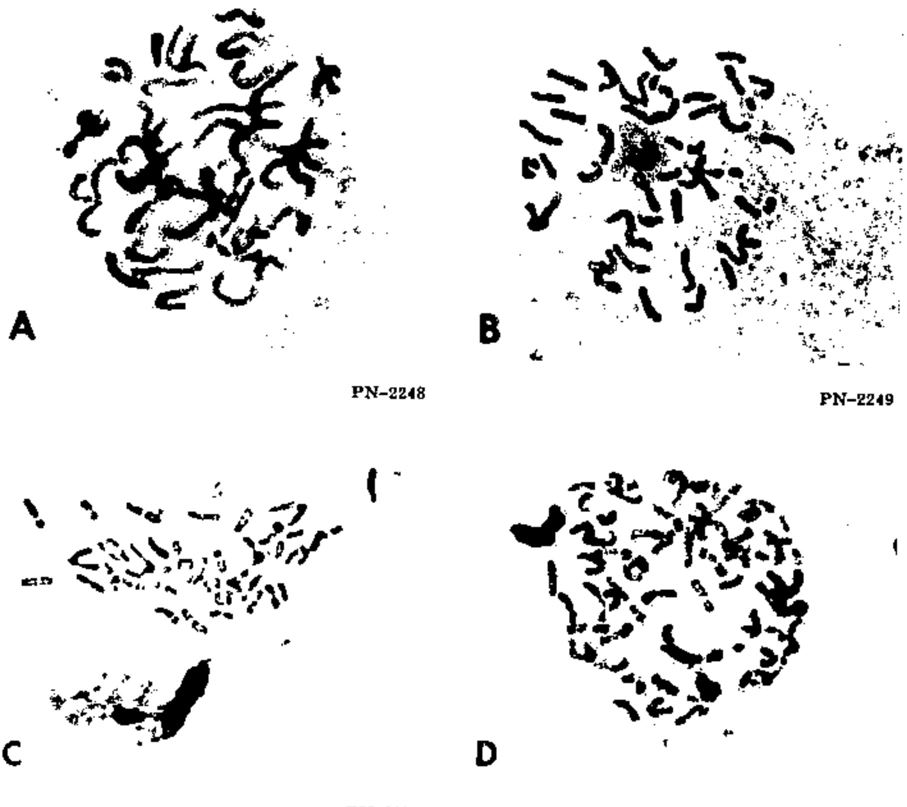
FIGURE 18.—Root-tip chromosomes of interspecific hybrids from crosses of diploid parents (× 2,300); *A*, Hybrid 5-37 of *C. japonica* × *C. hongkongensis*, 2x=30; *B*, hybrid 3-32 of *C. japonica* × *C. lutchuensis*, 2x=30; *C*, hybrid 5-1 of *C. japonica* × *C. saluenensis*, 2x=30; *D*, hybrid P-37 of *C. japonica* × *C. taliensis*, 2x=30; *E*, hybrid 5-69 of *C. kissi* × *C. rusticana*, 2x=30; *F*, hybrid 1-1 of *C. rusticana* × *C. lutchuensis*, 2x=30; *G*, hybrid 5-29 of *C. saluenensis* × *C. japonica*, 2x=30; *H*, hybrid P-42 of *C. pitardii* var. *pitardii* × *C. saluenensis*, 2x=30.

PN-2246 PN-2247

FIGURE 19.—Root-tip chromosomes of aneuploid hybrid of *C. japonica* × *C. lutchuensis* with 28 chromosomes (× 2,300): *A* and *B*, Two division figures from the aneuploid hybrid.

var. *pitardii*. Figure 20, *A*, *B*, and *C* show the chromosomal complements of the triploid hybrids resulting from crosses between *C. japonica* × *C. granthamiana*, *C. saluenensis* × *C. granthamiana*, and *C. pitardii* var. *pitardii* × *C. granthamiana*, and figure 20, *D* shows the complement of the tetraploid hybrid resulting from *C. pitardii* var. *pitardii* × *C. granthamiana*.

All but two of 18 hybrids studied from crosses between diploid female parents and hexaploid male parents resulted in tetraploid hybrids. Figure 21 shows the chromosomal complements of the tetraploid hybrids resulting from crosses between *C. japonica* × *C. fraterna*, *C. japonica* × *C. reticulata*, *C. japonica* × *C. rosaeflora*, *C. pitardii* var. *pitardii* × *C. fraterna*, *C. rusticana* ×



PN-2248 PN-2249

PN-2250 PN-2251

FIGURE 20.—Root-tip chromosomes of interspecific hybrids from crosses of diploid female parents and tetraploid male parents (× 2,300): *A*, Hybrid 7-96 of *C. japonica* × *C. granthamiana*, 3x=45; *B*, hybrid B-2 of *C. saluenensis* × *C. granthamiana*, 3x=45; *C*, hybrid P-56 of *C. pitardii* var. *pitardii* × *C. granthamiana*, 3x=45; *D*, hybrid B-6 of *C. pitardii* var. *pitardii* × *C. granthamiana*, 4x=60.

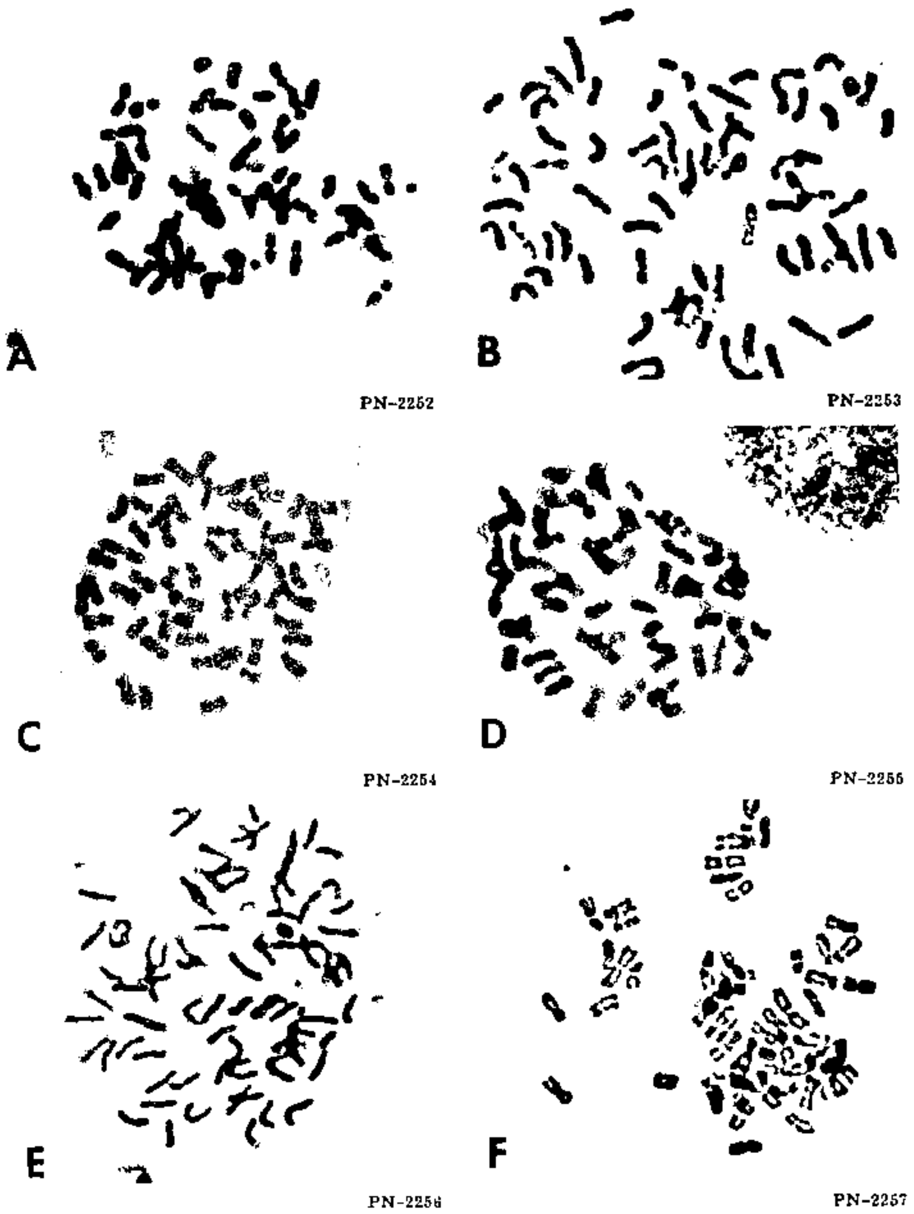


FIGURE 21.—Root-tip chromosomes of interspecific hybrids from crosses of diploid female parents and hexaploid male parents (× 2,300): *A*, Hybrid 4-4 of *C. japonica* × *C. fraterna*, 4x=60; *B*, hybrid P-13 of *C. japonica* × *C. reticulata*, 4x=60; *C*, hybrid P-46 of *C. japonica* × *C. rosaeflora*, 4x=60; *D*, hybrid 7-159 of *C. pitardii var. pitardii* × *C. fraterna*, 4x=60; *E.*, hybrid 3-2 of *C. rusticana* × *C. fraterna*, 4x=60; *F*, hybrid P-5 of *C. saluenensis* × *C. reticulata*, 4x=60.

*C. fraterna*, and *C. saluenensis* × *C. reticulata*. Two hybrids with aneuploid chromosome counts were observed, one with 56 chromosomes, the other with 59. Figure 22 shows the chromosomal complements of these two aneuploid hybrids.

Ten hybrids from crosses between hexaploid female and diploid male parents were tetraploid, whereas two hybrids were pentaploid. Tetraploid hybrids were obtained from *C. fraterna* × *C. japonica*, *C. reticulata* × *C. japonica*, *C. reticulata* × *C. pitardii* var. *pitardii*, *C. reticulata* × *C. rusticana*, *C. reticulata* × *C. saluenensis*, *C. sasanqua* × *C. japonica*, and *C. sasanqua* × *C. tenuiflora*. The two pentaploids were obtained from *C. reticulata* × *C. japonica*. If the somatic numbers of both parents were exactly halved during meiosis, only tetraploid hybrids would result. A possible explanation for the occurrence of the two pentaploids is the

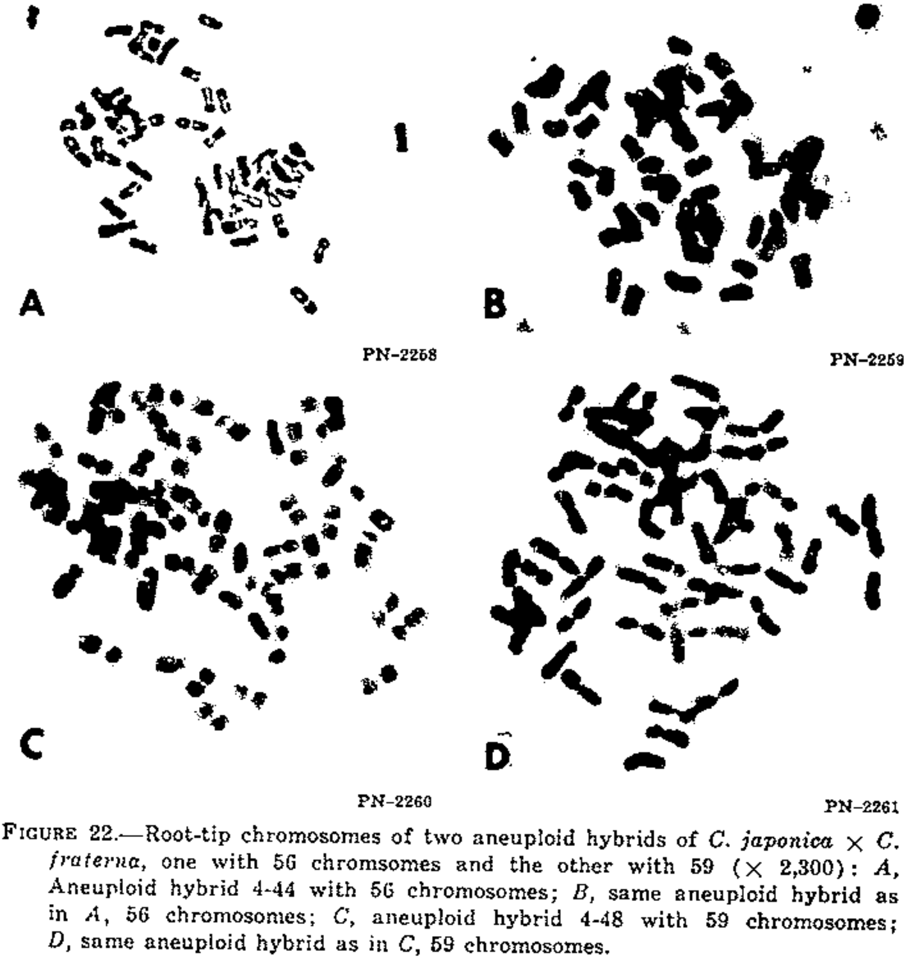


FIGURE 22.—Root-tip chromosomes of two aneuploid hybrids of *C. japonica* × *C. fraterna*, one with 56 chromsomes and the other with 59 (× 2,300): *A*, Aneuploid hybrid 4-44 with 56 chromosomes; *B*, same aneuploid hybrid as in *A*, 56 chromosomes; *C*, aneuploid hybrid 4-48 with 59 chromosomes; *D*, same aneuploid hybrid as in *C*, 59 chromosomes.

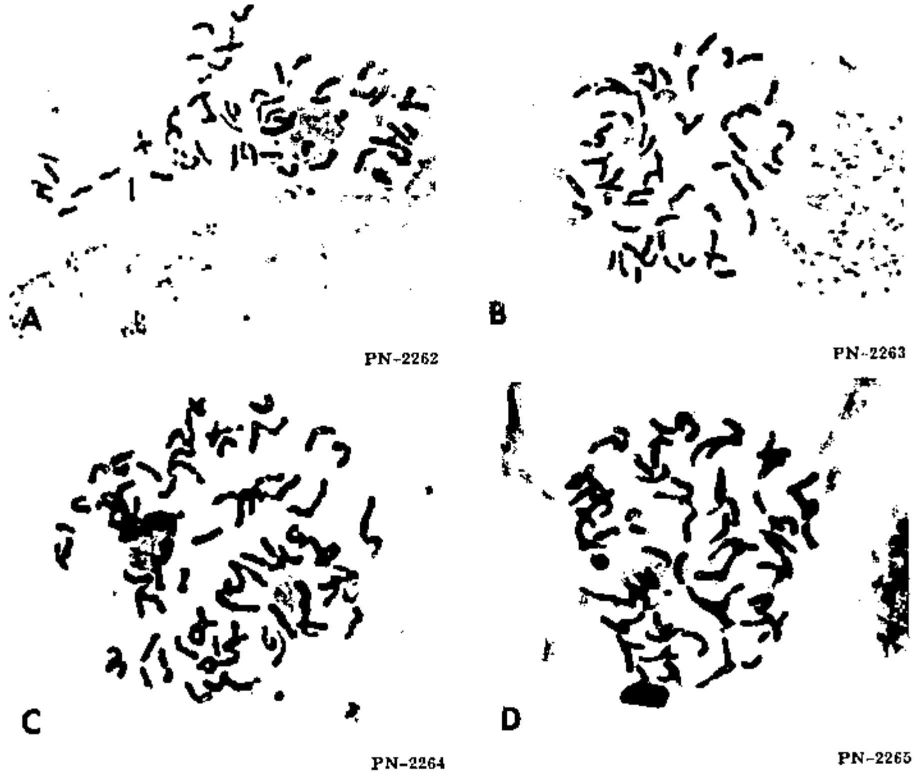


FIGURE 23.—Root-tip chromosomes of interspecific hybrids from crosses of hexaploid female parents and diploid male parents (× 2,300): *A*, Hybrid 5-58 of *C. reticulata* × *C. saluenensis*, 4x=60; *B*, hybrid A-6 of *C. reticulata* × *C. japonica*, 4x=60; *C*, hybrid A-8 of *C. reticulata* × *C. japonica*, 5x=75; *D*, hybrid A-14 of *C. reticulata* × *C. japonica*, 5x=75.

fertilization of the hexaploid female parent with unreduced pollen from the diploid parent. Figure 23 shows the chromosomal complements of tetraploid and pentaploid hybrids resulting from hexaploid × diploid crosses. Thus, crosses between *C. reticulata* × *C. japonica* can produce either tetraploid or pentaploid hybrids.

'Narumi-gata,' a pentaploid variety of *C. sasanqua*, produced hybrids when used as the female parent. However, the chromosome numbers of its hybrids seem unpredictable. A hybrid, A-24, resulting from *C. sasanqua* 'Narumi-gata' (5x=75) × *C. granthamiana* (4x=60) was tetraploid. The morphological characters of this hybrid were intermediate. It is generally difficult to assess accurately the contribution of each parent to the hybrid in crosses involving polyploid species without the aid of genetical or cytological markers. However, 'Narumi-gata' may have produced an egg with 30 chromosomes, which united with a sperm carrying 30 chromosomes from *C. granthamiana*. A hybrid of *C. sasanqua* 'Narumi-gata' × *C. reticulata* (6x=90) was hexaploid. In this case, 'Narumi-gata' may have produced an egg cell with 45 chromosomes. Figure 24 shows the chromosomal complements of both these hybrids.

Among 15 hybrids studied from crosses between two hexaploid species, all but one were hexaploids. Figure 25, *A*, *B*, *C*, and *D* show the chromosomal complements of the hybrids resulting from crosses between *C. sasanqua* × *C. miyagii*, *C. oleifera* × *C. miyagii*, *C. reticulata* × *C. fraterna*, and *C. sasanqua* × *C. oleifera*. In addition, one aneuploid hybrid with 86 chromosomes was found among the four hybrids of *C. sasanqua* × *C. miyagii*. Figure 25, *E* and *F* show the chromosomal complements of this aneuploid hybrid.

## Chromosome Numbers of Intergeneric Hybrids

Table 10 gives determinations of root-tip chromosome numbers of intergeneric hybrids. Among the hybrids of *Tutcheria virgata* (5x=75) × *Camellia miyagii* (6x=90), two hybrids each were found with 75 and 90 chromosomes, respectively, and one hybrid each with 80, 82, and 105 chromosomes. Figure 26 shows the chromosomal complements of these intergeneric hybrids. Little apparent difference was noted in general vigor and growth between the euploids and aneuploids of this cross.

Three hybrids of *T. virgata* (5x=75) × *C. granthamiana* (4x=60) had 75 chromosomes. Figure 27, *A*, *B*, and *C* show the chromosomal complements of these three hybrids. The chromosome numbers of these hybrids might suggest that they resulted from accidental selfing or apomictic development. However, the hy-

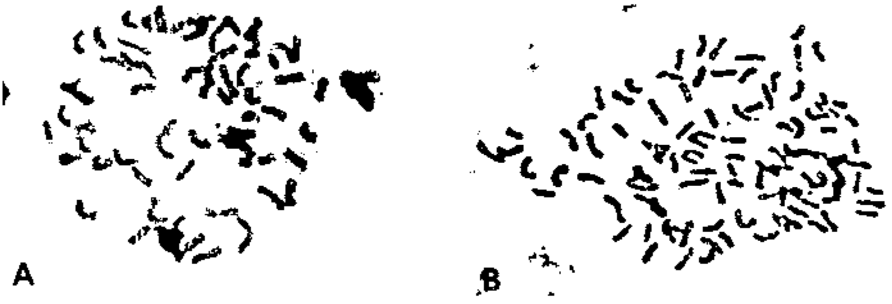


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FIGURE 24.—Root-tip chromosomes of interspecific hybrids from crosses of pentaploid female parent *C. sasanqua* 'Narumi-gata' with tetraploid and hexaploid male parents (× 2,300): *A*, Hybrid A-24 of *C. sasanqua* 'Narumi-gata' (5x=75) × *C. granthamiana* (4x=60), 4x=60; *B*, hybrid A-22 of *C. sasanqua* 'Narumi-gata' (5x=75) × *C. reticulata* (6x=90), 6x=90.

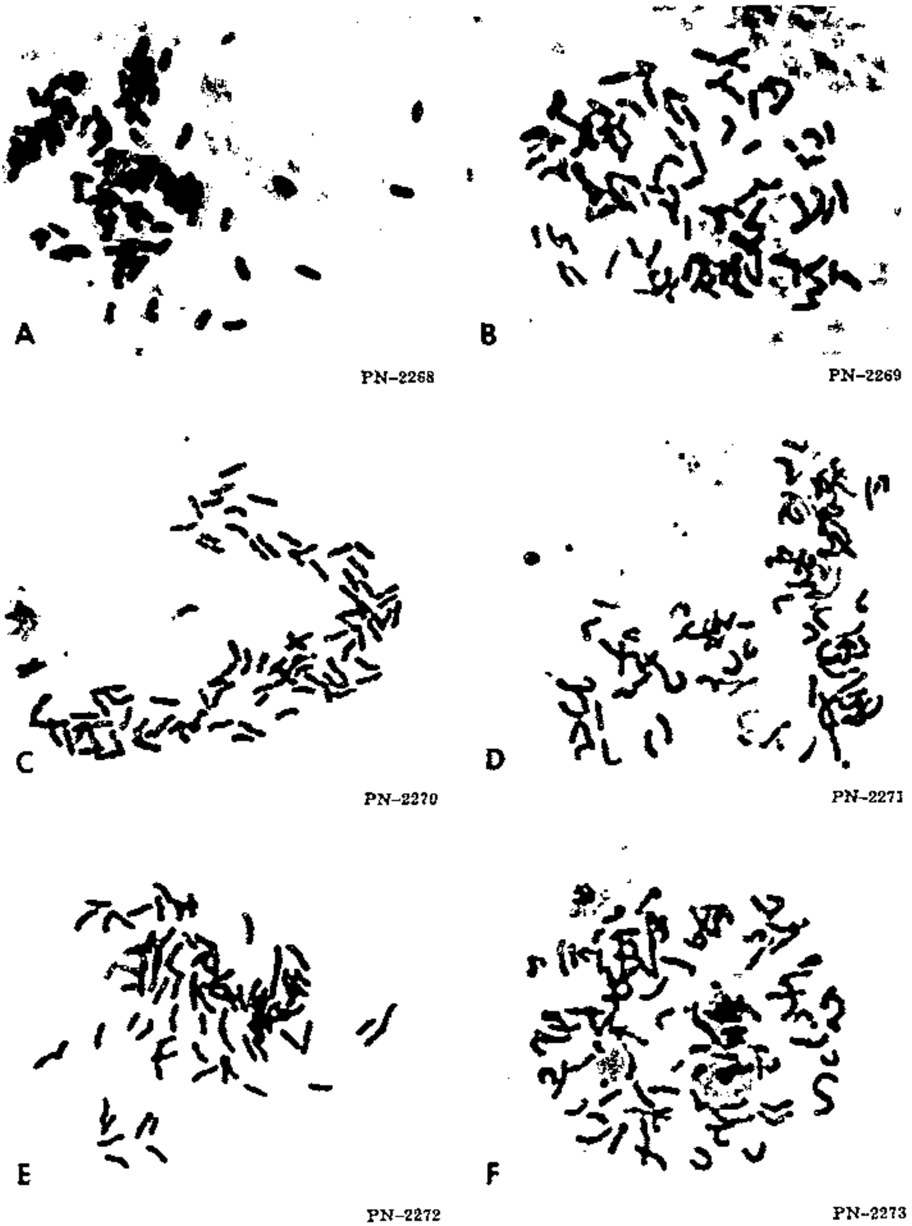
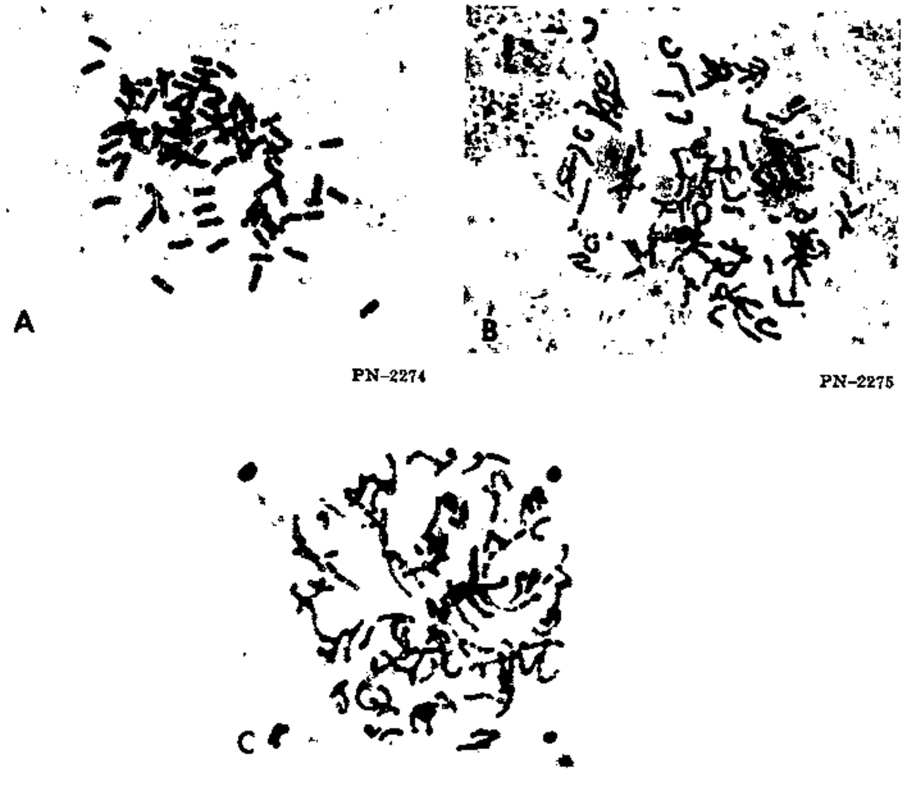


FIGURE 25.—Root-tip chromosomes of interspecific hybrids from crosses of hexaploid parents (× 2,300): *A*, Hybrid 5-52 of *C. sasanqua* × *C. miyagii*, 6x=90; *B*, hybrid 5-61 of *C. oleifera* × *C. miyagii*, 6x=90; *C*, hybrid 2-5 of *C. reticulata* × *C. fraterna*, 6x=90; *D*, hybrid B-1 of *C. sasanqua* × *C. oleifera*, 6x=90; *E*, aneuploid hybrid 5-55 of *C. sasanqua* × *C. miyagii* with 86 chromosomes; *F*, same aneuploid hybrid as in *E*, 86 chromosomes.

TABLE 10.—*Determinations of root-tip chromosome numbers of intergeneric hybrids of* Camellia *and* Tutcheria

| Crosses | Hybrids | Root-tip chromosomes |
|---|---|---|
| | *Number* | *Number* |
| Diploid × diploid (30 × 30): | | |
| *C. pilardii* var. *pilardii* × *T. spectabilis* | 1 | 30 |
| Pentaploid × tetraploid (75 × 60): | | |
| *T. virgata* × *C. granthamiana* | 3 | 75 |
| Pentaploid × hexaploid (75 × 90): | | |
| *T. virgata* × *C. miyagii* | 2 | 75 |
| Do | 1 | 80 |
| Do | 1 | 82 |
| Do | 2 | 90 |
| Do | 1 | 105 |



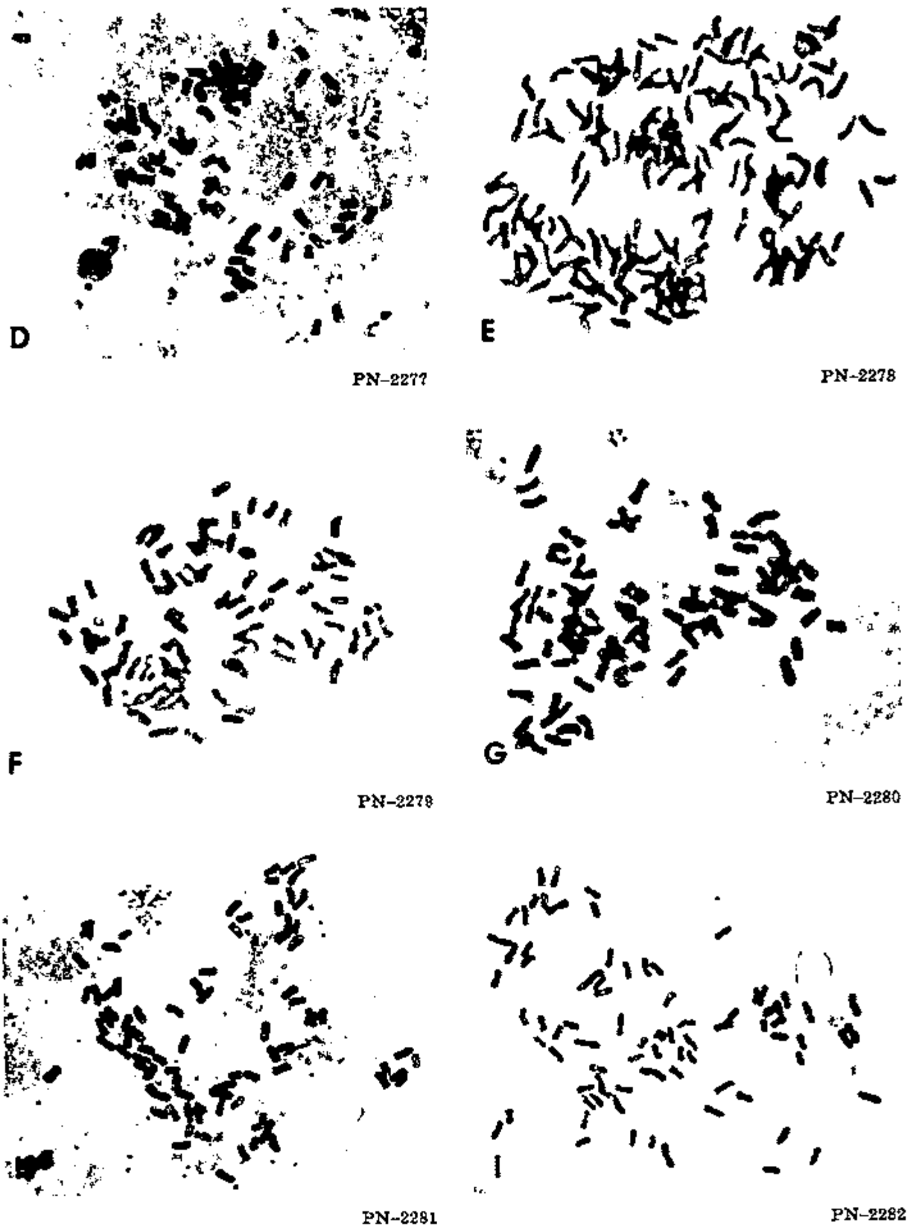


FIGURE 26.—Root-tip chromosomes of intergeneric hybrids of *Tutcheria virgata* × *Camellia miyagii* (× 2,300): *A*, Hybrid 5-62, 5x=75; *B*, hybrid 5-77, 5x=75; *C*, hybrid 5-70, 6x=90; *D*, hybrid 5-81, 6x=90; *E*, hybrid 5-80, 7x=105; *F*, aneuploid hybrid 5-76 with 80 chromosomes; *G*, same aneuploid hybrid as *F*, 80 chromosomes; *H*, aneuploid hybrid 5-82 with 82 chromosomes; *I*, same aneuploid hybrid as *H*, 82 chromosomes.

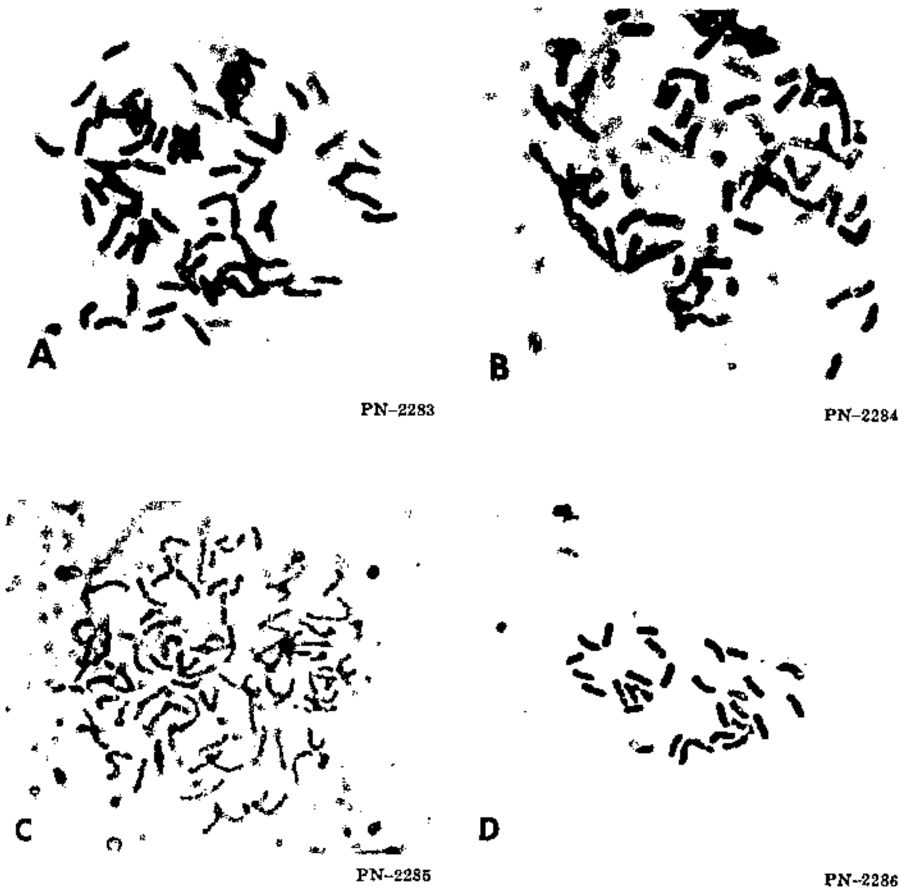


FIGURE 27.—Root-tip chromosomes of intergeneric hybrids of *Tutcheria virgata* × *Camellia granthamiana* and *C. pitardii* var. *pitardii* × *T. spectabilis* (× 2,300): *A*, Hybrid 7-233 of *T. virgata* × *C. granthamiana*, 5x=75; *B*, hybrid 7-235 of *T. virgata* × *C. granthamiana*, 5x=75; *C*, hybrid 7-255 of *T. virgata* × *C. granthamiana*, 5x=75; *D*, hybrid A-19 of *C. pitardii* var. *pitardii* × *T. spectabilis*, 2x=30.

brids showed transmission from *C. granthamiana* of vegetative characters as listed in appendix table 24 and illustrated in figure 10, *A*.

The one hybrid obtained from crosses between *C. pitardii* var. *pitardii* and *T. spectabilis* had 30 chromosomes like the two parents. Figure 27, *D* shows the chromosomal complement of this hybrid. As with the previously mentioned hybrids of *T. virgata* × *C. granthamiana*, the chromosome number cannot prove the validity of the hybrid. Again, the proof of hybridity rests on the vegetative morphology of the hybrid as listed in appendix table 24 and illustrated in figure 10, *C*.

## Chromosome Morphology

The major characteristics used to identify individual chromosomes were its total length and the position of the centromere. In most of the species the centromeres were relatively easy to locate. The centromeres themselves are achromatic and flanked on either side by chromatic regions.

Observations disclosed that whereas the shortest and longest pairs of homologs among the diploid species could be easily distinguished, the large group of medium-length chromosomes, comprising most of the complement, were very difficult to classify into individual pairs. Accurate identification of sets of homologs was not possible for polyploid species, so the study was confined to diploid species and hybrids.

Initially, we thought that, after the karyotypes of each of the diploid species had been established, the study could be extended to include the hybrids between different diploid species. The assumption was that the genome contribution of each parent could be identified in the hybrid. This line of reasoning was found to be an oversimplification and proved impractical for a number of reasons. For example, it was difficult to decide which of two or more possible mates should be assigned to a given parental species. Also, there was no assurance that two chromosomes from the same parent were not being assigned as mates. Therefore, the chromosome morphology studies were restricted to the diploid species.

Karyotypes of the somatic chromosomes of eight diploid species are illustrated in figures 28 through 35 with the chromosomes arranged in pairs of homologs from the longest to the shortest pair. All measurements for each pair of homologs within a species were essentially constant, though some minor differences were encountered. The data presented in tables 11 through 18 reflect the averages of any differences that may have occurred between homologs.

(1) *C. lutchuensis.* Table 11. The chromosomes range in size from 16.6 microns to 7.3 microns. The longest pair exceeds the next pair by 2.1 microns; the second longest pair exceeds the third longest pair by 2.3 microns. The other pairs decrease in length down to the shortest pair in rather even gradations. Five pairs were classified as median with indices from 1.00 to 1.19, four pairs were submedian with indices from 1.56 to 2.30, and six pairs were subterminal with indices from 2.44 to 7.00. Figure 28 show the karyotype of somatic chromosomes of *C. lutchuensis*.

(2) *C. rusticana.* Table 12. The chromosomes range in size from 15.6 microns to 7.3 microns. The longest pair exceeds the next pair by 2.5 microns. The other pairs decrease in length down to the

TABLE 11.—*Basic chromosomes of* C. lutchuensis

| Chromosome No. | Chromosome length | | | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | Total | Long arm | Short arm | | |
| | *Microns* | *Microns* | *Microns* | | |
| 1 | 16.6 | 14.4 | 2.2 | 100:15 | 6.55 |
| 2 | 14.5 | 11.8 | 2.7 | 100:23 | 4.37 |
| 3 | 12.2 | 8.3 | 3.9 | 100:47 | 2.13 |
| 4 | 11.8 | 6.1 | 5.7 | 100:93 | 1.07 |
| 5 | 11.2 | 9.8 | 1.4 | 100:14 | 7.00 |
| 6 | 11.1 | 5.9 | 5.2 | 100:88 | 1.13 |
| 7 | 11.0 | 7.8 | 3.2 | 100:41 | 2.44 |
| 8 | 10.5 | 5.7 | 4.8 | 100:84 | 1.19 |
| 9 | 10.4 | 7.5 | 2.9 | 100:39 | 2.58 |
| 10 | 10.0 | 5.0 | 5.0 | 100:100 | 1.00 |
| 11 | 9.7 | 6.9 | 2.8 | 100:41 | 2.46 |
| 12 | 9.3 | 4.8 | 4.5 | 100:94 | 1.06 |
| 13 | 8.9 | 6.2 | 2.7 | 100:44 | 2.30 |
| 14 | 8.2 | 5.0 | 3.2 | 100:64 | 1.56 |
| 15 | 7.3 | 5.0 | 2.3 | 100:46 | 2.17 |

TABLE 12.—*Basic chromosomes of* C. rusticana

| Chromosome No. | Chromosome length | | | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | Total | Long arm | Short arm | | |
| | *Microns* | *Microns* | *Microns* | | |
| 1 | 15.6 | 13.3 | 2.3 | 100:17 | 5.78 |
| 2 | 13.1 | 11.1 | 2.0 | 100:18 | 5.55 |
| 3 | 11.8 | 9.5 | 2.3 | 100:24 | 4.13 |
| 4 | 11.4 | 6.1 | 5.3 | 100:87 | 1.15 |
| 5 | 11.1 | 8.8 | 2.3 | 100:26 | 3.83 |
| 6 | 10.8 | 5.5 | 5.3 | 100:96 | 1.04 |
| 7 | 10.7 | 8.9 | 1.8 | 100:20 | 4.94 |
| 8 | 10.6 | 6.1 | 4.5 | 100:74 | 1.36 |
| 9 | 10.5 | 8.4 | 2.1 | 100:25 | 4.00 |
| 10 | 10.4 | 6.5 | 3.9 | 100:60 | 1.67 |
| 11 | 9.6 | 7.1 | 2.5 | 100:35 | 2.84 |
| 12 | 9.2 | 5.4 | 3.8 | 100:70 | 1.42 |
| 13 | 8.9 | 6.1 | 2.8 | 100:46 | 2.18 |
| 14 | 7.8 | 4.6 | 3.2 | 100:70 | 1.44 |
| 15 | 7.3 | 4.1 | 3.2 | 100:78 | 1.28 |

shortest pair in rather even gradations. Two pairs were classified as median with indices of 1.04 and 1.15, six pairs were submedian with indices from 1.28 to 2.18, and seven were subterminal with indices from 2.84 to 5.78. Figure 29 shows the karyotype of somatic chromosomes of *C. rusticana*.

(3) *C. japonica*. Table 13. The chromosomes range in size from 16.4 microns to 7.3 microns. The

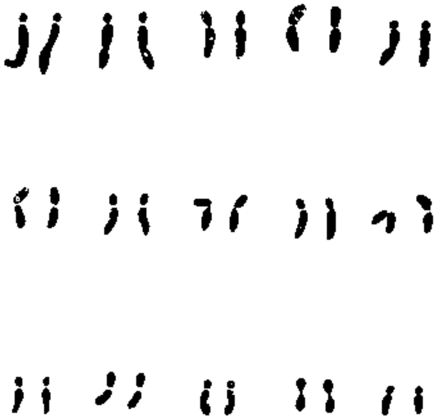


FIGURE 28.—Karotype of somatic chromosomes of C. *lutchuensis*.

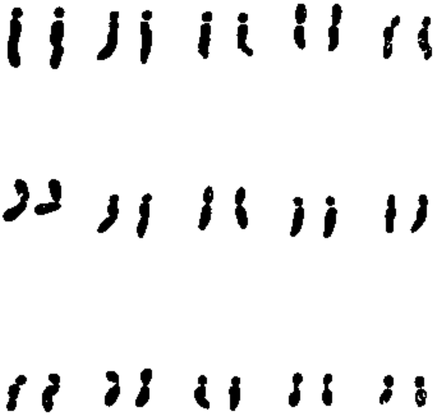


FIGURE 29.—Karotype of somatic chromosomes of *C. rusticana*.

TABLE 13.—*Basic chromosomes of* C. japonica

| Chromosome No. | Chromosome length Total | Long arm | Short arm | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | *Microns* | *Microns* | *Microns* | | |
| 1. | 16.4 | 13.9 | 2.5 | 100:18 | 5.56 |
| 2. | 13.7 | 11.4 | 2.3 | 100:20 | 4.96 |
| 3. | 13.0 | 10.5 | 2.5 | 100:24 | 4.20 |
| 4. | 12.7 | 7.1 | 5.6 | 100:79 | 1.27 |
| 5. | 12.0 | 9.5 | 2.5 | 100:26 | 3.80 |
| 6. | 11.4 | 6.4 | 5.0 | 100:78 | 1.28 |
| 7. | 11.0 | 8.8 | 2.2 | 100:25 | 4.00 |
| 8. | 10.7 | 6.5 | 4.2 | 100:65 | 1.55 |
| 9. | 10.2 | 8.1 | 2.1 | 100:26 | 3.86 |
| 10. | 9.7 | 5.4 | 4.3 | 100:80 | 1.26 |
| 11. | 9.6 | 7.2 | 2.4 | 100:33 | 3.06 |
| 12. | 8.7 | 4.7 | 4.0 | 100:85 | 1.18 |
| 13. | 8.6 | 4.9 | 3.7 | 100:76 | 1.32 |
| 14. | 8.2 | 4.7 | 3.5 | 100:74 | 1.34 |
| 15. | 7.3 | 5.2 | 2.1 | 100:40 | 2.48 |

longest pair exceeds the next pair by 2.7 microns. The other pairs decrease in length down to the shortest pair in rather even gradations. One pair was classified as median with an index of 1.18, six pairs were submedian with indices from 1.26 to 1.55, and eight pairs were subterminal with indices from 2.48 to 5.56. Figure 30 shows the karyotype of somatic chromosomes of *C. japonica.*

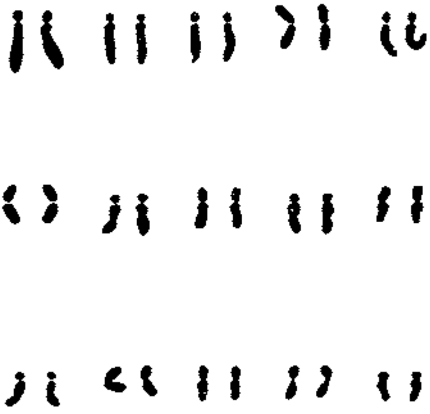


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FIGURE 30.—Karotype of somatic chromosomes of *C. japonica.*

(4) *C. saluenensis.* Table 14. The chromosomes range in size from 12.8 microns to 4.8 microns. The longest pair exceeds the next pair by 2.2 microns. The other pairs decrease in length down to the shortest pair in rather even gradations. Two pairs were classified as median with indices of 1.00 and 1.16, five pairs were submedian with indices from 1.25 to 2.24, and eight pairs were subterminal with indices from 2.60 to 5.24. Figure 31 shows the kary-

TABLE 14.—*Basic chromosomes of* C. saluenensis

| Chromosome No. | Chromosome length: Total | Chromosome length: Long arm | Chromosome length: Short arm | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | *Microns* | *Microns* | *Microns* | | |
| 1 | 12.8 | 10.6 | 2.2 | 100:21 | 4.82 |
| 2 | 10.6 | 8.9 | 1.7 | 100:19 | 5.24 |
| 3 | 10.4 | 7.9 | 2.5 | 100:32 | 3.16 |
| 4 | 10.1 | 7.3 | 2.8 | 100:38 | 2.60 |
| 5 | 9.4 | 7.7 | 1.7 | 100:22 | 4.53 |
| 6 | 9.0 | 5.0 | 4.0 | 100:80 | 1.25 |
| 7 | 8.2 | 6.8 | 1.4 | 100:21 | 4.86 |
| 8 | 8.0 | 4.3 | 3.7 | 100:86 | 1.16 |
| 9 | 7.6 | 6.3 | 1.3 | 100:21 | 4.85 |
| 10 | 7.0 | 4.0 | 3.0 | 100:75 | 1.33 |
| 11 | 6.8 | 4.7 | 2.1 | 100:45 | 2.24 |
| 12 | 6.4 | 3.2 | 3.2 | 100:100 | 1.00 |
| 13 | 6.1 | 4.8 | 1.3 | 100:27 | 3.69 |
| 14 | 5.5 | 3.1 | 2.4 | 100:77 | 1.29 |
| 15 | 4.8 | 3.1 | 1.7 | 100:55 | 1.82 |

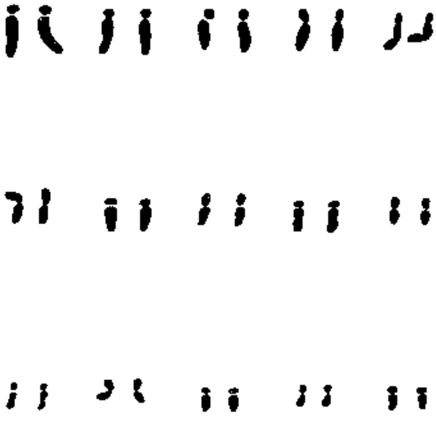

FIGURE 31.—Karotype of somatic chromosomes of *C. saluenensis.*

otype of somatic chromosomes of *C. saluenensis.*

(5) *C. sinensis.* Table 15. The chromosomes range in size from 17.0 microns to 7.5 microns. The longest pair exceeds the next pair by 2.0 microns. The other pairs decrease in length down to the shortest pair in rather even gradations. Two pairs were classified as median with indices of 1.00 and 1.12, five pairs were submedian with indices from 1.27 to 1.71, and eight pairs were subterminal with indices from 2.75 to 4.60. Figure 32 shows the karyotype of somatic chromosomes of *C. sinensis.*

(6) *C. pitardii* var. *pitardii.* Table 16. The chromosomes range in size from 16.5 microns to 6.7 microns. The longest pair exceeds the next pair by 1.5 microns; the second longest pair exceeds the third longest pair by 1.8 microns. The other pairs decrease in length down to the shortest pair

TABLE 15.—*Basic chromosomes of* C. sinensis

| Chromosome No. | Chromosome length Total | Long arm | Short arm | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | *Microns* | *Microns* | *Microns* | | |
| 1. | 17.0 | 13.0 | 4.0 | 100:31 | 3.25 |
| 2. | 15.0 | 11.5 | 3.5 | 100:30 | 3.29 |
| 3. | 14.0 | 10.5 | 3.5 | 100:33 | 3.00 |
| 4 | 12.7 | 8.0 | 4.7 | 100:59 | 1.70 |
| 5. | 12.0 | 9.0 | 3.0 | 100:33 | 3.00 |
| 6. | 11.7 | 7.0 | 4.7 | 100:67 | 1.49 |
| 7. | 11.2 | 9.2 | 2.0 | 100:22 | 4.60 |
| 8. | 11.0 | 5.8 | 5.2 | 100:90 | 1.12 |
| 9. | 10.8 | 6.6 | 4.2 | 100:64 | 1.57 |
| 10. | 10.2 | 5.7 | 4.5 | 100:79 | 1.27 |
| 11. | 10.0 | 8.0 | 2.0 | 100:25 | 4.00 |
| 12. | 9.5 | 6.0 | 3.5 | 100:58 | 1.71 |
| 13. | 9.0 | 4.5 | 4.5 | 100:100 | 1.00 |
| 14. | 8.5 | 6.5 | 2.0 | 100:31 | 3.25 |
| 15. | 7.5 | 5.5 | 2.0 | 100:36 | 2.75 |

in rather even gradations. Three pairs were classified as median with indices from 1.16 to 1.20, three pairs were submedian with indices from 1.25 to 2.31, and nine pairs were subterminal with indices from 2.72 to 7.25. Figure 33 shows the karyotype of somatic chromosomes of *C. pitardii* var. *pitardii.*

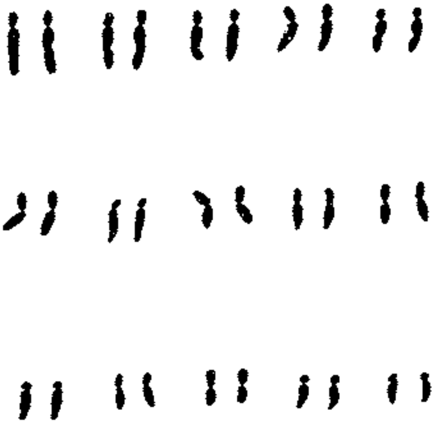

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FIGURE 32.—Karotype of somatic chromosomes of *C. sinensis.*

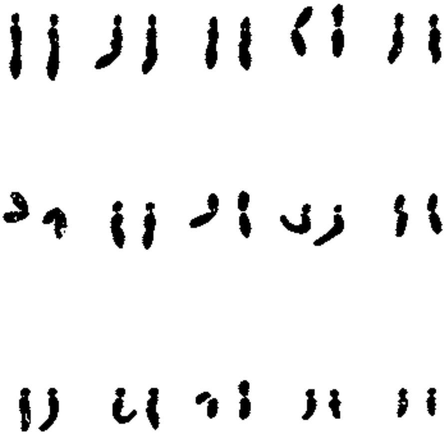

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FIGURE 33.—Karotype of somatic chromosomes of *C. pitardii* var. *pitardii.*

TABLE 16.—*Basic chromosomes of* C. pitardii *var.* pitardii

| Chromosome No. | Chromosome length: Total | Chromosome length: Long arm | Chromosome length: Short arm | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | *Microns* | *Microns* | *Microns* | | |
| 1 | 16.7 | 14.5 | 2.0 | 100:14 | 7.25 |
| 2 | 15.0 | 12.3 | 2.7 | 100:22 | 4.56 |
| 3 | 13.2 | 10.7 | 2.5 | 100:23 | 4.28 |
| 4 | 13.0 | 7.0 | 6.0 | 100:86 | 1.17 |
| 5 | 12.9 | 9.0 | 3.9 | 100:43 | 2.31 |
| 6 | 12.5 | 6.7 | 5.8 | 100:87 | 1.16 |
| 7 | 12.1 | 9.8 | 2.3 | 100:23 | 4.26 |
| 8 | 11.8 | 6.6 | 5.2 | 100:79 | 1.27 |
| 9 | 11.5 | 10.0 | 1.5 | 100:15 | 6.67 |
| 10 | 11.0 | 6.0 | 5.0 | 100:83 | 1.20 |
| 11 | 10.8 | 9.3 | 1.5 | 100:16 | 6.20 |
| 12 | 10.5 | 8.5 | 2.0 | 100:24 | 4.25 |
| 13 | 9.0 | 5.0 | 4.0 | 100:80 | 1.25 |
| 14 | 7.3 | 5.8 | 1.5 | 100:26 | 3.87 |
| 15 | 6.7 | 4.9 | 1.8 | 100:37 | 2.72 |

TABLE 17.—*Basic chromosomes of* C. kissi

| Chromosome No. | Chromosome length Total | Long arm | Short arm | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | *Microns* | *Microns* | *Microns* | | |
| 1 | 17.5 | 15.0 | 2.5 | 100:17 | 6.00 |
| 2 | 15.0 | 12.0 | 3.0 | 100:25 | 4.00 |
| 3 | 14.0 | 11.5 | 2.5 | 100:22 | 4.60 |
| 4 | 13.5 | 7.5 | 6.0 | 100:80 | 1.25 |
| 5 | 13.0 | 10.1 | 2.9 | 100:29 | 3.48 |
| 6 | 12.8 | 6.8 | 6.0 | 100:88 | 1.13 |
| 7 | 12.0 | 9.3 | 2.7 | 100:29 | 3.44 |
| 8 | 11.7 | 8.0 | 3.7 | 100:46 | 2.16 |
| 9 | 11.0 | 8.5 | 2.5 | 100:29 | 3.40 |
| 10 | 10.1 | 5.1 | 5.0 | 100:98 | 1.02 |
| 11 | 10.0 | 7.8 | 2.2 | 100:28 | 3.55 |
| 12 | 9.9 | 6.4 | 3.5 | 100:55 | 1.83 |
| 13 | 8.5 | 6.1 | 2.4 | 100:39 | 2.54 |
| 14 | 7.7 | 4.2 | 3.5 | 100:83 | 1.20 |
| 15 | 7.5 | 5.4 | 2.1 | 100:39 | 2.57 |

(7) *C. kissi.* Table 17. The chromosomes range in size from 17.5 microns to 7.5 microns. The longest pair exceeds the next pair by 2.5 microns. The other pairs decrease in length down to the shortest pair in rather even gradations. Three pairs were classified as median with indices from 1.02 to 1.20, three pairs were submedian with indices from 1.25 to 2.16, and nine pairs were subterminal with indices from 2.54 to 6.00. Figure 34 shows the karyotype of somatic chromosomes of *C. kissi.*

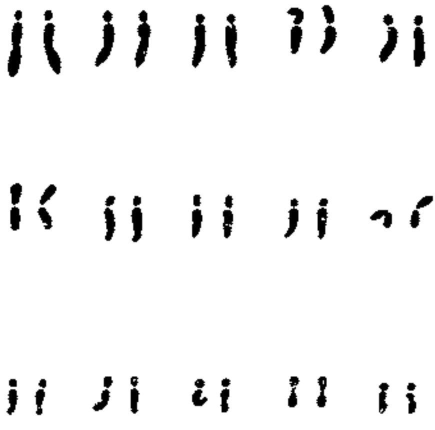

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FIGURE 34.—Karotype of somatic chromosomes of *C. kissi.*

(8) *C. salicifolia.* Table 18. The chromosomes range in size from 17.5 microns to 5.8 microns. The longest pair of homologs possess a microsatellite. The longest pair of chromosomes exceeds the next pair by 1.7 microns. The other pairs decrease in length down to the shortest pair in rather even gradations. Three pairs were classified as median with indices

TABLE 18.—*Basic chromosomes of* C. salicifolia

| Chromosome No. | Chromosome length: Total | Chromosome length: Long arm | Chromosome length: Short arm | Arm length ratio | Long arm to short arm index |
|---|---|---|---|---|---|
| | *Microns* | *Microns* | *Microns* | | |
| 1 | 17.5 | 15.0 | 2.5 | 100:17 | 6.00 |
| 2 | 15.8 | 12.3 | 3.5 | 100:28 | 3.51 |
| 3 | 15.0 | 12.5 | 2.5 | 100:20 | 5.00 |
| 4 | 14.0 | 8.5 | 5.5 | 100:65 | 1.55 |
| 5 | 13.3 | 11.0 | 2.6 | 100:24 | 4.23 |
| 6 | 12.7 | 6.5 | 6.2 | 100:95 | 1.05 |
| 7 | 12.5 | 10.5 | 2.0 | 100:19 | 5.25 |
| 8 | 11.2 | 8.7 | 2.5 | 100:29 | 3.48 |
| 9 | 10.5 | 7.5 | 3.0 | 100:40 | 2.50 |
| 10 | 10.0 | 7.0 | 3.0 | 100:43 | 2.33 |
| 11 | 9.5 | 5.0 | 4.5 | 100:90 | 1.11 |
| 12 | 9.0 | 5.0 | 4.0 | 100:80 | 1.25 |
| 13 | 7.0 | 5.0 | 2.0 | 100:40 | 2.50 |
| 14 | 6.4 | 3.2 | 3.2 | 100:100 | 1.00 |
| 15 | 5.8 | 4.3 | 1.5 | 100:35 | 2.87 |

from 1.00 to 1.11, three pairs were submedian with indices from 1.25 to 2.33, and nine pairs were subterminal with indices from 2.50 to 6.00 Figure 35 shows the karyotype of somatic chromosomes of *C. salicifolia.*

An analysis of the karyotypes of the basic chromosomes of eight diploid species of *Camellia* is given in table 19. The species are listed in the table in ascending order of the number of subterminal chromosomes in each.

Chromosomes 1, 2, and 7 are subterminal in all eight species; whereas chromosome 3 is subterminal in all species except *C. lutchuensis*; chromosome 5 is subterminal in all except *C. pitardii* var. *pitardii,* and chromosome 9 is subterminal in all except *C. sinensis.* Chromosomes 6 and 10 are either median or submedian in all eight species; whereas chro-

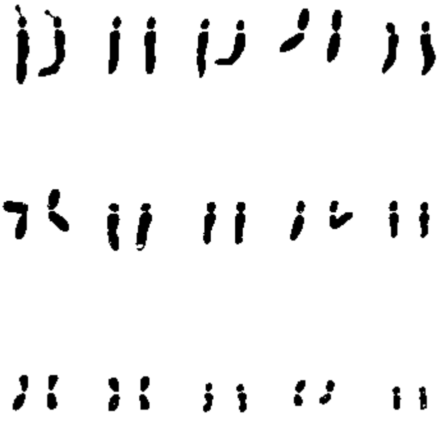

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FIGURE 35.—Karotype of somatic chromosomes of *C. salicifolia.*

TABLE 19.—*Analysis of karyotypes of basic chromosomes of 8 diploid species of* Camellia [1]

| Species | Chromosome No. | | | | | | | | | | | | | | | Type chromosome | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | m | sm | st |
| | | | | | | | | | | | | | | | | *Number* | *Number* | *Number* |
| *C. lutchuensis* | st | st | sm | m | st | m | st | m | st | m | st | m | sm | sm | sm | 5 | 4 | 6 |
| *C. rusticana* | st | st | st | m | st | m | st | sm | st | sm | st | sm | sm | sm | sm | 2 | 6 | 7 |
| *C. japonica* | st | st | st | sm | st | sm | st | sm | st | sm | st | m | sm | sm | st | 1 | 6 | 8 |
| *C. saluenensis* | st | st | st | st | st | sm | st | m | st | sm | sm | m | st | sm | sm | 2 | 5 | 8 |
| *C. sinensis* | st | st | st | sm | st | sm | st | m | sm | sm | st | sm | m | st | st | 2 | 5 | 8 |
| *C. pitardii* var. *pitardii* | st | st | st | m | sm | m | st | sm | st | m | st | st | sm | st | st | 3 | 3 | 9 |
| *C. kissi* | st | st | st | sm | st | m | st | sm | st | m | st | sm | st | m | st | 3 | 3 | 9 |
| *C. salicifolia* | st | st | st | sm | st | m | st | st | st | sm | m | sm | st | m | st | 3 | 3 | 9 |

[1] m = median; sm = submedian; st = subterminal.

mosome 4 is median or submedian in all except *C. saluenensis*; chromosome 8 is median or submedian in all except *C. salicifolia*; and chromosome 12 is median or submedian in all except *C. pitardii* var. *pitardii*. Chromosome 11 is subterminal in all except two species, chromosome 14 is median or submedian in all except two species, chromosome 13 is median or submedian in all except three species, and chromosome 15 is subterminal in all except three species. Thus, more variability appears to exist among the short chromosomes than among the long ones.

## DISCUSSION AND CONCLUSIONS

Rather wide differences were observed in the percentages of hybrids developed per pollination between the reciprocals of interspecific crosses, as shown in tables 2 and 3. In most cases, the numbers of pollinations and hybrids were not sufficiently large to establish significance by chi-square, but differences were significant for six of 54 reciprocal combinations shown in table 3. The six reciprocal crosses showing significant or highly significant differences were: diploid with diploid crosses *C. japonica* with *C. lutchuensis* and *C. rusticana* with *C. lutchuensis;* diploid with hexaploid crosses, *C. japonica* with *C. reticulata, C. rusticana* with *C. reticulata,* and *C. kissi* with *C. rosaeflora;* and hexaploid with hexaploid crosses, *C. fraterna* with *C. reticulata.*

The diploid *C. lutchuensis* as the female parent produced fewer progeny in crosses with *C. japonica* and *C. rusticana* than did either *C. japonica* or *C. rusticana.* Similarly, the hexaploid *C. fraterna* was less fertile as the female than was hexaploid *C. reticulata.* Also, hexaploid *C. rosaeflora* was less fertile as the female than diploid *C. kissi.* Three of the species that performed poorly as females, *C. fraterna, C. lutchuensis,* and *C. rosaeflora,* are of section Theopsis. *C. fraterna* and *C. lutchuensis* at least may require higher temperatures than other species of *Camellia* for success when used as the female parent. *C. lutchuensis* was highly fertile when used as the female parent in Gonzales, La.,[5] and Long Beach, Calif.,[6] but was poorly fertile at Berkeley, Calif.[7] Similarly, *C. fraterna* was highly fertile at Los Angeles, Calif.[8]

When used as the female parent in reciprocal crosses with *C. japonica* and *C. rusticana,* the hexaploid *C. reticulata* was supe-

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[5] Palmer, F. A., Jr. 1969. [Personal correspondence.]

[6] Neptune, H. 1969. [Personal correspondence.]

[7] Cutter, R. K. 1966-69. [Personal correspondence.]

[8] Parks, C. R. 1967-68. [Personal correspondence.]

rior to both of these diploid species.

The percentages of aborted pollen produced by the hybrids generally exceeded those of the parents. Individual hybrids with totally aborted pollen were obtained from *C. japonica* × *C. lutchuensis*, *C. rusticana* × *C. lutchuensis*, and *C. saluenensis* × *C. granthamiana*. Eleven of the interspecific crosses produced hybrids having averages of 90 percent or more aborted pollen. In contrast, some of the clones of the diploids *C. japonica*, *C. kissi*, and *C. rusticana* had more than 50 percent aborted pollen as did the tetraploid *C. granthamiana*. Although reduced fertility in polyploids often can be attributed to irregular meiotic distribution of chromosomes, varying frequencies of aborted pollen encountered among different clones of the parental diploids also suggest the presence of chromosomal structural changes or segregation of genes affecting fertility in *Camellia*. The variation in frequencies of aborted pollen among the parents undoubtedly was a factor in differences in fertility of hybrids obtained from the same interspecific cross. Success in the interspecific transfer of desirable genes in future hybridization programs requires some degree of fertility in the $F_1$ hybrids. Although the hybrids exhibited reduced fertility in comparison with the parental species, all successful crosses except the triploid hybrid of *C. saluenensis* × *C. granthamiana* produced some partly fertile hybrids.

The same factors that cause reduced pollen fertility may also be expected to cause reduced megaspore or egg fertility. Therefore, attempts to successfully cross one hybrid of low pollen fertility with another hybrid of similar low fertility are usually very difficult. In instances where the desired genetic characteristic has been secured in the hybrid, a more productive procedure may be to use hybrids of low fertility as male parents in crosses with female clones of high fertility and possessing other desirable characteristics lacking in the hybrid.

Compatibility relationships of species within subgeneric sections and between sections were investigated. Within the section Camellia there is a close relationship between *C. japonica*, *C. pitardii* var. *pitardii*, *C. reticulata*, *C. rusticana*, and *C. saluenensis*. All of these species hybridize quite readily with each other. *C. hongkongensis*, on the other hand, failed to hybridize in one-half of the reciprocal combinations attempted, as shown in figure 14. Therefore *C. hongkongensis* apparently is the least compatible species within the section. This observation agrees with Parks and Griffiths (*1966*) who stated that from both chemotaxonomic and cross-compatibility criteria, *C. hongkongensis* is apart from other species in this section. Thus, five of the species seem to be closely related ecospecies and *C. hongkongensis* a possible cenospecies in relation to the others.

The three species, *C. kissi, C. oleifera* and *C. sasanqua,* within section Paracamellia all hybridize freely with each other, indicating a close relationship typical of ecospecies.

*C. fraterna, C. lutchuensis,* and *C. rosaeflora* of section Theopsis were the most difficult of the intrasectional crosses to hybridize. Their behavior, typical of cenospecies, suggests the existence of genetic isolation barriers more typical of intersectional species crosses than that expected of crosses within a single section. A factor that may play a part here is that all three species are poor female parents. Seed set has always been low, regardless of type of pollination. A rather large number of reciprocal crosses involving one of these species combined with another species from a different section showed that invariably the number of hybrids was always much higher where the Theopsis species was the male parent. A possible explanation for this deficiency was previously discussed on page 78.

*C. hiemalis* and *C. miyagii* of section Dubiae hybridize readily between themselves and also with species within section Paracamellia. A lack of any apparent genetic isolation barriers suggests that *C. hiemalis* and *C. miyagii* are ecospecies and that they are more closely related to species within section Paracamellia than with species within any other section. Actually, the compatibility ratios of these two species with those of Paracamellia is 18 percent for *C. miyagii* and 13 percent for *C. hiemalis.* This compares with 9 percent for intrasectional crosses of species within section Camellia. Compatibility evidence thus suggests that these two species might in fact belong within section Paracamellia.

Section Thea appears more closely related to section Paracamellia and to *C. hiemalis* and *C. miyagii* of Dubiae than to species of other sections.

Section Camellia shows a somewhat closer compatibility relationship with Heterogenea, Theopsis, and Camelliopsis than with Paracamellia or Thea, although at least some hybrids were possible from all combinations. High pollen abortion among the hybrids indicates that the species of each of these sections act as cenospecies in relation to species of other sections.

*C. granthamiana* of section Heterogenea is most closely associated with species of section Camellia and will hybridize with difficulty with *C. sasanqua* of section Paracamellia, but not at all with species of other sections. In general, *C. granthamiana* showed a higher overall incompatibility in intersectional crosses than did any of the other species tested.

In summary, the subgeneric sections appeared to fall into two more-or-less distinct groups. In the first, species of Paracamellia, Thea, and Dubiae appear to be more generally compatible with each other than with species of the other sections. In the second, species of Theopsis and Camelliopsis appear to be closely related to each other and in turn more closely compatible with Camellia than with other sections. Heterogenea would appear to fall within this second group because of its closer association with Camellia than with any other section.

Determinations of chromosome numbers were made for the 88 interspecific hybrids of *Camellia* that produced root tips suitable for study. Among these, four hybrids had aneuploid chromosome complements; all others had multiples of the basic chromosome number of 15. Only one aneuploid was found reported in the literature; Longley and Tourje (*1959*) list the hybrid variety 'Salutation' from *C. saluenensis* × *C. reticulata* as having 53±2 chromosomes. However, this variety had been reported earlier by Janaki Ammal (*1952*) as being a tetraploid with 60 chromosomes. Because of the loss of vital genes and genetic imbalance, the absence of a single chromosome is usually lethal in diploid plants (Muntzing, *1961*). An aneuploid, deficient for two chromosomes, occurred among the hybrids of the diploids *C. japonica* × *C. lutchuensis*. The aneuploid had small distorted leaves, was very weak in growth, and subsequently died. Two aneuploids, hybrid 4-44 with 56 chromosomes and hybrid 4-48 with 59 chromosomes, resulted from *C. japonica* (2x=30) × *C. fraterna* (6x=90). These two hybrids developed from separate seed capsules grown on the same *C. japonica* parent and pollinated the same day in 1964. Both hybrids survive and resemble the hexaploid male parent in most vegetative characters (appendix table 22), the exceptions being leaf veination and margins for 4-44 and leaf veination for 4-48. General vigor and growth of both of these hybrids are comparable with those of the other eight hybrids of this cross. Both hybrids produced 98 percent aborted pollen, suggesting considerable irregularities in meiosis of the unbalanced chromosomal complements.

Among four hybrids of the hexaploid cross *C. sasanqua* × *C. miyagii*, hybrid 5-55 had a complement of 86 chromosomes. This aneuploid survives and shows greater similarity to the female parent, *C. sasanqua*, than do the other three hybrids of this cross. Of eight vegetative characteristics listed in table 22, hybrid 5-55 resembles the female parent in four of these and the male parent in the other four. As with the other polyploid hybrids with aneuploid chromosome numbers, and in contrast to the 2x-2 aneuploid, there is little apparent difference in vigor and growth between hybrid 5-55 and the three euploid hybrids of this cross. Pollen abortion was 88 percent, somewhat lower than that for the other aneuploids.

Observations of the pollen of the *Camellia* species used as parents disclosed that the production of large, presumably unreduced, grains is very common in the genus. Only five of 66 introductions listed in table 4 did not produce at least some unreduced pollen. Spontaneous polyploidy through the production of functional unreduced gametes is not unique in *Camellia* but has been reported in a number of horticultural plants including *Dianthus* by Brooks and Mehlquist (*1961*); *Malus* by Einset (*1952*); *Narcissus* and *Iris* by Emsweller and Uhring (*1960*); and *Vitis* by Olmo (*1952*). The occurrence of spontaneous triploids in diploid species is attributed to the functioning of unreduced gametes (Elliott, *1958*).

Triploidy in *Camellia* was first detected in *C. sinensis*. Karasawa (*1932, 1935*) found a large-leaved plant of tea, which had 45 chromosomes. Patterson, Longley, and Robertson (*1950*) first reported the existence of triploids among cultivated varieties of *C. japonica*. The three triploids found by Patterson, Longley, and Robertson had irregular meiotic association. Univalents were detected, and more than the normal number of four spores from a single microsporocyte often occurred, resulting in the production of aneuploid, aborted pollen. In addition to the expected tetrads of microspores, diploid varieties occasionally produced dyads and sporads with one or two extra small spores. Patterson, Longley, and Robertson suggested that the triploids originated after the functioning of unreduced diploid pollen developed from dyads of spores. Other triploids in *Camellia* have also been detected. Darlington and Wylie (*1961*) reported the triploid number for *C. japonica* var. *grandiflora*. Longley and Tourje (*1959, 1960*) listed chromosome counts for 59 cultivated varieties of *C. japonica*, and 12 were triploids. *C. vernalis* 'Hirya' was reported to be triploid by the same authors. Further evidence for the functioning of unreduced gametes in *Camellia* is provided by the pentaploid hybrid 'Inamorata' derived from *C. saluenensis* (2x=30) × *C. reticulata* (6x=90). Janaki Ammal (*1952*) attributed the origin of the pentaploid to the functioning of an unreduced egg from the diploid parent.

The functioning of an unreduced egg from a diploid parent is also indicated in this study. Among five hybrids of the cross *C. pitardii* var. *pitardii* (2x=30) × *C. granthamiana* (4x=60), a tetraploid hybrid was obtained. As shown in table 4, *C. pitardii* var. *pitardii* was observed to produce 9 percent large, unreduced pollen. Presumably, meiosis would be similar in microsporocytes and megasporocytes, and unreduced megaspores occurred, resulting in a diploid egg produced by *C. pitardii* var. *pitardii*.

Two pentaploid hybrids resulted from crosses of *C. reticulata* (6x=90) × *C. japonica* (2x=30). All of the 21 clones of *C. japonica* produced large, unreduced pollen in percentages ranging from 1 to 22. With the exception of one hybrid with the unpredictable pentaploid *C. sasanqua* 'Narumi-gata,' all of the other hybrids involving *C. reticulata* as one parent, and listed in table 9, had the expected chromosome numbers. Accordingly, the origin of the two pentaploids is attributed to the functioning of unreduced pollen of *C. japonica.*

With the exception of the pentaploid *C. sansanqua* 'Narumi-gata,' all species of *Camellia* used as parents had even multiples of the basic chromosome number. Because 'Narumi-gata' is pentaploid, varying chromosomal contributions to its hybrids may be expected. *C. reticulata* is hexaploid and, as shown in table 9, in crosses with other species with even multiples of the basic chromosome number, produced 16 hybrids having expected chromosome numbers. The hybrid *C. sasanqua* 'Narumi-gata' × *C. reticulata* had 90 chromosomes. Accordingly, it seems likely that 'Narumi-gata' produced a functional egg cell with three sets of chromosomes. The functioning of an egg cell with two sets of chromosomes may account for the origin of the tetraploid hybrid obtained from *C. sasanqua* 'Narumi-gata' × *C. granthamiana*, a tetraploid species.

Similar to the unpredictable behavior of *C. sasanqua* 'Narumi-gata' was that of another pentaploid, *Tutcheria virgata,* when used as the female parent in intergeneric crosses with *C. granthamiana* (4x=60) and *C. miyagii* (6x=90). Three pentaploid hybrids resulted from crosses of *T. virgata* (5x=75) × *C. granthamiana* (4x=60). Pentaploids are more erratic in meiotic behavior than tetraploids. Assuming that tetraploid *C. granthamiana* produced reduced diploid sperms, the production of eggs with three sets of chromosomes by *T. virgata* could account for the origin of the pentaploid intergeneric hybrids.

The seven intergeneric hybrids resulting from crosses of *T. virgata* (5x=75) × *C. miyagii* (6x=90) gave greater variation in their chromosome complements than any of the interspecific combinations. As shown in table 10, two hybrids had 75 chromosomes, two had 90, and one had a complement of 105. In addition, two hybrids had aneuploid numbers of 80 and 82 chromosomes, respectively. The source of variation in chromosome numbers of all these hybrids is difficult to assess. Atypical chromosome numbers would be expected in the eggs of the pentaploid female parent. Although the hexaploid male parent produced six hybrids with the expected chromosome numbers in crosses with other *Camellia* species, an aneuploid hybrid had 86 chromosomes rather than the expected number of 90 when *C. myiagii* was used as the male parent in a cross with *C. sasanqua*. In consideration of the instability of both parents and the absence of adequate cytological markers, the chromosomal contributions of the parents is quite speculative, particularly in regard to the two aneuploids. If *C. miyagii* contributed the reduced number of 45, as it apparently did in six of seven interspecific hybrids, the two pentaploid intergeneric hybrids would have been derived from eggs carrying 30 chromosomes produced by the pentaploid female parent. Similarly, eggs carrying three sets of chromosomes would have functioned in the development of the hexaploid hybrids.

It seems quite unlikely that the hybrid with 105 chromosomes, exactly seven times the basic number, could have arisen from two gametes carrying unbalanced chromosome numbers. Assuming the functioning of gametes carrying multiples of the basic number, the following possible chromosomal contributions exist, with the chromosomes from the female parent listed first: 75 × 30, 60 × 45, 45 × 60, 30 × 75, and 15 × 90. The last combination would require the union of a monoploid egg from the pentaploid *T. virgata* and an unreduced sperm from *C. miyagii*. Only 1 percent unreduced pollen was detected in *C. miyagii*. Furthermore, the hybrid might be expected to show considerably phenotypic similarities to the male parent. Of the seven hybrids from the cross, hybrid 5-80 with 105 chromosomes was the only one to resemble the female parent in floral form (fig. 11), and similarly resembled the female parent more than the male in vegetative characters (appendix table 24). Accordingly, the combination of 15 chromosomes from the female parent and 90 from the male seems most unlikely. With the exception of one aneuploid, all 14 other hybrids of hexaploid × hexaploid crosses resulted in the expected chromosome numbers. Excluding the contribution of 45 chromosomes by *C. miyagii*, the other combinations would require a degree of gametic variability in chromosome number unsupported from the results of hexaploid × hexaploid crosses. Therefore, the most likely explanation of the origin of the hybrid with 105 chromosomes is the union of an egg carrying 60 chromosomes from *T. virgata* with a normal sperm from *C. miyagii*.

Studies of chromosome morphology were intended primarily to ascertain whether karyotype analysis in *Camellia* would be fruitful in distinguishing species and in elucidating phylogenetic relationships. Thus, representative diploid species were investigated without attempting to establish fine differences through a statistical approach.

Some differences were noted in

chromosome size. Particularly obvious was the shorter length of the chromosomes of *C. saluenensis*. This condition may have been more apparent than real and the result of greater colchicine penetration of these root-tip preparations. The main differences encountered were in relation to centromere position and in one case to the presence of a microsatellite.

Although there were striking similarities between the genomes of all of the species in respect to centromere position, there were also marked differences, indicating that the species can be distinguished from each other through careful karyotype analysis.

There are a number of serious limitations in comparing similarities and differences of karyotypes of various species with known external morphological relationships. However, such comparisons do offer one more tool in the classification of species and may help clarify relationships that cannot be detected by the taxonomist.

The karyotypes of *C. japonica* and *C. rusticana* appeared the most similar among the eight species studied. Here, the differences are perhaps more surprising than the similarities. Some taxonomists, including Sealy (*1958*), consider *C. rusticana* to be a subspecies of *C. japonica*. The vegetative morphology of the two species is rather similar. Comparison of the indices of tables 12 and 13 shows a number of minor dissimilarities, but the largest differences in centromere position appear to exist between chromosomes 13 and 15, where the contrast in arm length is greater in *C. rusticana* for chromosome 13 and greater in *C. japonica* for chromosome 15.

Species known to be closely related are *C. japonica*, *C. pitardii* var. *pitardii*, *C. rusticana*, and *C. saluenensis*. Sealy (*1958*) places these species among others in the subgeneric section Camellia. Therefore, the karyotypes of these species would be expected to be more similar to each other than to other species. Ignoring possible chromosome size differences, this is certainly true for *C. saluenensis*, whose long arm to short arm indices (table 14) compare quite favorably with those of both *C. japonica* and *C. rusticana*. Major differences in centromere position are apparent only in chromosomes 4 and 13. The karyotype of *C. pitardii* var. *pitardii*, however, appears distinctly different from those of other species within section Camellia. At least six chromosomes (1, 5, 9, 11, 12, and 14) appear quite distinct from their counterparts in the other species.

Among the species outside the section Camellia, *C. kissi* and *C. lutchuensis* appear more similar, at least superficially, to those within this section than do *C. salicifolia* or *C. sinensis*. *C. lutchuensis* hybridizes fairly readily with species of the section Camellia, but many of the hybrids are largely sterile. The karyotype of

*C. salicifolia* is perhaps the most dissimilar in relation to all other species. Also, here the first evidence was found of a chromosome pair with a satellite.

In general, there was only a rough correlation between the visual appearance of the karyotypes of the various species and their ability to hybridize and produce fertile hybrid plants. The lack of more positive correlation would appear to indicate that structural and genetic differences affecting hybridization exist, which are not visible in the karyotypes.

## SUMMARY

Twenty species were used as parents for interspecific crosses in *Camellia*, resulting in 459 hybrids from 106 combinations. Analysis by chi-square disclosed that one parent was superior in six of 54 reciprocal crosses in the numbers of hybrids obtained per pollination. Intergeneric crosses were also made involving *Camellia* and *Franklinia alatamaha, Stewartia ovata, Tutcheria spectabilis*, and *T. virgata*. Eleven hybrids were obtained from crosses of *Camellia* species with *Tutcheria spectabilis* and *T. virgata*, and six as yet unvalidated plants were obtained from *Franklinia alatamaha* × *Camellia hongkongensis*.

In a substantial number of crosses, seed capsules developed to apparent maturity, but contained partly developed or aborted embryos. Many of the former were grown to normal plants through the use of embryo culture techniques.

The first evidence of validity of a young hybrid plant is the comparison of its vegetative morphological characters with those of its parents. The identification of 211 interspecific and 11 intergeneric hybrids was based on vegetative characters. Certain characters were found to be strongly dominant. Among these, the most useful were pubescent stems of certain species, the indented midrib and veination of the leaves of *C. granthamiana*, and the narrow, elongated leaf character of *C. hongkongensis*.

Floral characters proved to be a valuable supplement to vegetative characters. Certain species transmitted their floral characters more strongly than others. *C. granthamiana* transmitted frilled petals to the majority of its progeny. *C. hongkongensis* transmitted trumpet-shaped flowers and rough, grey perules to many of its progeny. Floral scent is restricted to seven species, *C. fraterna, C. kissi, C. lutchuensis, C. miyagii, C. oleifera, C. sasanqua*, and *C. tsaii*. As an inherited character, floral scent was transmitted to most of the progeny of these species.

The use of hybrids in the inter-

specific or intergeneric transfer of desirable characters depends upon fertility. Also, a greatly increased frequency of aborted pollen produced by a presumptive hybrid in comparison with frequencies produced by the parents provides corroborative evidence of hybridity. Thus, percentages of aborted pollen, after staining with acetocarmine, were determined for all parental species and those hybrids that flowered. Although the percentages of aborted pollen in the hybrids generally exceeded those in the parental species, enough fertility was indicated to suggest the use of the hybrids in the transfer of desirable characters. Observation of the pollen also disclosed that the production of large, presumably unreduced grains is very common in *Camellia*. Only five of 66 parental species or clones observed did not produce at least some unreduced pollen. Unreduced pollen was found in 112 of 134 interspecific hybrids examined. *Tutcheria spectabilis* and *T. virgata* also produced unreduced pollen. Unreduced pollen was found in five of the eight intergeneric hybrids of *Tutcheria* and *Camellia* that flowered.

Species compatibility relationships were based on Sealy's (*1958*) division of the genus into sections. Representatives of six subgeneric sections and the unplaced group Dubiae were studied for the number of valid hybrids in relation to the total number of reciprocal cross-pollinations for each parental combination. Pollen sterility among the hybrids was also considered, but these data were far from complete because many hybrids were too young to flower.

Intrasectional hybridization within section Camellia showed a close compatibility relationship between *C. japonica, C. pitardii* var. *pitardii, C. reticulata, C. rusticana,* and *C. saluenensis. C. hongkongensis,* on the other hand, was more difficult to hybridize with other members of this section, indicating a more distant relationship. Species within section Paracamellia hybridized more readily with each other than those of any other section. In contrast, species of section Theopsis were the most difficult to hybridize with each other. Two species of Dubiae, *C. hiemalis* and *C. miyagii,* very readily hybridized in either reciprocal direction.

Analyses of the intersectional compatibility relationships suggest that the seven sections fall into two more-or-less distinct groups. In the first group, species of Paracamellia, Thea, and Dubiae appear to be more generally related to each other than with species of the other sections. In the second, species of Theopsis and Cammeliopsis appear to be closely related to each other and, in turn, more closely compatible with Camellia than with other sections. Heterogenea would appear to fall within this second group because of its closer compatibility with Camellia than with any other section.

Root-tip chromosomes were examined in parental species and hybrids. Chromosome numbers not previously reported were determined for the diploid *C. lutchuensis* and the hexaploids *C. miyagii* and *C. rosaeflora*. *T. virgata*, previously reported as diploid, was found to be pentaploid.

Determinations of chromosome numbers were made for 88 interspecific and 11 intergeneric hybrids that produced root tips suitable for study. Chromosome counts of 43 hybrids resulting from crosses between diploid species disclosed one variant from the diploid number. An aneuploid hybrid with 28 chromosomes occurred from a cross of *C. japonica* × *C. lutchuensis*.

Hybrids resulting from crosses between diploid female parents and tetraploid male parents resulted in triploids in four out of five hybrids studied. One hybrid of *C. pitardii* var. *pitardii* × *C. granthamiana* was tetraploid. All but two of 18 hybrids from crosses between diploid female parents and hexaploid male parents were tetraploids. Two hybrids with aneuploid chromosome counts were observed; one had 56 chromosomes, and the other 59.

Ten hybrids from crosses between hexaploid female and diploid male parents were tetraploid and two hybrids were pentaploid. *C. sasanqua* 'Narumi-gata,' a pentaploid variety, produced hybrids when used as the female parent. However, the chromosome numbers of its hybrids were unpredictable. A hybrid of *C. sasanqua* 'Narumi-gata' ($5x=75$) × *C. granthamiana* ($4x=60$) was tetraploid. A hybrid of *C. sasanqua* 'Narumi-gata' × *C. reticulata* ($6x=90$) was hexaploid. Among 15 hybrids studied from crosses between hexaploid species, all but one were hexaploids. One hybrid with an aneuploid chromosome count of 86 was observed among the four hybrids of *C. sasanqua* × *C. miyagii*.

Three hybrids of *Tutcheria virgata* ($5x=75$) × *C. granthamiana* ($4x=60$) had 75 chromosomes. Among the hybrids of *T. virgata* × *C. miyagii* ($6x=90$), two hybrids had 75 chromosomes and two had 90. Individual hybrids with 80, 82, and 105 chromosomes also occurred. The one hybrid obtained from the diploids *C. pitardii* var. *pitardii* × *T. spectabilis* was also diploid.

The probable origins of the complements of euploid variants among the interspecific and intergeneric hybrids are discussed. The functioning of unreduced gametes is indicated in three interspecific hybrids.

Studies of chromosome morphology were intended primarily to ascertain whether karyotype analysis in *Camellia* would be fruitful in distinguishing species and in elucidating phytogenetic relationships. The major characteristics used to identify individual chromosomes were its total length and the position of the centromere. Accurate identification of sets of homologs was not possible for polyploid species, so the study was confined to eight diploid species.

Although there were striking similarities between the genomes of all of the species in respect to centromere position, there were also marked differences, indicating that the species can be distinguished from each other through careful karyotype analysis.

Species known to be closely related are *C. japonica, C. pitardii* var. *pitardii, C. rusticana,* and *C. saluenensis.* The major differences in the karyotypes of *C. japonica* and *C. rusticana* appeared in the position of the centromere in chromosomes 13 and 15. The karyotype of *C. saluenensis* differed from that of *C. japonica* and *C. rusticana* primarily in chromosomes 4, 11, and 13. However, *C. pitardii* var. *pitardii* differed from *C. japonica* and *C. rusticana* in the centromere position of six chromosomes.

Among the species outside the section Camellia, *C. kissi* and *C. lutchuensis* appear more similar, at least superficially, to those within this section than do *C. salicifolia* and *C. sinensis.* The karyotype of *C. salicifolia* showed the least similarity to those of the other species.

In general, there was only a rough correlation between karyotypes of the various species and their ability to hybridize. The lack of more positive correlation indicates that structural and genetic differences affecting hybridization exist, which are not visible in the karyotypes.

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# APPENDIX

TABLE 20.—*Interspecific crosses in* Camellia *resulting in no hybrid plants*

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | |
|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. fraterna* × *C. granthamiana* | 63 | 2 | 3.2 | 0 | 0 |
| *C. fraterna* × *C. hiemalis* | 20 | 1 | 5.0 | 0 | 0 |
| *C. fraterna* × *C. hongkongensis* | 18 | 0 | 0 | 0 | 0 |
| Reciprocal | 15 | 0 | 0 | 0 | 0 |
| *C. fraterna* × *C. kissi* | 25 | 0 | 0 | 0 | 0 |
| Reciprocal | 25 | 4 | 16.0 | 0 | 0 |
| *C. fraterna* × *C. miyagii* | 49 | 3 | 6.1 | 2 | 4.1 |
| *C. fraterna* × *C. oleifera* | 19 | 8 | 42.1 | 1 | 5.3 |
| *C. fraterna* × *C. pitardii* var. *pitardii* | 25 | 0 | 0 | 0 | 0 |
| *C. fraterna* × *C. rosaeflora* | 26 | 0 | 0 | 0 | 0 |
| *C. fraterna* × *C. rusticana* | 50 | 4 | 8.0 | 2 | 4.0 |
| *C. fraterna* × *C. salicifolia* | 25 | 1 | 4.0 | 2 | 8.0 |
| *C. fraterna* × *C. saluenensis* | 18 | 1 | 5.6 | 3 | 16.7 |
| *C. fraterna* × *C. sasanqua* | 34 | 1 | 2.9 | 0 | 0 |
| Reciprocal | 31 | 0 | 0 | 0 | 0 |
| *C. fraterna* × *C. sinensis* | 27 | 0 | 0 | 0 | 0 |
| *C. fraterna* × *C. taliensis* | 16 | 0 | 0 | 0 | 0 |
| *C. granthamiana* × *C. japonica* | 11 | 0 | 0 | 0 | 0 |

TABLE 20.—*Interspecific crosses in* Camellia *resulting in no hybrid plants*—Continued

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | |
|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. granthamiana* × *C. miyagii* | 18 | 0 | 0 | 0 | 0 |
| Reciprocal | 54 | 4 | 7.4 | 3 | 5.6 |
| *C. granthamiana* × *C. oleifera* | 16 | 0 | 0 | 0 | 0 |
| Reciprocal | 25 | 1 | 4.0 | 1 | 4.0 |
| *C. granthamiana* × *C. sasanqua* | 6 | 1 | 16.7 | 0 | 0 |
| *C. granthamiana* × *C. sinensis* | 8 | 0 | 0 | 0 | 0 |
| *C. hiemalis* × *C. japonica* | 26 | 2 | 7.7 | 0 | 0 |
| *C. hiemalis* × *C. lutchuensis* | 17 | 0 | 0 | 0 | 0 |
| Reciprocal | 29 | 0 | 0 | 0 | 0 |
| *C. hiemalis* × *C. pitardii* var. *pitardii* | 11 | 1 | 9.1 | 0 | 0 |
| *C. hiemalis* × *C. reticulata* | 23 | 0 | 0 | 0 | 0 |
| Reciprocal | 4 | 0 | 0 | 0 | 0 |
| *C. hiemalis* × *C. sinensis* | 12 | 0 | 0 | 0 | 0 |
| *C. hongkongensis* × *C. fraterna* | 15 | 1 | 6.7 | 0 | 0 |
| *C. hongkongensis* × *C. granthamiana* | 20 | 2 | 10.0 | 2 | 10.0 |
| *C. hongkongensis* × *C. hiemalis* | 16 | 1 | 6.3 | 0 | 0 |
| *C. hongkongensis* × *C. japonica* | 18 | 0 | 0 | 0 | 0 |
| *C. hongkongensis* × *C. kissi* | 11 | 0 | 0 | 0 | 0 |
| Reciprocal | 31 | 2 | 6.4 | 1 | 3.2 |
| *C. hongkongensis* × *C. lutchuensis* | 12 | 0 | 0 | 0 | 0 |
| Reciprocal | 12 | 0 | 0 | 0 | 0 |
| *C. hongkongensis* × *C. miyagii* | 21 | 0 | 0 | 0 | 0 |

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|  |  |  |  |  |  |
|---|---|---|---|---|---|
| *C. hongkongensis* × *C. oleifera* | 24 | 0 | 0 | 0 | 0 |
| Reciprocal | 42 | 2 | 4.8 | 0 | 0 |
| *C. hongkongensis* × *C. pitardii* var. *pitardii* | 14 | 0 | 0 | 0 | 0 |
| Reciprocal | 25 | 0 | 0 | 0 | 0 |
| *C. hongkongensis* × *C. saluenensis* | 36 | 2 | 5.6 | 0 | 0 |
| *C. japonica* × *C. oleifera* | 18 | 2 | 11.0 | 1 | 5.5 |
| Reciprocal | 28 | 1 | 3.6 | 0 | 0 |
| *C. japonica* × *C. rosaeflora* | 24 | 0 | 0 | 0 | 0 |
| Reciprocal | 24 | 0 | 0 | 0 | 0 |
| *C. japonica* × *C. salicifolia* | 16 | 0 | 0 | 0 | 0 |
| *C. japonica* × *C. sasanqua* | 29 | 2 | 6.9 | 2 | 6.9 |
| *C. kissi* × *C. fraterna* | 25 | 1 | 4.0 | 0 | 0 |
| *C. kissi* × *C. granthamiana* | 66 | 5 | 7.6 | 7 | 10.6 |
| *C. kissi* × *C. lutchuensis* | 108 | 31 | 28.7 | 0 | 0 |
| Reciprocal | 21 | 0 | 0 | 0 | 0 |
| *C. kissi* × *C. pitardii* var. *pitardii* | 17 | 1 | 5.9 | 0 | 0 |
| *C. lutchuensis* × *C. granthamiana* | 14 | 0 | 0 | 0 | 0 |
| *C. lutchuensis* × *C. hiemalis* | 29 | 2 | 6.9 | 1 | 3.4 |
| *C. lutchuensis* × *C. hongkongensis* | 12 | 0 | 0 | 0 | 0 |
| *C. lutchuensis* × *C. miyagii* | 49 | 0 | 0 | 0 | 0 |
| *C. lutchuensis* × *C. oleifera* | 26 | 0 | 0 | 0 | 0 |
| Reciprocal | 65 | 6 | 9.2 | 3 | 4.6 |
| *C. lutchuensis* × *C. reticulata* | 38 | 3 | 7.9 | 2 | 5.3 |
| Reciprocal | 55 | 3 | 5.5 | 0 | 0 |
| *C. lutchuensis* × *C. saluenensis* | 14 | 0 | 0 | 0 | 0 |
| *C. lutchuensis* × *C. sasanqua* | 32 | 0 | 0 | 0 | 0 |
| Reciprocal | 12 | 0 | 0 | 0 | 0 |
| *C. lutchuensis* × *C. sinensis* | 26 | 0 | 0 | 0 | 0 |
| Reciprocal | 23 | 2 | 8.7 | 0 | 0 |

TABLE 20.—*Interspecific crosses in* Camellia *resulting in no hybrid plants*—Continued

| Interspecific crosses | Pollinations | Seed capsules produced | | Seeds started in culture | |
|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent per pollination* | *Number* | *Percent per pollination* |
| *C. miyagii* × *C. japonica* | 21 | 0 | 0 | 0 | 0 |
| *C. miyagii* × *C. rosaeflora* | 30 | 2 | 6.7 | 0 | 0 |
| Reciprocal | 23 | 0 | 0 | 0 | 0 |
| *C. miyagii* × *C. rusticana* | 42 | 5 | 11.9 | 0 | 0 |
| Reciprocal | 26 | 1 | 3.8 | 0 | 0 |
| *C. miyagii* × *C. sinensis* | 17 | 6 | 35.3 | 0 | 0 |
| *C. oleifera* × *C. granthamiana* | 12 | 1 | 8.3 | 0 | 0 |
| *C. oleifera* × *C. japonica* | 28 | 1 | 3.6 | 2 | 7.1 |
| *C. oleifera* × *C. pitardii* var. *pitardii* | 27 | 2 | 7.4 | 0 | 0 |
| *C. pitardii* var. *pitardii* × *C. rosaeflora* | 20 | 0 | 0 | 0 | 0 |
| *C. pitardii* var. *pitardii* × *C. salicifolia* | 22 | 0 | 0 | 0 | 0 |
| *C. pitardii* var. *pitardii* × *C. taliensis* | 25 | 0 | 0 | 0 | 0 |
| *C. reticulata* × *C. hiemalis* | 14 | 0 | 0 | 0 | 0 |
| *C. reticulata* × *C. hongkongensis* | 19 | 2 | 10.5 | 0 | 0 |
| *C. reticulata* × *C. kissi* | 28 | 3 | 10.7 | 2 | 7.1 |
| *C. reticulata* × *C. miyagii* | 11 | 0 | 0 | 0 | 0 |
| *C. reticulata* × *C. salicifolia* | 22 | 0 | 0 | 0 | 0 |
| *C. reticulata* × *C. sasanqua* | 31 | 0 | 0 | 0 | 0 |
| *C. rosaeflora* × *C. granthamiana* | 26 | 0 | 0 | 0 | 0 |
| *C. rosaeflora* × *C. hongkongensis* | 21 | 0 | 0 | 0 | 0 |
| *C. rosaeflora* × *C. kissi* | 83 | 2 | 2.4 | 0 | 0 |

| | | | | | |
|---|---|---|---|---|---|
| *C. rosaeflora* × *C. lutchuensis* | 24 | 0 | 0 | 0 | 0 |
| *C. rosaeflora* × *C. reticulata* | 34 | 0 | 0 | 0 | 0 |
| *C. rusticana* × *C. hiemalis* | 19 | 1 | 5.3 | 0 | 0 |
| *C. rusticana* × *C. reticulata* | 48 | 0 | 0 | 0 | 0 |
| *C. rusticana* × *C. sasanqua* | 29 | 0 | 0 | 0 | 0 |
| Reciprocal | 22 | 0 | 0 | 0 | 0 |
| *C. rusticana* × *C. sinensis* | 23 | 0 | 0 | 0 | 0 |
| Reciprocal | 18 | 1 | 5.6 | 0 | 0 |
| *C. salicifolia* × *C. pitardii* var. *pitardii* | 16 | 0 | 0 | 0 | 0 |
| *C. saluenensis* × *C. salicifolia* | 20 | 0 | 0 | 0 | 0 |
| *C. sasanqua* × *C. hongkongensis* | 22 | 0 | 0 | 0 | 0 |
| *C. sasanqua* × *C. pitardii* var. *pitardii* | 20 | 0 | 0 | 0 | 0 |
| *C. sasanqua* × *C. rosaeflora* | 12 | 0 | 0 | 0 | 0 |
| *C. sasanqua* × *C. saluenensis* | 33 | 2 | 6.1 | 0 | 0 |
| *C. sasanqua* × *C. sinensis* | 12 | 1 | 8.3 | 0 | 0 |
| *C. sasanqua* × *C. taliensis* | 20 | 0 | 0 | 0 | 0 |
| *C. sinensis* × *C. hongkongensis* | 30 | 2 | 6.7 | 0 | 0 |
| *C. sinensis* × *C. lutchuensis* | 33 | 5 | 15.2 | 3 | 9.1 |
| *C. sinensis* × *C. pitardii* var. *pitardii* | 16 | 0 | 0 | 0 | 0 |
| *C. sinensis* × *C. reticulata* | 20 | 1 | 5.0 | 0 | 0 |
| *C. sinensis* × *C. rusticana* | 18 | 0 | 0 | 0 | 0 |

TABLE 21.—*Vegetative characters of parental species of* Camellia *useful for identification of hybrids*

| Species | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. fraterna* | Pubescent | Thin, willowy, spreading | Pink to red | Dull, grey green | Raised, fairly prominent | Obscure | Basal ⅓ smooth, bluntly serrulate | Medium long, pointed, pubescent. |
| *C. granthamiana* | Pubescent | Medium thin, intermediate | Light green | Glossy, bright green | Very highly raised, prominent | Very highly raised, prominent | Bluntly serrulate | Medium short, bluntly pointed, pubescent. |
| *C. hiemalis* | Pubescent | Medium stout, intermediate | Light green | Glossy, bright green | Slightly raised, apparent | Apparent as dark lines only | Mostly crenate, some serrate | Long, sharply pointed, pubescent. |
| *C. hongkongensis* | Glabrous | Stout, upright | Dark purple | Dull, grey green | Highly raised, prominent | Slightly raised, dark lined | Very bluntly shallow, crenate | Short, stout, bluntly pointed, glabrous. |
| *C. japonica* | Glabrous | Stout, upright | Bright green | Glossy, bright green | Raised, prominent | Not raised, but apparent | Bluntly denticulate to crenate-denticulate | Long, sharply pointed, glabrous. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. kissi* | Pubescent | Medium thin, intermediate | Pink to red | Semi-glossy, medium green | Raised, prominent | Apparent as dark lines only | Basal ¼ to ⅓ smooth, serrulate | Short, stout at base, sharply pointed, pubescent. |
| *C. lutchuensis* | Pubescent | Thin, willowy, spreading | Pink to red | Dull, olive green | Not raised, but apparent | Obscure | Bluntly serrulate | Short, bluntly pointed, pubescent. |
| *C. miyagii* | Pubescent or glabrous | Thin, spreading | Pink | Semi-glossy, medium green | Not raised, but apparent | Obscure | Crenate | Short, stout, bluntly pointed, glabrous. |
| *C. oleifera* | Mostly pubescent | Thin, spreading | Light green | Semi-glossy, bright green | Slightly raised, apparent | Obscure | Serrate | Short, stout, bluntly pointed, pubescent. |
| *C. pitardii* var. *pitardii* | Glabrous | Very stout, upright | Light green | Glossy, bright green | Raised, prominent | Raised, dark lined, prominent | Serrulate to serrate | Short, stout, bluntly pointed, pubescent. |
| *C. reticulata* | Glabrous | Stout, upright, rigid, open | Pink | Semi-glossy, dark green | Raised, prominent | Raised, dark lined, prominent | Basal ⅕ smooth, serrulate | Short, stout, bluntly pointed, glabrous. |

TABLE 21.—*Vegetative characters of parental species of* Camellia *useful for identification of hybrids*—Con.

| Species | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. rosaeflora* | Pubescent | Medium thin, lax, straggly | Pink | Glossy, dark green | Slightly raised, apparent | Obscure | Widely crenulate-serrulate, teeth 2–3 mm. apart | Medium long, pointed, pubescent. |
| *C. rusticana* | Glabrous | Stout, upright | Bright green | Glossy, dark green | Raised, prominent | Not raised, but apparent | Coarsely crenate to serrate | Medium long, sharply pointed, glabrous. |
| *C. salicifolia* | Pubescent | Thin, willowy, spreading, pendulous | Pink to red | Semi-glossy, olive green | Raised, prominent | Raised, prominent | Widely and shallowly serrulate, teeth incurved, black tipped | Short, slender, sharply pointed, highly pubescent. |
| *C. saluenensis* | Pubescent | Stout, upright, densely leaved | Pink | Semi glossy, olive green | Slightly raised, apparent | Slightly raised, dark lined, apparent | Serrulate | Medium long, pointed, pubescent. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. sasanqua* | Mostly pubescent | Stout, upright | Light green | Glossy, bright green | Raised, fairly prominent | Not raised, dark lined, apparent | Variable, crenately serrate | Medium short, bluntly pointed, pubescent. |
| *C. sinensis* | Mostly glabrous | Medium to stout, upright | Light green | Glossy, dark green | Highly raised, prominent | Raised, prominent | Bluntly serrulate to sinuate-serrulate, teeth incurved, black tipped | Long, pointed, pubescent. |
| *C. taliensis* | Glabrous | Stout | Light green | Glossy, bright green | Raised, prominent | Raised, prominent | Bluntly serrulate | Long, pointed, pubescent. |
| *C. tenuiflora* | Pubescent, then glabrous | Thin, spreading | Light green | Semi-glossy, medium green | Slightly raised, apparent | Obscure | Crenulate, denticulate | Short, bluntly pointed, glabrous. |

Source: Information partly from narrative description in Sealy (*1958*) and partly from author's observations at Plant Introduction Station, Glenn Dale, Md.

TABLE 22.—*Vegetative characters of* Camellia *used for initial identification of interspecific hybrids*[1]

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. fraterna* × *C. japonica:* | | | | | | | | |
| B-7 | f | i | f | f | s | m | m | f |
| *C. japonica* × *C. fraterna:* | | | | | | | | |
| 4-2 | m | m | m | m | s | m | m | m |
| 4-4 | m | m | m | m | s | f | f | m |
| 4-5 | m | m | m | m | s | i | m | m |
| 4-7 | m | m | m | m | s | m | m | m |
| 4-8 | m | i | f | m | s | m | m | m |
| 4-9 | m | m | ---------- | m | s | i | f | m |
| 4-43 | m | i | ---------- | m | s | f | m | m |
| 4-44 | m | m | m | m | s | i | f | m |
| 4-47 | m | m | m | m | s | i | m | m |
| 4-48 | m | m | m | m | s | f | m | m |
| *C. fraterna* × *C. lutchuensis:* | | | | | | | | |
| 1-3 | s | s | s | f | m | s | m | f |
| *C. lutchuensis* × *C. fraterna* | | | | | | | | |
| 2-1 | s | s | s | m | f | s | f | m |
| *C. fracterna* × *C. reticulata:* | | | | | | | | |
| 3-25 | f | i | s | m | s | m | s | f |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. reticulata* × *C. fraterna:* | | | | | | | | |
| 2-4 | m | i | s | m | s | i | s | m |
| 2-5 | m | i | s | m | s | m | s | m |
| 2-7 | m | i | s | m | s | m | s | m |
| *C. japonica* × *C. granthamiana:* | | | | | | | | |
| 7-67 | m | f | s | s | m | i | m | m |
| 7-96 | m | f | s | s | m | i | m | m |
| B-3 | m | i | s | s | m | m | m | m |
| *C. japonica* × *C. hiemalis:* | | | | | | | | |
| 5-84 | m | f | s | s | f | m | m | m |
| *C. japonica* × *C. hongkongensis:* | | | | | | | | |
| 5-10 | s | s | ---------- | m | i | m | f | m |
| 5-12 | s | s | m | m | m | m | f | m |
| 5-37 | s | s | ---------- | m | i | m | f | m |
| 5-41 | s | s | m | m | i | f | f | f |
| 5-47 | s | s | m | m | i | m | f | m |
| 5-48 | s | s | m | m | m | i | f | m |
| 5-49 | s | s | m | m | i | m | f | m |
| *C. japonica* × *C. kissi:* | | | | | | | | |
| 5-26 | m | f | f | f | s | m | f | m |
| 5-27 | m | f | m | f | s | f | m | m |
| *C. japonica* × *C. lutchuensis:* | | | | | | | | |
| 3-6 | m | f | m | m | m | f | m | m |
| 3-7 | m | i | m | m | m | f | m | m |
| 3-8 | m | f | m | i | m | f | m | m |
| 3-12 | m | i | m | m | m | f | m | m |
| 3-13 | m | i | m | i | m | f | f | m |

**See footnote at end of table.**

TABLE 22.—*Vegetative characters of* Camellia *used for initial identification of interspecific hybrids* [1]—Con.

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. japonica* × *C. lutchuensis*—Con.: | | | | | | | | |
| 3–14 | m | i | m | m | m | f | m | m |
| 3–15 | m | f | f | f | m | f | m | m |
| 3–16 | m | i | m | i | m | f | m | m |
| 3–17 | m | i | m | m | m | f | m | m |
| 3–18 | m | i | m | m | i | f | m | m |
| 3–19 | m | i | m | i | m | f | m | m |
| 3–20 | m | i | m | m | m | f | m | m |
| 3–21 | m | i | f | m | m | f | f | m |
| 3–23 | m | i | m | i | i | f | m | m |
| 3–24 | m | i | m | m | m | f | m | m |
| 3–26 | m | i | m | m | m | m | m | m |
| 3–28 | m | i | ---------- | m | f | f | m | m |
| 3–29 | m | i | m | f | f | f | m | m |
| 3–30 | m | i | m | m | m | f | m | m |
| 3–32 | m | i | m | m | m | f | f | m |
| 4–16 | m | i | f | i | m | f | m | m |
| 4–19 | m | i | f | m | m | f | m | m |
| 4–20 | m | i | m | m | m | f | f | m |
| 4–21 | m | i | m | m | m | f | f | m |
| 4–23 | m | i | m | m | m | f | m | m |
| 4–31 | m | i | m | m | i | f | f | m |
| 4–32 | m | i | m | i | m | f | m | m |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 4-33 | m | i | f | m | m | f | m | m |
| 4-35 | m | i | m | m | f | f | m | m |
| 4-36 | m | i | f | m | m | f | m | m |
| 4-40 | m | i | m | m | m | f | m | m |
| 4-41 | m | i | m | i | m | f | m | m |
| 4-42 | m | i | i | m | m | f | m | m |
| 4-45 | m | i | f | m | m | f | f | m |
| 4-46 | m | i | m | f | m | f | m | m |
| 4-53 | m | i | m | i | m | f | m | m |
| 4-54 | m | i | m | m | m | f | f | m |
| 4-55 | m | i | m | m | f | f | f | m |
| 4-56 | m | i | f | m | f | f | m | m |
| 4-57 | m | i | f | m | i | f | m | m |
| 4-58 | m | i | m | m | i | f | f | m |
| 4-59 | m | i | f | m | m | f | m | m |
| 4-60 | m | i | f | i | i | f | m | m |
| 4-61 | m | i | m | m | m | f | m | m |
| 4-62 | m | i | m | m | m | f | i | m |
| 4-63 | m | i | m | m | i | f | m | m |
| 4-64 | m | i | m | m | m | f | m | m |
| 4-65 | m | i | ---------- | m | m | f | m | m |
| 4-66 | m | i | m | m | m | f | m | m |
| 4-67 | m | i | m | m | m | f | m | m |
| 4-68 | m | i | m | m | m | m | m | m |
| 4-69 | m | i | m | i | m | f | m | m |
| 4-70 | m | i | m | m | m | f | m | m |
| 4-71 | m | i | f | i | m | f | m | m |
| 4-72 | m | i | ---------- | m | m | f | m | m |
| 4-73 | m | i | m | m | m | f | m | m |

See footnote at end of table.

TABLE 22.—*Vegetative characters of* Camellia *used for initial identification of interspecific hybrids* [1]—Con.

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. japonica* × *C. lutchuensis*—Con.: | | | | | | | | |
| 4–74 | m | i | m | f | m | f | m | m |
| 4–75 | m | i | f | m | m | f | m | m |
| 4–76 | m | i | m | m | i | f | m | m |
| 4–77 | m | i | ---------- | i | m | f | m | m |
| 5–3 | m | i | f | m | i | f | f | m |
| 5–4 | m | i | m | m | m | f | m | m |
| *C. lutchuensis* × *C. japonica:* | | | | | | | | |
| 5–20 | f | i | m | m | m | m | f | f |
| 5–23 | f | i | m | m | m | m | f | f |
| *C. japonica* × *C. miyagii:* | | | | | | | | |
| 5–7 | m | i | f | f | m | f | f | i |
| 5–9 | m | i | f | m | m | f | f | m |
| *C. japonica* × *C. pitardii* var. *pitardii:* | | | | | | | | |
| P–2 | s | f | s | s | s | m | f | m |
| P–3 | s | f | s | s | s | m | m | m |
| *C. pitardii* var. *pitardii* × *C. japonica:* | | | | | | | | |
| A–16 | s | s | s | s | s | m | m | f |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. japonica* × *C. reticulata:* | | | | | | | | |
| 3–22 | s | m | m | m | s | m | m | m |
| 3–23 | s | m | ---------- | m | s | m | m | f |
| 3–31 | s | f | f | m | s | f | m | f |
| P–13 | s | i | f | m | s | m | f | m |
| P–16 | s | m | ---------- | f | s | m | m | m |
| *C. reticulata* × *C. japonica:* | | | | | | | | |
| A–2 | s | m | f | f | s | f | f | m |
| A–6 | s | m | f | m | s | f | f | m |
| A–8 | s | i | m | f | s | f | m | m |
| A–9 | s | i | f | m | s | f | m | f |
| A–11 | s | i | f | f | s | i | m | m |
| A–13 | s | f | m | f | s | f | f | m |
| A–14 | s | i | m | f | s | f | m | m |
| *C. japonica* × *C. rosaeflora:* | | | | | | | | |
| P–46 | m | f | m | f | m | f | f | m |
| *C. japonica* × *C. rusticana:* | | | | | | | | |
| 5–13 | s | s | s | m | s | s | m | s |
| 5–14 | s | s | s | m | s | s | m | s |
| 5–24 | s | s | s | m | s | s | m | s |
| 5–25 | s | s | s | m | s | s | m | s |
| *C. rusticana* × *C. japonica:* | | | | | | | | |
| 5–28 | s | s | s | f | s | s | m | s |
| *C. japonica* × *C. saluenensis:* | | | | | | | | |
| 5–1 | m | i | f | f | f | m | m | m |
| 5–5 | m | i | f | f | m | m | m | m |
| 5–6 | m | f | m | f | m | m | m | m |
| 5–42 | m | f | f | f | f | m | m | m |

See footnote at end of table.

TABLE 22.—*Vegetative characters of* Camellia *used for initial identification of interspecific hybrids* [1]—Con.

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. japonica* × *C. saluenensis*—Con.: | | | | | | | | |
| 5–44 | m | i | f | f | f | m | m | m |
| 5–45 | m | f | m | m | m | m | m | m |
| 5–46 | m | f | m | f | m | m | m | m |
| *C. saluenensis* × *C. japonica:* | | | | | | | | |
| 5–29 | f | m | --------- | m | m | f | m | f |
| *C. japonica* × *C. sinensis:* | | | | | | | | |
| 5–17 | f | s | s | f | m | m | m | m |
| 5–22 | m | s | s | f | f | f | f | m |
| 7–250 | m | s | s | m | m | m | f | m |
| *C. japonica* × *C. taliensis:* | | | | | | | | |
| P–37 | s | s | s | s | s | m | m | m |
| *C. kissi* × *C. rusticana:* | | | | | | | | |
| 5–69 | f | m | f | m | s | m | m | f |
| *C. rusticana* × *C. kissi:* | | | | | | | | |
| 5–51 | m | m | --------- | f | s | m | m | m |
| *C. lutchuensis* × *C. rusticana:* | | | | | | | | |
| 1–4 | f | m | --------- | f | m | m | m | f |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. rusticana* × *C. lutchuensis:* | | | | | | | | |
| 1–1 | m | i | m | i | f | f | m | m |
| 1–3 | m | i | m | m | m | f | m | m |
| 1–5 | m | f | m | f | m | m | m | m |
| 2–2 | m | i | m | m | m | f | m | m |
| 2–3 | m | i | m | m | f | f | f | m |
| 2–6 | m | f | m | i | f | f | m | m |
| 2–10 | m | i | m | m | m | f | m | m |
| 2–11 | m | i | m | m | f | f | m | m |
| 3–9 | m | i | m | m | m | f | f | m |
| 3–11 | m | f | m | m | f | m | m | m |
| 3–27 | m | i | m | m | m | f | f | m |
| 4–1 | m | i | m | f | f | f | f | m |
| 4–3 | m | i | m | m | f | f | m | m |
| 4–6 | m | i | m | m | m | f | m | m |
| 4–10 | m | f | m | i | f | f | f | m |
| 4–13 | m | i | m | m | i | f | m | m |
| 4–14 | m | i | m | m | f | f | f | m |
| 4–15 | m | i | m | m | m | f | m | m |
| 4–17 | m | i | m | i | i | f | f | m |
| 4–18 | m | i | m | m | f | f | f | m |
| 4–37 | m | i | m | m | f | f | m | m |
| 4–38 | m | i | m | i | f | f | m | m |
| 4–39 | m | f | m | m | i | f | m | m |
| 5–39 | m | i | m | i | m | f | m | m |
| *C. miyagii* × *C. lutchuensis:* | | | | | | | | |
| 7–168 | m | s | s | i | s | s | f | m |
| 7–180 | m | s | s | m | s | s | f | m |
| 7–182 | m | s | s | m | s | s | f | m |
| 7–248 | s | s | s | m | s | s | f | m |

See footnote at end of table.

TABLE 22.—*Vegetative characters of* Camellia *used for initial identification of interspecific hybrids* [1]—Con.

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. oleifera* × *C. hiemalis:* | | | | | | | | |
| C-1 | s | f | s | s | s | m | m | m |
| *C. oleifera* × *C. miyagii:* | | | | | | | | |
| 5-60 | f | s | m | s | m | s | f | f |
| 5-61 | f | s | m | s | m | s | f | f |
| *C. pitardii* var. *pitardii* × *C. fraterna:* | | | | | | | | |
| 7-159 | m | f | m | f | s | f | f | i |
| P-19 | m | i | m | m | s | f | f | m |
| *C. pitardii* var. *pitardii* × *C. granthamiana:* | | | | | | | | |
| B-6 | m | m | s | s | m | m | s | s |
| P-56 | m | f | s | s | m | m | s | s |
| *C. pitardii* var. *pitardii* × *C. lutchuensis:* | | | | | | | | |
| P-8 | m | m | f | m | i | f | s | s |
| P-9 | m | m | ---------- | m | m | f | s | s |
| *C. pitardii* var. *pitardii* × *C. reticulata:* | | | | | | | | |
| P-24 | s | f | f | m | s | s | m | f |
| *C. reticulata* × *C. pitardii* var. *pitardii:* | | | | | | | | |
| P-55 | s | m | m | f | s | s | f | m |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. pitardii* var. *pitardii* × *C. saluenensis:* | | | | | | | | |
| P-42 | m | m | f | f | m | f | s | m |
| *C. saluenensis* × *C. pitardii* var. *pitardii:* | | | | | | | | |
| P-45 | f | f | m | m | f | m | s | f |
| *C. reticulata* × *C. granthamiana:* | | | | | | | | |
| B-5 | m | i | f | m | m | m | m | m |
| *C. reticulata* × *C. rosaeflora:* | | | | | | | | |
| P-57 | m | i | s | f | m | m | f | m |
| *C. reticulata* × *C. rusticana:* | | | | | | | | |
| 5-50 | s | f | m | f | s | m | m | f |
| *C. reticulata* × *C. saluenensis:* | | | | | | | | |
| 5-58 | m | i | s | m | f | s | m | m |
| 5-65 | m | f | s | f | m | s | m | m |
| 5-83 | m | f | s | f | f | s | m | m |
| *C. rosaeflora* × *C. fraterna:* | | | | | | | | |
| 7-266 | s | m | s | m | m | s | f | s |
| 7-267 | s | m | s | m | m | s | f | s |
| *C. rusticana* × *C. fraterna:* | | | | | | | | |
| 3-1 | m | i | f | m | s | i | f | m |
| 3-2 | m | i | m | m | s | i | m | m |
| 4-49 | m | i | m | m | s | i | m | m |
| *C. rusticana* × *C. hongkongensis:* | | | | | | | | |
| 7-1 | s | s | ---------- | m | m | m | f | i |
| 7-5 | s | s | ---------- | m | m | m | m | f |

See footnote at end of table.

TABLE 22.—*Vegetative characters of* Camellia *used for initial identification of interspecific hybrids* [1]—Con.

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | | | | | Lower surface | | | |
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Midrib | Veins | Margins | |
| *C. rusticana* × *C. saluenensis:* | | | | | | | | |
| 4-77 | m | f | ---------- | m | f | m | f | m |
| *C. saluenensis* × *C. fraterna:* | | | | | | | | |
| 7-302 | s | m | s | m | f | f | m | s |
| *C. saluenensis* × *C. granthamiana:* | | | | | | | | |
| B-2 | s | i | f | m | m | m | s | f |
| *C. saluenensis* × *C. hongkongensis:* | | | | | | | | |
| P-48 | f | f | m | m | m | s | f | f |
| *C. saluenensis* × *C. lutchuensis:* | | | | | | | | |
| A-26 | s | m | s | m | m | f | s | m |
| *C. saluenensis* × *C. reticulata:* | | | | | | | | |
| P-4 | f | i | s | m | m | m | f | f |
| P-5 | f | i | s | m | m | m | f | f |
| *C. saluenensis* × *C. roseaflora:* | | | | | | | | |
| 5-85 | s | m | s | f | s | m | m | s |
| *C. saluenensis* × *C. taliensis:* | | | | | | | | |
| 7-249 | f | m | ---------- | m | m | m | s | f |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *C. sasanqua* × *C. granthamiana:* | | | | | | | | |
| A-24 | m | m | s | s | f | f | s | s |
| B-4 | m | i | s | s | i | i | s | s |
| *C. sasanqua* × *C. hiemalis:* | | | | | | | | |
| 6-41 | s | m | s | s | f | m | s | m |
| *C. sasanqua* × *C. japonica:* | | | | | | | | |
| P-33 | f | s | s | s | s | f | m | f |
| P-34 | f | s | s | s | s | f | m | f |
| P-36 | m | s | s | s | s | f | m | f |
| *C. sasanqua* × *C. miyagii:* | | | | | | | | |
| 5-52 | f | m | m | m | m | m | f | f |
| 5-53 | f | m | m | m | m | m | s | f |
| 5-55 | f | m | m | m | m | f | f | f |
| 5-56 | f | m | m | m | m | f | s | f |
| *C. sasanqua* × *C. oleifera:* | | | | | | | | |
| B-1 | m | i | s | ---------- | m | m | s | m |
| *C. sasanqua* × *C. reticulata:* | | | | | | | | |
| A-21 | f | m | ---------- | m | s | m | m | f |
| A-22 | m | m | m | m | s | m | m | f |
| A-23 | f | f | m | m | s | f | m | f |
| *C. sasanqua* × *C. tenuiflora* | | | | | | | | |
| P-29 | s | f | s | m | m | m | f | f |
| P-32 | s | i | s | m | m | f | f | f |

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[1] m = resemblance to male parent; f = resemblance to female parent; i = intermediate characters; s = characters similar to both parents.

TABLE 23.—*Vegetative characters of parental species of* Tutcheria *useful for identification of hybrids*

| Species | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *T. spectabilis* | Pubescent | Stout, upright, rigid, open | Red to purple | Dull, olive green | Very highly raised, prominent | Slightly raised, dark lined, prominent | Widely shallow, crenate | Long, very sharply pointed, pubescent. |
| *T. virgata* | Glabrous | Medium to stout, upright, rigid, open | Red to purple | Dull, olive green | Raised, prominent | Obscure | Widely shallow, crenate | Long, very sharply pointed, pubescent. |

TABLE 24.—*Vegetative characters used for initial identification of intergeneric hybrids*[1]

| Code of hybrids | Twigs and young shoots | | | Leaves | | | | Terminal vegetative buds |
|---|---|---|---|---|---|---|---|---|
| | Pubescence | Habit of growth | Color of new growth | Color of upper surface | Lower surface | | Margins | |
| | | | | | Midrib | Veins | | |
| *C. pitardii* var. *pitardii* × *T. spectabilis:* | | | | | | | | |
| A–19 | m | i | ---------- | m | f | s | f | m |
| *T. virgata* × *C. granthamiana:* | | | | | | | | |
| 7–233 | m | m | f | m | f | f | m | i |
| 7–235 | m | i | ---------- | m | f | f | m | m |
| 7–255 | m | i | f | m | f | f | m | m |
| *T. virgata* × *C. miyagii* | | | | | | | | |
| 5–62 | m | i | f | m | m | s | f | i |
| 5–70 | m | i | m | m | m | s | f | i |
| 5 76 | m | m | ---------- | m | m | s | f | i |
| 5–77 | m | m | f | m | m | s | f | m |
| 5–80 | f | i | f | m | m | s | f | i |
| 5–81 | m | i | f | m | m | s | f | i |
| 5–82 | m | m | f | m | m | s | f | m |

[1] m = resemblance to male parent; f = resemblance to female parent; i = intermediate characters; s = characters similar to both parents.

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